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Author

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1 **Space-Time Equivalence in the Fossil Record, with a Case Study from Pleistocene Australia**

2 Julien Louys^{1,*}, Gilbert J. Price², Kenny J. Travouillon³

3 ¹ Australian Research Centre for Human Evolution, Griffith University, Brisbane 4111, Queensland,
4 Australia

5 ² School of Earth and Environmental Science, The University of Queensland, Brisbane, Queensland
6 4072, Australia

7 ³ Western Australian Museum, Locked Bag 49, Welshpool DC, WA, 6986 Australia

8 *To whom correspondence should be addressed: j.louys@griffith.edu.au

9
10 **Abstract**

11 Ecological processes operating across the spatial scale can be equivalently found operating across
12 the temporal scale. Such processes may affect community structure and species richness
13 relationships in ways that can be analysed using the fossil record. The best studied involve the
14 combination of the Species-Area-Relationship and the Species-Time-Relationship into a single space-
15 time equivalence of species richness. This equivalence has been recorded in modern and fossil
16 systems, providing insights into underlying ecological processes controlling species turnover through
17 space and time. The analysis of space-time equivalence has received less attention for community
18 structure, and we outline a framework wherein this could be examined. The inclusion of fossil data
19 to investigations into space-time equivalence are important for revealing emergent properties of
20 ecosystems that are not possible using only modern ecological data. They reveal complexities in the
21 nature of the equivalence across distinct geographical and temporal thresholds and are impacted by
22 environmental heterogeneity. In particular, the examination of space-time equivalence for
23 Quaternary systems highlights the uniqueness of the Holocene with respect to the Pleistocene.
24 Understanding how and why species are found together across large spatial and temporal scales can
25 provide information important for conservation efforts, however, the few cases of space-time
26 equivalence reported using fossil records indicates that this remains a poorly studied area in
27 palaeoecology.

28 **Introduction**

29 The widespread loss of ecosystem function due to anthropogenic disturbance and concerns over the
30 effects of climate change on biodiversity have accelerated efforts at reconciling conservation
31 practice and ecological theory (Flather et al. 2011; Sætersdal and Gjerde, 2011; Driscoll and
32 Lindenmayer, 2012). Understanding how ecosystems respond to perturbations, climatic changes,
33 and outright devastation requires knowledge of underlying mechanisms controlling how and why
34 species and species associations are (or are not) found in time and space (Mace 2013; Sutherland et
35 al. 2013). Because ecological processes and patterns can be observed equivalently through space
36 and time (Du and Behrensmeier, 2018), the space-time connection is increasingly being used to
37 predict climate-driven changes in species diversity, distributions, and co-occurrences, with spatial
38 patterns of turnover projected into the future (Elith and Leathwick, 2009; Fitzpatrick et al. 2011;
39 Maguire et al. 2015).

40 Significant changes in species composition through space and time are usually the result of large,
41 directional environmental changes that disrupt background conditions (Brown et al. 2001, Raia et al.
42 2011). The fossil record has a critical role to play in such investigations. Despite the patchiness of this
43 record, and difficulties in matching fossil data with modern ecological observations, only fossils can
44 provide the temporal depth required to study some ecological phenomena, many of which only
45 become emergent at scales larger than any ecological experiment (Louys et al. 2012; Tomašových et
46 al. 2014).

47 Palaeontological data are thus imperative to validate any ecological patterns observed across space
48 and time, allow extensions beyond regional and/or decadal scales, and identify phenomena
49 emergent beyond modern ecological study sites. Space-time equivalences hold promise for
50 understanding deep-time ecological phenomena in neo-ecological terms. Conversely, spatial
51 phenomena established through modern ecological studies might find their equivalent in the
52 geological record. Here, we review studies that have sought to establish space-time equivalence
53 using the fossil record. We provide a case study from the Pleistocene of Australia, examining
54 mammal community structure equivalence through space and time. Finally, we discuss the
55 usefulness and implications of this research for understanding ecological processes and applications
56 to conservation.

57 **Species Richness Relationships through Time and Space**

58 *The Space-Time-Area Relationship*

59 Species diversity is one of the most important and well-studied ecological attributes of an
60 ecosystem. It is an emergent property that remains constant provided conditions related to
61 availability of energy, impact of environmental changes on the region species pool, and how
62 resources that are divided amongst species are maintained (Brown et al., 2001). Although a
63 relationship between species richness and either space (SAR) or time (STR) had been well
64 established, and it was long theorised that there existed a relationship between both of them
65 (Preston, 1960), it was not until the early 2000s that this was first empirically demonstrated under a
66 unified relationship (termed the space-time-area relationship, or STAR) by Adler and Laurenroth
67 (2003). In their study, species numbers for grassland plots spanning 35 years and fifteen 1 x 1 m
68 quadrants were modelled as a function of the area and time of sampling, as well as their interaction.
69 Adler and Laurenton (2003) found a negative interaction between space and time, meaning that the
70 rate of species accumulation (often equated to species turnover) decreases as time span increases,

71 and that species accumulation decreases over time as spatial span increases. This relationship takes
72 the form

$$73 \quad \log S = \log c + z_1 \log A + w_1 \log T + u(\log A)(\log T)$$

74 where S is species richness, c is the intercept, A is the sampled area, T is the sampled time span, z_1 is
75 the scaling exponent of the SAR at the unit time scale, w_1 is the scaling exponent of the STR at the
76 unit spatial scale, and u is the fitted interaction parameter. (It is worth noting here that scale can be
77 divided into two kinds: grain and extent, with SAR, STR, and STAR referring to grain.) This finding was
78 generalised in a “scales of time-area equivalence” concept, defined as the combination of sampled
79 area and time where the rates of turnover are equal (Adler et al. 2005). These equivalences were
80 recorded in very different modern communities including plants, algae, zooplankton, and small
81 mammals (Adler et al. 2005). However, equivalence differed, in some cases by several orders of
82 magnitude, depending on the system studied. This was attributed to the scale of heterogeneity –
83 spatial and/or temporal – that exists between the systems studied, and potentially confounded by
84 life history differences between the modelled organisms (Adler et al. 2005).

85 Empirically, time-by-area interactions are negative regardless of the community examined,
86 indicating similar underlying processes operating across both scales. However, stochastic modelling
87 assuming species neutrality produced positive interactions as well as patterns qualitatively similar to
88 empirical models, suggesting that a neutral model could explain the space-time interaction, and thus
89 that no underlying processes needed to be invoked (McGlenn & Palmer 2009). Such modelling
90 further indicated that the magnitude of the negative interaction depended on how closely the
91 accumulated richness approached the size of the regional species pool.

92
93 White et al. (2010), however, noted that neutral models fail to generate realistic predictions for STR
94 and SAR when these are examined separately (Adler 2004). The exponent of the SAR can however be
95 accurately predicted by a maximum entropy model (Harte et al. 2008, 2009). In such a model, the
96 SAR exponent, expected to vary as a function of the ratio of the total number of individuals N to the
97 total species richness S , declines with scale due to how linearly N compares to the less linear S as
98 both increase with spatial scale (White et al. 2010). In other words, because N increases with area in
99 a linear fashion, but S increases less linearly with the same increase in area, the rate at which S
100 accumulates as a function of N (the SAR component) decreases as area increases. White et al. (2010)
101 extended this concept by suggesting that some of the processes producing these spatial patterns,
102 namely the clustering of individuals in two-dimensional space, could be extended to a third
103 dimension, time. They predicted (although did not test) that the exponent of the SAR should
104 decrease with temporal scale, because, like the spatial scale, N also increases linearly with time
105 while S increases less than linearly. Thus, in the same way as SAR, the exponent of the STR should
106 decrease with spatial scale, and thus be indicative of similar underlying ecological processes
107 controlling this phenomenon.

108 109 *Examples using Palaeontological Data*

110 To bridge the gap between the patterns observed in modern records and fossil assemblages, Du and
111 Behrensmeyer (2018) examined the STAR model for a death assemblage of mammals from Amboseli
112 National Park in Kenya. The examination of death assemblages straddles neoecology and
113 palaeoecology by considering a temporal scale commensurate with previous modern studies but
114 incorporating some of the sampling biases introduced through the process of fossil site formation.
115 Unsurprisingly, patterns observed in Amboseli are comparable to those detailed by Adler et al.
116 (2005), namely that a model with an interactive term combining space and time performed best, and
117 this term was negative.

118 The generality of the STAR model at the intersection between modern and fossil communities
119 suggested to Du and Behrensmeyer (2018) that increased space and time sampling are simply two
120 alternative ways of sampling the underlying regional species pool, and the accumulation of species
121 should be seen as a two-phase process. The first occurs at smaller temporal and spatial scales, such
122 as those commonly expected in many modern ecological studies, with increasing space and time
123 revealing a functionally static species pool; the second sampling a species pool that is itself changing
124 and turning over. At large enough temporal and spatial scales, sampling will move beyond the
125 regional species pool and will encounter new or multiple species pools, altering the shapes of the
126 species-area and species-time relationships (Scheiner et al. 2011). Thus, an examination of STAR in
127 the fossil record could potentially reveal over which time scales regional species pools change as a
128 result of evolutionary and climatic processes, or when some species pool threshold has been crossed
129 in space or time.

130 Because fossil identifications are often only resolvable at higher taxonomic levels than that studied
131 by modern ecologists, i.e. species or subspecies, Du and Behrensmeyer (2018) extended the bridge
132 between modern ecology and palaeontology further by examining the role of taxonomic scale, in
133 addition to spatial and temporal scale, in the STAR model. This was achieved by running the STAR
134 analyses with taxa grouped at the genus, family, and order level. They found that as taxonomic scale
135 increases (e.g. moving from species to genus to family), model intercepts, coefficients, and
136 interaction terms all decreased. This makes sense, as taxonomic averaging effectively decreases the
137 number of taxa available to be discovered as area or time increases. As Du and Behrensmeyer (2018)
138 point out, this is an important consideration to palaeoecologists interested in examining rates of
139 turnover from the fossil record. The examination of a fully interactive Taxon-Time-Area-Relationship
140 model might yield further insights into the effects of taxonomic hierarchy on richness scaling, or
141 alternatively one could incorporate some measure of phylogenetic scaling or cladistic nestedness in
142 the models. This could be a rich future research direction for palaeoecology.

143 Hadly and Maurer (2001), working with Holocene records, examined the small mammal fossil record
144 of Lamar Cave through 16 stratigraphically-stacked strata, comparing species makeup and
145 abundances through time with 19 modern comparable mountaintop communities. Because of their
146 focus on the late Holocene, they were able to directly compare taxonomic identities in space and
147 time. They demonstrated that taxonomic identity and relative abundance in space and time are non-
148 random properties of communities sourced from the same regional species pool. They also found
149 that the species with larger ranges were the ones found in more places and to persist through time.
150 They further predicted that Pleistocene 'non-analogue' communities are caused by few taxa and
151 thus do not fundamentally alter community structure. While demonstrating similar patterns across
152 space and time, they did not directly determine an equivalence in space-time for their observed
153 small mammal diversities, nor any interactive term between them (i.e. STAR). Nevertheless, from
154 their results it is clear such a relationship likely exists (Hadly and Maurer, 2001: figure 2). Although
155 not discussed in detail, it is interesting that the amount of variance in species number explained was
156 larger for sampled time (76%) than by area of habitat (43%), but both share the same exponent.
157 Thus, the STR observed in these data more closely approaches the theoretical 'true' relationship
158 between species richness and time than does the SAR. This implies that no major change in turnover
159 rates has been experienced during the time sampled, while species turnover across space behaved
160 less predictably. This might be the result of differences in the degree of ecological heterogeneity in
161 the space sampled versus time – the last 3,000 years have been relatively stable climatically while in
162 the mountaintops differences and changes in altitude between different sampled sites could have
163 resulted in more variable turnover.

164 A quantitative examination of the relationship between species richness, time, and space in
165 palaeontology was provided by Raia et al. (2011), who calculated STRs, SARs, and STAR for Plio-
166 Holocene large mammal communities in Europe. The goal of their study was to examine the effects
167 of Pleistocene climatic changes on species accumulation rates. Previous research had demonstrated
168 that Italian mammal communities had undergone greater turnover rates as climates cooled, in
169 particular, in response to the mid-Pleistocene transition that saw global temperatures drop in
170 response to the changes in amplitude and frequency of glacial cycles (Raia et al. 2005; Meloro et al.
171 2008). Raia et al. (2011) demonstrated an increasing slope in SAR in the relatively more benign
172 Pliocene and middle Pleistocene, and an increase in slope in STR during the climatically harsher late
173 Pleistocene, in accordance with their predictions. Like other studies before them, Raia et al. (2011)
174 related patterns of richness accumulation observed under different spatial and temporal scale in
175 largely separate but complementary treatments: they compared and discussed the implications of
176 STR and SAR for the Pliocene to Holocene mammals of Europe but did not delve into what their STAR
177 model meant for these ecosystems. This speaks to the difficulty of directly relating space and time
178 interactions in theoretical models to palaeoecological, palaeoenvironmental, and palaeobiological
179 observations. However, such explorations are important if space-time models such as STAR are to
180 provide any insights into understanding evolutionary ecological processes from fossil data.

181 Like neoecologists, Raia et al. (2011) recorded a negative interaction factor in their STAR model.
182 They recorded a significantly lower z exponent for their STAR than their SAR. Their w exponent for
183 their STAR was also lower than their STR component, although they noted that it was comparable to
184 those reported by Rosenzweig (1998) for STRs calculated over evolutionary time. However, this w
185 exponent of their STAR ($w = 0.680$) is within the confidence interval of the w exponent of STRs
186 calculated using 2 and 4 cells (their temporal grain, each cell equal to 500,000 km²) of in their total
187 and 'South' dataset (total $w = 0.160-1.901$ and $w = 0.630-1.454$, 'South' $w = 0.155-4.839$ and $w =$
188 $0.130-1.865$), and just within the interval for STRs calculated using up to 8 cells in their 'North'
189 dataset ($w = 0.647-1.213$). This means that S , species richness, for their STAR is likely to be
190 equivalent (but offset by the difference in c , the intersect values) to S for their STRs calculated using
191 2, 4, and in the 'North' case, 8 cells, at least somewhere within the confidence interval. In other
192 words, the contribution to diversity from increased area of sampling at these spatial scales is more
193 or less independent of time.

194 Because STR is an indirect proxy for temporal turnover (Rosenzweig 1998, White 2004), these data
195 suggest that turnover in European mammal communities over the Plio-Holocene predominately
196 occurred as a result of temporal changes regardless of spatial scale, up to 4 cells in area (8 for
197 'North'). Thus, a comparison of STAR and STR exponents reveals the scale at which temporal
198 turnover can be examined without needing to explicitly consider spatial turnover in these
199 communities. Moreover, these results indicate important differences between 'North' and 'South' –
200 specifically, that temporal turnover can be considered largely independent of spatial turnover at
201 larger spatial scales in the north compared to the south. In other words, spatial turnover (i.e. SAR
202 slope) is lower in the north, an observation also made and discussed by Raia et al. (2011) and
203 attributed to the influence of the homogenous mammoth steppe biome in northern Europe. The
204 subtle additional insight revealed by also considering STAR is that this biome is homogenous only up
205 to a given area, which can be specified across time, and that beyond that area spatial turnover (and
206 space-time interaction) will increase as the limits of the biome are exceeded.

207 Blois et al. (2013) took a different approach in modelling drivers of composition turnover by
208 explicitly examining the extent to which turnover is related to climate. They examined how well
209 pollen turnover records compared to predictions in 'time-for-time' substitutions compared to

210 'space-for-time'. They predicted that if climate affects turnover through time in a similar way to its
211 effects on turnover through space, then the following should hold: (I) the substitutions should give
212 equivalent results; (II) the same environmental factors should impact turnover in space and through
213 time; and (III) rates and magnitudes of turnover along environmental gradients should be the same
214 across both scales. For the first prediction, they found that the substitutions produced comparably
215 accurate results for the Quaternary as a whole, however, the "space-for-time" substitution
216 performed much more poorly for the Holocene than either the Quaternary (that is, both Pleistocene
217 and Holocene considered together) or the late Pleistocene. This highlights the problems of scale
218 mismatch in attempting to predict time from space, or vice versa. Predictions break down when the
219 magnitude, nature, and impact of climatic changes differ too much across time versus space (Blois et
220 al. 2013). In their study, the magnitudes of turnover predicted by the models in space were not
221 observed in the Holocene and attributed to the relatively small climatic changes that occurred
222 during this epoch. Thus, this speaks to their third prediction, which was found to hold, but only at
223 certain spatial and temporal scales.

224 Regarding their second prediction, Blois et al. (2013) found that climatic factors explained the
225 majority of compositional turnover in both space and time. However, the magnitude of the
226 individual climatic components differed in how much deviance was explained. For time, all variables
227 examined were significant predictors, whereas in space, summer temperature and precipitation
228 seasonality dominated. Thus, while processes operating across space can have similar ultimate
229 impacts on turnover to those operating through time, emergent properties can proximally impact
230 turnover differently. In Blois et al.'s (2013) study for example, summer temperature was a significant
231 predictor of variation in compositional turnover across both spatial and temporal models. However,
232 the rates and magnitude of turnover along the summer temperature gradient were only similar at
233 the lowest temperatures and differed markedly at higher temperatures. If turnover operating across
234 space or time were examined only in cold ecosystems, a close relationship between turnover and
235 temperature might be observed, but different rates and magnitude of turnover at higher
236 temperatures across space versus time may not. Thus, emergent properties may not necessarily be
237 predictable without empirical tests and may also differ across organisms and systems.

238 **Community Assembly through Time and Space**

239 The ecological structure of any given animal community can be expressed in n -dimensional space
240 (ecospace) by n discrete variables that describe how animals inhabit or use the environment or
241 landscape in which they are found (Louys et al. 2015). This is fundamentally a niche-based definition
242 of why animals are found together and is one that can be examined within a quantitative framework
243 (Jongman et al. 1995; Kovarovic et al 2018). Animals occupying a niche will have adaptive traits that
244 allow successful exploitation of that niche, and because selection acts on these traits, community
245 structure will ultimately be optimised for a particular set of environmental conditions (Fuentes,
246 1976, Wilson and Whittaker 1995, Wilson et al. 1995, Louys et al. 2011).

247 Regularities in community structure in the same environments suggests that, like diversity,
248 underlying ecological processes control community assembly. Common structures have been
249 observed occurring through space at local (Fuentes, 1976, Wilson and Whittaker 1995, Wilson et al.
250 1995) and global scales (Louys et al. 2011, Lintulaakso and Kovarovic, 2016). For example, Louys and
251 Meijaard (2010) found that Asian mammal communities from modern rainforest reserves and
252 national parks were more similar to each other than to communities from open environments.

253 Community structures have been more intensively studied by palaeontologists as a means of
254 reconstructing palaeoenvironments from fossil mammal communities, demonstrating the

255 occurrence of common structures through time (Andrews, 1989, 1996; Kay and Madden, 1997;
256 Reed, 1997, 1998; Mendoza et al., 2004, 2005; Travouillon et al. 2009; Louys & Meijaard, 2010;
257 Kovarovic et al. 2018). This implies that processes controlling assembly could be acting equivalently
258 across space and time, however, unlike the species richness analyses discussed above, we know of
259 no examination of space-time equivalence of community structure.

260 Nevertheless, in the same way that species distributions change along an environmental gradient
261 (e.g. Whittaker, 1975), community structure should show continuous and overlapping variation
262 through environmental change, whether temporal or spatial. When environments change,
263 environmental conditions will be autocorrelated across either space or time because new conditions
264 are likely to fall within the range of conditions already existing at nearby sites or close in time
265 (Brown et al. 2001). Because the structure of a community defined by niche space is dependent on
266 the environment present, community structure should also be autocorrelated along that gradient.
267 The distance between sites or sampled time intervals should therefore reflect the difference in the
268 structure of communities in a predictable fashion, such that communities further apart on an
269 environmental gradient, either spatially or temporally, will be further apart in multidimensional
270 ecospace (Figure 1). Thus, there should exist some conditions where the degree of change across
271 space is equivalent to that observed through time (Figure 2). In other words, for any given record of
272 community change through successive stratigraphic layers, can we find an equivalent expression of
273 community change through successive modern sites?

274 **Case Study**

275 Southern Australia is today comprised of several botanical regions, including the South-western
276 Temperate and the South-eastern Temperate, but is dominated by dry open landscapes and an arid
277 climate (Burbridge, 1960). However, during the Pleistocene several lines of evidence, including from
278 fossil faunas, speleothems, and phytogeography, suggest the presence of a wetter, more wooded
279 biome harbouring related climatic, vegetation, and mammal communities stretching from the south-
280 eastern tip of South Australia, through the southern Eremaean, and across to the south-west of the
281 continent (Prideaux et al. 2007a, b, 2010, Macken et al. 2011, Ayliffe et al. 1998, González-Orozco et
282 al. 2014). Stratified fossil records document a progressive drying of the landscape and concomitant
283 extinction or range reductions of several mammalian species, signifying significant community
284 structural changes through time (Prideaux et al. 2007a, b, 2010, Faith and O'Connell 2011, Faith et
285 al. 2017, Macken et al. 2012).

286 While no single site in Australia's south currently spans the entire Quaternary, sites with deep
287 stratigraphic records do span considerable portions of the Middle and Late Pleistocene. The fossil
288 record of Cathedral Cave, Naracoorte Caves World Heritage Area, represents a well-dated and
289 stratigraphically constrained deposit spanning from approximately 500 ka to 200 ka. Diverse
290 mammalian species are preserved in five successive layers and together they document changing
291 communities in response to the long-term climatic trends discussed above (Prideaux et al. 2007).
292 The palaeocommunities from Tight Entrance Cave (Prideaux et al. 2010a), situated in south-western
293 Australia, appear to have been subjected to the same broad ecological processes (Faith et al. 2017).
294 Fossils from successive layers from this site span the period between the last layer of Cathedral Cave
295 through to just prior to the Last Glacial Maximum, i.e. approximately 140 ka to 30 ka.

296 We classified each of the mammal species found in these sites according to their functional traits
297 corresponding to trophic (primary or secondary consumer) and locomotor (strictly terrestrial or
298 arboreal) guilds as well as their body mass (tiny, small, medium, large, very large). This follows the
299 methodology described in detail in Louys et al. (2011, 2015). The structure of a single

300 palaeocommunity is represented by the proportion of species from that community belonging to
301 these combined functional groups, with tiny mammals excluded for taphonomic and sampling
302 reasons (see Kovarovic et al. 2018). Similarly, we classified modern mammalian communities found
303 in Australian national parks (derived from Travouillon and Legendre, 2009) according to the same
304 ecological criteria (Supplementary Information). In order to build an Australian mammal community
305 ecospace, fossil and modern mammal communities were subjected to a Principal Components
306 Analysis (Figure 3; Table 1). We consider only the first 3 principal coordinates in our analyses (Table
307 2), with all statistics calculated using PAST ver. 2.13c (Hammer et al. 2001).

308 An ecospace distance between each fossil community and the nearest modern community was
309 calculated by examining the magnitude of the vector connecting the fossil to the modern community
310 (Table 3). In the case of Cathedral Cave the closest national park is Little Desert National Park, for
311 Tight Entrance Cave it is Stirling Range National Park. Each successive fossil community was
312 compared to the same modern community. Both time (median age in ka) and distance (km) were
313 standardised by calculating the z-score for each variable (Table 3). The median age of each
314 community from successive fossil layers was plotted against ecospace distance (Figure 4). Shapiro-
315 Wilk tests indicate that all variables are normally distributed (at $\alpha = 0.05$), however, due to small
316 sample sizes we report both parametric and non-parametric correlation coefficients. A linear trend is
317 observable for both Cathedral Cave and Tight Entrance Cave ($r^2 = 0.47$ and 0.39 , respectively),
318 although only the Cathedral Cave record is statistically significant (Pearson's $r = 0.69$, $p = 0.20$;
319 Spearman's $\rho = 0.9$, $p = 0.02$). Contrary to expectations, the oldest sites were closest in structure to
320 modern communities, indicating increasing resemblance to the present going back in time. An
321 examination of the slopes for both sites indicates that they are equal (ANCOVA $F(1,8) = 6.32$, $p =$
322 0.04 , homogeneity of slopes $F = 0.01$, $p = 0.91$), suggesting that community structural changes
323 observable through time for both Cathedral Cave and Tight Entrance Cave are tracking the same
324 environmental gradient. However, the ANCOVA may be overfitted, and further stratified fossil
325 deposits from southern Australia are needed to determine whether this result holds for the region.

326 The question is, can we find a set of successive modern sites that show equivalent changes in
327 community structure through space that were exhibited through time? Iterative analyses of sites
328 radiating out from Little Desert National Park suggests that only in some directions are there
329 equivalent community changes. The best performing trajectory extends in a north-westerly direction
330 and includes Mount Remarkable National Park, Flinders Ranges National Park, Vulkathunha-
331 Gammon National Park, and Simpson Desert National Park. Plotting standardised spatial distance
332 (calculated from park coordinates) against ecospace distance produced a linear relationship
333 (Pearson's $r = 0.99$, $p = 0.01$, Spearman's $\rho = 0.8$, $p = 0.08$) that had a slope equivalent to that
334 observed in the fossil communities through time (each fossil site considered separately) (ANCOVA F
335 $(2,11) = 4.45$, $p = 0.04$, homogeneity of slopes $F = 2.09$, $p = 0.18$).

336 Assuming both Cathedral and Tight Entrance Caves are recording the same gradient of community
337 structural changes through time for southern Australia in response to vegetation changes, we can
338 compare their combined linear relationship with that of the modern community trajectory identified
339 above in order to derive a time-space community equivalence relationship. Thus

$$340 \quad m = 0.05t_s + 0.266 \quad (1) \quad \text{and}$$

$$341 \quad m = 0.096d_s + 0.322 \quad (2)$$

342 where m is the magnitude of ecospace distance in the shared community ecospace, t_s is equal to
343 time (expressed as the standardised value of negative ka), and d_s is the spatial distance (expressed as
344 the standardised value of km). This resolves to

$$345 \quad t_s \approx 1.92d_s + 1.12 \quad (3)$$

346 In other words, going back 1000 years in time ($t = -1$, $t_s \approx 2.60$) is equivalent to a point ~ 925 km ($d_s =$
347 0.77) along the identified trajectory towards Little Desert National Park. The equivalence holds for
348 the Pleistocene; however the location of the origin relative to the trend in time in Figure 4a suggests
349 that the Holocene exhibits properties unlike those present during the rest of the Quaternary. It
350 should be noted that this approach differs importantly from those used by STAR. The STAR models
351 discussed in this review rely on nested plots, whereas the approach outlined above uses non-nested
352 data, and thus the equivalences are not directly comparable.

353 **Discussion**

354 Changes in species richness relationships, beyond those observed simply by just counting more
355 individuals, can result from changes in environmental heterogeneity and ecological processes. For
356 example, the slope of species richness relationships may be positively related to the rate of change
357 of texture of the environment (Environmental Texture Hypothesis: Palmer, 2007, McGlenn and
358 Palmer, 2011). Such slopes can be determined from well-stratified fossil deposits and could thus be
359 compared between different sites in order to move from simply attributing palaeobiological change
360 to major habitat differences, to examining the effects of changes in the structure of the
361 environment. In at least this respect they may be of interest to palaeoecologists seeking to
362 understanding the structure and evolution of past environments. While species richness
363 relationships cannot be used in and of themselves to distinguish between different ecological
364 mechanisms, species richness relationships do provide a framework over which processes operating
365 over different scales can be inferred from any patterns observed (Adler and Levine, 2007; Scheiner
366 et al. 2011).

367 The relationship between richness and one of its primary regulators—productivity (Brown et al.
368 2001)—is more similar across both space and time when it is examined at either predictable (in
369 terms of temporal variation of productivity) or coarse-grained scales (White et al. 2010). Thus,
370 deviation from examining these patterns at comparable scales results in a mismatch between space
371 and time that can obscure any underlying equivalence (Blois et al. 2013). An important insight that
372 emerges from examining the fossil record of space-time equivalence is that ecological processes
373 operating over space may be proximally different, at least in magnitude, from those occurring over
374 time even if they have the same ultimate outcome. In other words, space-time equivalence probably
375 suffers from equifinality. The extent to which equifinality impacts equivalent observations made
376 through space and time can only be meaningfully addressed by the inclusion of longer time scales
377 than can be observed in modern systems. Thus, the relative importance of local and regional spatial
378 scale processes is dependent on time scale of analysis and ultimately, without including
379 palaeontological data, it's not possible to understand how space and time interact in their entirety
380 (White et al. 2010).

381 Examination of species richness values can also provide insights into community dynamics. For
382 example, communities with low alpha diversities can be considered closed due to niche-based
383 filtering; conversely, high alpha diversity indicates relatively open communities where neutral
384 assembly rules are expected; such neutral assemblies will also exhibit high beta diversities (Weiher
385 et al. 2011). However, richness is influenced by many factors such that a less rich community does

386 not automatically suggest niche-based filtering, or vice versa. Empirical examinations of species
387 richness relationships can also provide insights into the response of species diversity to historic,
388 abiotic, biotic, and geographical factors (Brown et al. 2001; although they are also affected by
389 sampling design and measurement error – see Scheiner et al. 2011). Increases in the temporal or
390 spatial scale of sampling increases the likelihood that more environmental variation will be
391 encountered. This is because, if the functional diversity of a community is related to species number,
392 then more time and/or space will reveal more niche space and thus more species (Triantis et al.
393 2003). Most species rare in diverse communities (Weiher et al. 2011), and only sufficient spatial or
394 temporal sampling will reveal specialised or rare species (Hadley and Maurer 2001).

395 Community assembly, and thus species diversity, which is the outcome of assembly, is affected by
396 drift, selection, dispersal, and speciation (Weiher et al. 2011, Vellend 2010, 2016). Across space, it is
397 thought that long term biogeographical processes such as colonisation and extinction dominate,
398 while across time demographic processes within established populations will exert more influence
399 (Adler and Levine, 2007). This is because, at local to regional scales, species sorting will be a product
400 of niche requirements, migration rates, and distances, but over long periods of time, evolutionary
401 processes will create niche differentiation (Scheiner et al. 2011). Selection shapes the structure of
402 communities by acting on ecological similarities and differences of organisms and species (Cadotte
403 et al. 2011, 2013, Jablonski 2008, Jablonski and Sepkoski 1996). The influence of selection on
404 assembly dynamics has benefited from the application and examination of trait-based frameworks,
405 for example, models that can integrate data on species traits, niches, phylogenetic relationships, and
406 variation and covariation among species occurrences (Rapacciuolo and Blois, 2019). Trait-based
407 models are particularly useful in examining spatiotemporal drivers of community structure that
408 incorporates fossil data, as traits are the common currency that allow discussions across global and
409 geological scales (Barnosky et al. 2017). Such models provide a quantitative framework for
410 investigating where community structure space-time equivalence holds. When such equivalences
411 are identified, they may be useful for predicting changes in communities under scenarios of future
412 climate change. Most likely, however, the value of such equivalences lie not so much in the absolute
413 values of the coefficient and constants calculated for any specific region, but rather as a point of
414 comparison for other regions or organisms. Like for species richness relationships, this provides a
415 means to get at fundamental understandings of underlying processes of community assembly at
416 different scales.

417 Determinants of community assembly are commonly divided into different processes: interaction,
418 environment, and neutral, with palaeontological data providing the strongest support for
419 environmental determinism of assembly (Jackson and Blois, 2015). Neutral assembly processes
420 result from historical contingencies, although only phylogeny and dispersal are considered in most
421 models (Jackson and Blois, 2015). Mammal community assemblages are suggested to be more
422 structured across space and time than predicted by neutral theory (McGill et al. 2005), but the
423 influence of historical contingency on community assembly may only be discernible at large spatial
424 and temporal scales (Louys et al. 2011). Community assembly is deterministic from a functional
425 perspective but historically contingent from taxonomic perspective (Li and Shipley, 2018). As stress
426 and environmental disturbance increases, taxonomic historical contingency decreases in importance
427 and this drives functional convergence of communities. Thus, community structural coherence is
428 likely only true at certain spatial, temporal, and organismic scales. An examination of time-space
429 equivalence in community structure may reveal at what scales interaction, environment, or neutral
430 rules of assembly hold or dominate, and where there is scale mismatch between process and
431 outcome. Only the fossil record provides insights into how these processes manifest over thousands
432 of years.

433 The fossil record also provides some points of caution for direct interpretation of space for time, and
434 vice versa. For the Quaternary fossil record, the Holocene emerges as very different from either the
435 Pleistocene or the Quaternary taken as a whole. This is observed both in studies examining richness
436 relationships (Raia et al. 2010, Blois et al. 2013) and our case study examining community structure.
437 The uniqueness of the Holocene is a result of important changes in the nature and magnitude of
438 climatic changes in this epoch compared to the Pleistocene. While this result is expected from our
439 understanding of the ecological theory underpinning time-space equivalence, it does provide some
440 limitations in using this theory to aid in biological conservation. An added problem is the precision of
441 dating techniques beyond the Holocene. For example, $300 \text{ ka} \pm 10 \text{ ka}$ at 2 SD error is only 3.3%
442 (which is exceptional precision), but still represents a 20,000-year period of uncertainty – nearly
443 double that of the entire Holocene. Extrapolating space for time in predicting the impacts of climate
444 and anthropogenic effects on species diversity and community structure beyond the Holocene
445 should be carefully considered and will almost certainly be region specific. The examination of fossil
446 records for regions of interest will provide suitable frameworks for understanding how well space-
447 time equivalences hold beyond spatial scales equivalent to the Holocene.

448 Nevertheless, understanding how space and time interact in structuring communities and species
449 turnover over geological timescales has important implications for biological conservation. Perhaps
450 nowhere is this more noteworthy than island ecosystems – the original arenas where the species-
451 area relationship was first formalised. Fossil and archaeological records have in many cases
452 fundamentally altered our perception of diversity on islands by recording past natural and
453 anthropogenically-driven extinctions. For example, the deep time records of the Caribbean islands
454 have established multiple turnovers over the past 7,000 years associated with serial human
455 colonisation events. These dramatically altered vertebrate communities in both direct and in-direct
456 ways acting differently across islands (Kemp et al. 2020). Determining the conditions for restoration
457 of island ecosystems based on SAR, STR, or STAR models established using only modern data of
458 these islands would be highly skewed and unrepresentative.

459 Conversely, establishing STAR or space-time equivalences in community structure using fossil data
460 could address one of the fundamental conservation challenges, namely the choice of baseline or
461 reference condition. Palaeoecological studies, particularly those in island ecosystems, have
462 emphasised the need to consider multiple baselines in order to prioritise the different goals of
463 conservation (Nogué et al. 2017; Wood et al. 2017; Kemp et al. 2020). A consideration of space-time
464 equivalence using the deep-time record could advance this by potentially defining a continuous, as
465 opposed to multiple discrete, baselines. At the very least, an examination of space-time equivalence
466 in specific ecosystems may reveal which past events have produced fundamental shifts in turnover
467 rates or how communities are structured within a fully integrated space-time framework, allowing
468 policy makers to determine which baseline state might be most appropriate as a conservation goal.
469 Integrating the large temporal scales available through fossil records is an important aspect of the
470 growing discipline of conservation palaeobiology.

471 Despite the importance of the fossil record for understanding ecological processes over space and
472 time, investigations in this area remains scarce, as can be seen by the limited number of papers
473 discussed above. While part of the problem is finding suitable fossil sites for analysis – these need to
474 be well-dated, well-resolved temporally and taxonomically, and extend back sufficiently in time – the
475 main issue remains one of bridging disciplines (Louys et al. 2012, Jackson and Blois 2015). Indeed,
476 the examination of space-time equivalence using the fossil record makes important contributions
477 not just to palaeontology and ecology, but by providing an evaluation of evolutionary processes on
478 regional species pools and species turnover, it also provides a framework for a greater integration of

479 these disciplines with evolutionary and conservation biology. It is a rich area of study that promises
480 to provide novel insights into how and why species are found together, and what will happen to
481 them in a rapidly changing world.

482

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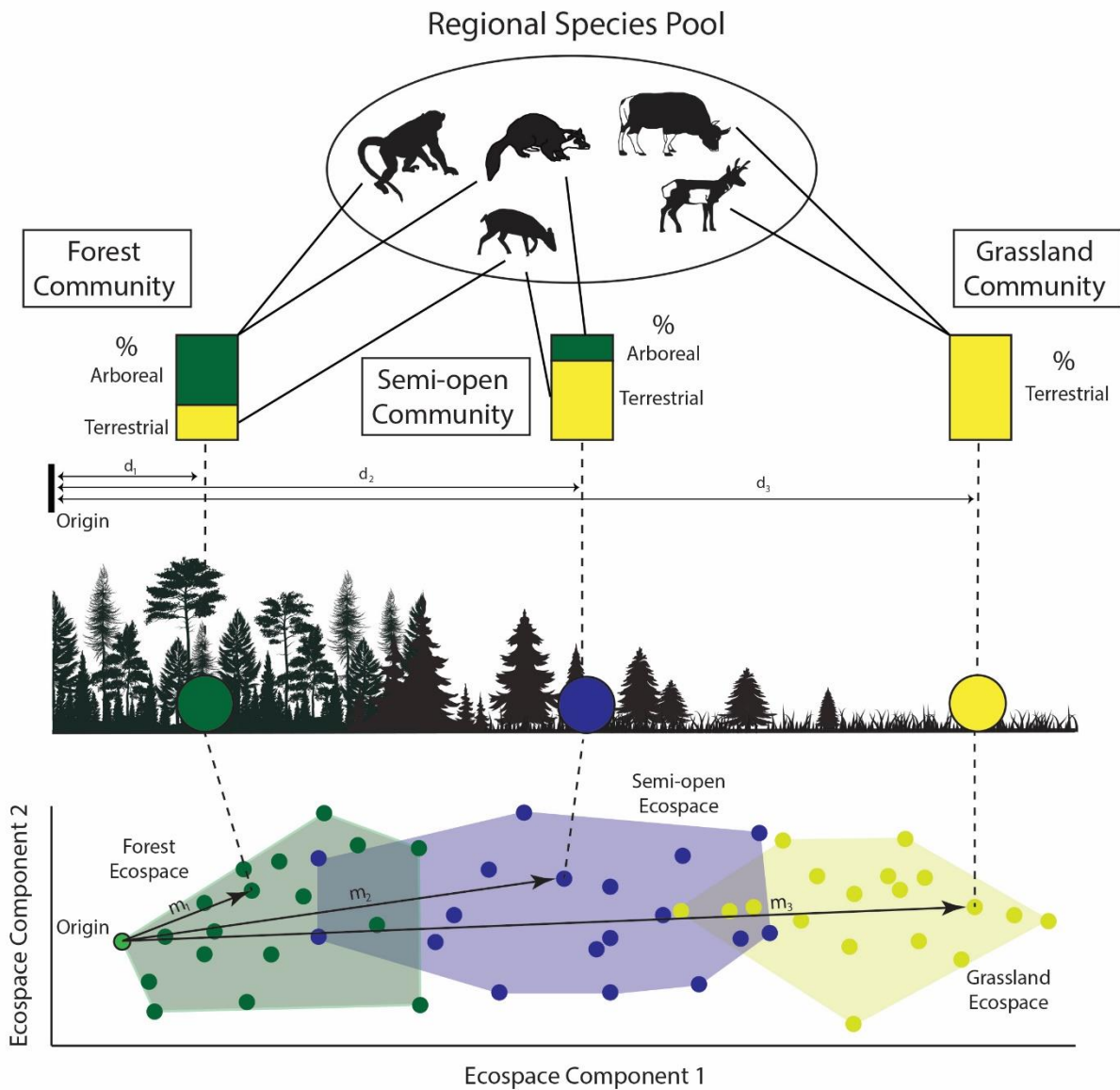
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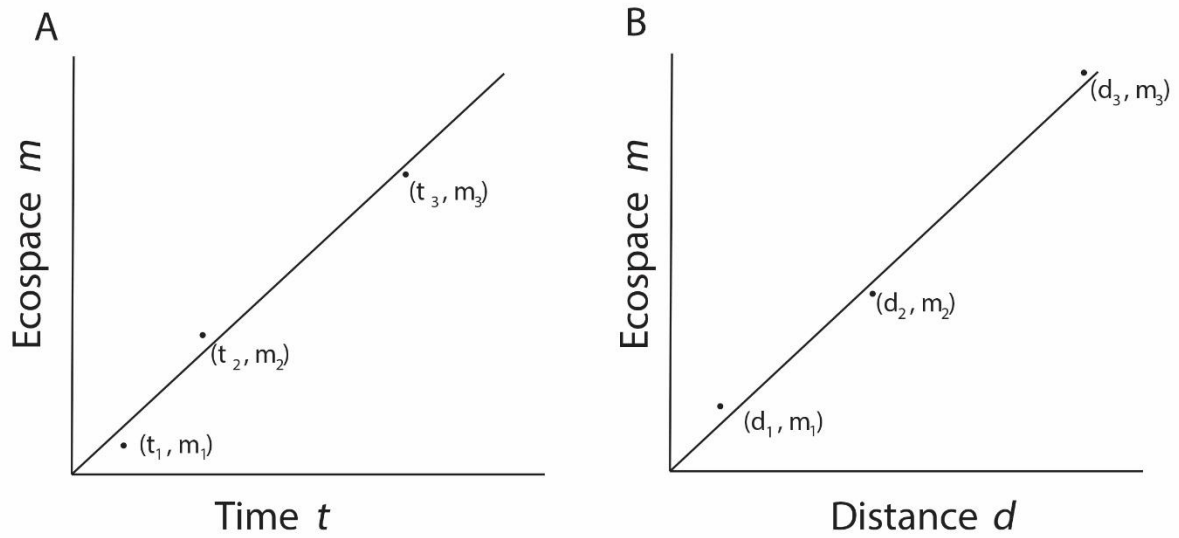
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675

676 Figure 1. Hypothetical schematic representing community structure through space. Local
 677 communities are constructed from the regional species pool and can be classified according to their
 678 functional groups. In theory any combination of functional groups could be used to describe a
 679 community, in this example locomotor guilds only are shown. Green represents more forested
 680 habitats, blue mixed habitats, and yellow open habitats such as grasslands. Such a schematic could
 681 equally be drawn showing community structure through time by considering a stratigraphic column
 682 instead of a transect.

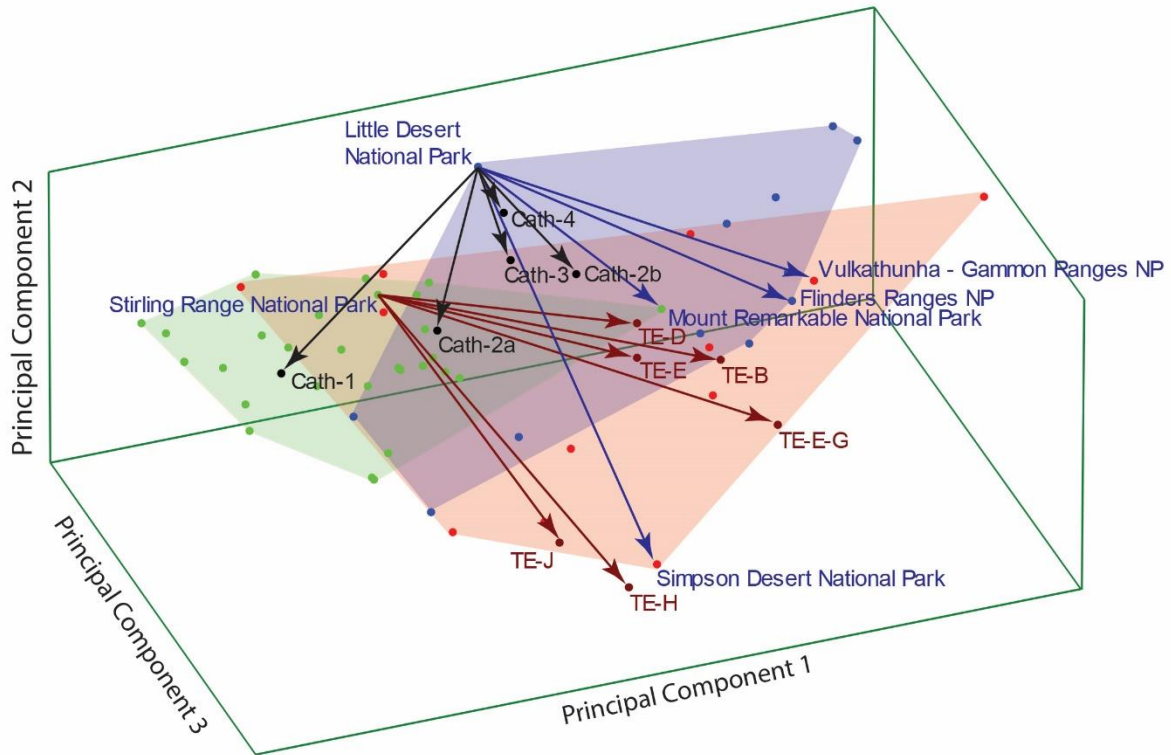
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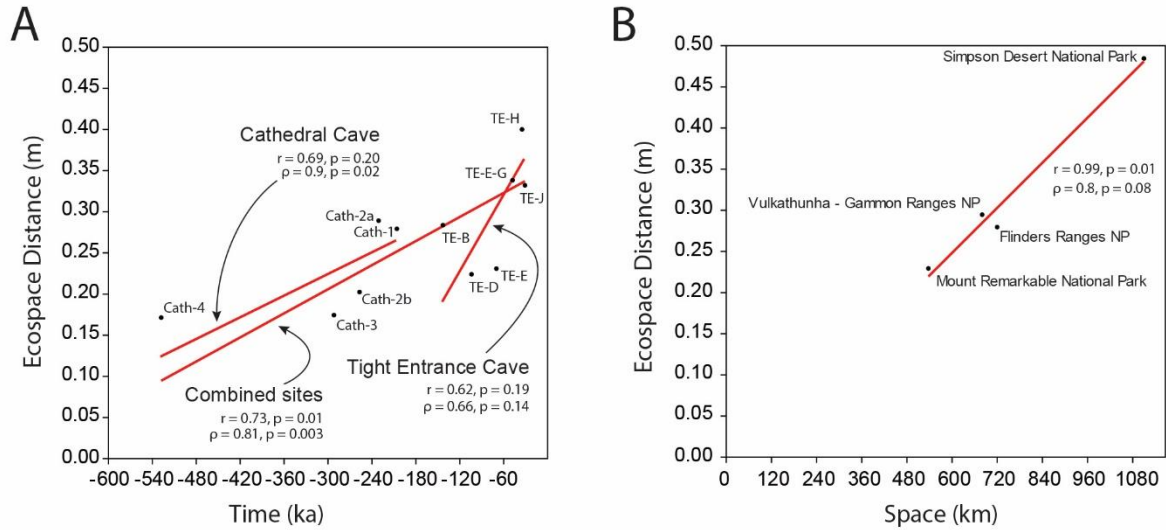
685 Figure 2. Hypothetical relationship of ecospace distance (represented by the magnitude of the
 686 vector between a point of origin and each community) versus (A) time; and (B) space.

687



688

689 Figure 3. Example of space-time equivalence calculations for southern Australian mammal
 690 communities described in the text. First three principal component values for each national park and
 691 fossil site are listed in Table 2. Green represents forested habitats, blue semi-open habitats, and red
 692 open habitats. Abbreviations: Cath – Cathedral Cave; TE – Tight Entrance Cave, suffixes represent
 693 different stratigraphic units for these sites.



694

695 Figure 4. Relationship between ecospace distance versus (A) time, and (B) space for southern
 696 Australian mammal communities. Note that time and space are listed on the x-axis as raw values for
 697 ease of interpretation (standardised values are used in Equations 1-3). Abbreviations: m – magnitude
 698 of ecospace distance in the shared community ecospace; r – Pearson correlation coefficient; ρ –
 699 Spearman rank-order correlation coefficient; Cath – Cathedral Cave; TE – Tight Entrance Cave,
 700 suffixes represent different stratigraphic units for these sites.

701

702 **Tables**

703

PC	Eigenvalue	% variance
1	0.025239	41.09
2	0.01231	20.54
3	0.008813	14.35
4	0.006766	11.02
5	0.003717	6.05
6	0.002318	3.77
7	0.00111	1.81
8	0.000858	1.40
9	0.000183	0.30
10	0.000103	0.17
11	1.21×10^{-5}	0.02
12	7.75×10^{-20}	1.26×10^{-16}

713 Table 1. Principal Components Analysis of modern Australian national park and fossil communities
 714 discussed in the text. Each species in a community was assigned to trophic, locomotor, and body-size
 715 functional groups, with input values equal to proportion of species in each functional group (see
 716 Supplementary Information).

717

Faunal Community	PC 1	PC 2	PC 3
Cath-4	0.09	-0.03	0.20
Cath-3	0.07	-0.05	0.15
Cath-2b	0.12	-0.06	0.13
Cath-2a	0.02	-0.16	0.17
Cath-1	-0.14	-0.07	0.08
TE-B	0.16	-0.02	-0.06
TE-D	0.12	-0.01	0.00
TE-E	0.11	-0.03	-0.03
TE-E-G	0.18	-0.04	-0.15
TE-H	-0.02	0.00	-0.36
TE-J	-0.06	0.03	-0.30
Mutawintji National Park	0.24	0.14	0.02
Kinchega National Park	0.20	0.09	0.03
Mungo National Park	0.30	0.19	0.06
Little Desert National Park	0.05	0.13	0.15
Mount Buffalo National Park	-0.22	0.04	-0.08
Snowy River National Park	-0.04	-0.01	-0.01
Wyperfeld National Park	0.18	-0.08	0.03
Gundabooka National Park	0.22	0.10	-0.06
Lamington National Park	-0.22	0.06	-0.01
Yumberra Conservation Park	-0.07	0.09	0.06
Bundjalung National Park	-0.05	0.02	-0.02
Currawinya National Park	0.20	-0.03	-0.04
Yuraygir National Park	-0.13	-0.04	0.03
Diamantina National Park	0.19	-0.12	0.04
Deua National Park	-0.15	0.06	0.11
Carnarvon National Park	-0.07	-0.02	0.01
Wadbilliga National Park	-0.16	0.07	0.00
Flinders Ranges National Park	0.23	0.04	-0.05
South East Forest National Park	-0.04	0.03	0.02
Gawler Ranges National Park	0.39	0.13	-0.03
Mungkan Kandju National Park	-0.10	-0.10	-0.04
Vulkathunha-Gammon Ranges National Park	0.27	-0.02	0.02
Iron Range National Park	-0.19	-0.05	0.03
Witjira National Park	0.08	-0.23	0.03
Mount Barney National Park	-0.11	0.00	-0.02
Millstream-Chichester National Park	0.11	0.08	-0.19
Main Range National Park	-0.12	0.06	-0.01
Kalbarri National Park	0.17	0.10	0.02
Boodjamulla National Park	0.02	-0.15	-0.01
Karijini National Park	0.00	-0.15	-0.12
Abercrombie	-0.05	-0.01	0.13
Blue Mountains	-0.05	-0.02	0.01

Ku-ring-gai	-0.11	0.02	0.08
Bookmark	0.32	0.17	0.05
Croajingolong	-0.17	0.06	0.03
Fitzgerald River National Park	-0.15	0.01	0.14
Grampians National Park	-0.03	0.05	0.06
Kosciuszko National Park	-0.03	-0.03	-0.01
Prince Regent River Nature Reserve	-0.13	-0.01	-0.05
Purnululu National Park	-0.05	-0.24	-0.04
Shoalwater and Corio Bays Area Ramsar Site	-0.06	-0.04	0.03
Uluru National Park	-0.09	0.10	0.00
Wilson's Promontory National Park	-0.05	0.08	0.03
Simpson Desert National Park	0.09	-0.28	-0.11
Savage River National Park	-0.28	0.15	0.00
Ben Lomond National Park	-0.26	0.14	-0.05
Gregory National Park	-0.03	-0.30	0.03
Nitmiluk National Park	-0.09	-0.18	0.00
Kakadu National Park	-0.10	-0.15	-0.02
Stirling Range National Park	-0.08	0.09	0.03
Mount Field National Park	-0.27	0.16	-0.02
Douglas-Apsley National Park	-0.26	0.14	-0.05
Mount Remarkable National Park	0.11	0.10	-0.07

719

720 Table 2. Principal Component Scores (listed to two decimal places) for each Australian modern and
721 fossil community, used in the analysis of ecospace distance and space-time equivalence calculations.

722

Time	Ecospace (m)	Time (ka)	z-score	Combined sites z-score
Cath-4 to LD	0.171373	-528	-1.93886	-2.46848
Cath-3 to LD	0.174404	-292	0.092983	-0.80962
Cath-2b to LD	0.202466	-257	0.394316	-0.5636
Cath-2a to LD	0.289228	-231	0.618163	-0.38085
Cath-1 to LD	0.279277	-206	0.833401	-0.20512
TE-B to SR	0.283719	-143	-1.77044	0.23771
TE-D to SR	0.224049	-104	-0.80022	0.511843
TE-E to SR	0.230933	-70	0.045609	0.750831
TE-E-G to SR	0.338351	-48	0.592912	0.90547
TE-H to SR	0.400088	-35	0.916319	0.996848
TE-J to SR	0.332099	-31	1.015828	1.024964
Space	Ecospace (m)	Distance (km)	z-score	
LD to Remarkable	0.229413	537	-1.05853	
LD to Vulk	0.294723	680	-0.38502	
LD to Flinders	0.279587	720	-0.1973	
LD to Simpsons	0.484514	1110	1.640841	

723

724 Table 3. Variables used in the calculation of the space-time equivalency for community structure.
725 Abbreviations: m – magnitude of ecospace distance in the shared community ecospace; LD – Little
726 Desert National Park; SR – Stirling Range National Park; Cath – Cathedral Cave; TE – Tight Entrance
727 Cave, suffixes represent different stratigraphic units for these sites.