The role of behavioural flexibility in primate diversification

Maria J.A. Creighton^a, Dan A. Greenberg^b, Simon M. Reader^a & Arne Ø. Mooers^b

^aDepartment of Biology, McGill University, Montreal, Quebec, Canada

^bDepartment of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, Canada

*Author for correspondence: maria.creighton@mail.mcgill.ca; ph: +1-514 398 7020; McGill University, Stewart Biology Building 1205 ave Docteur Penfield, Montreal, QC Canada, H3A 1B1 ORCID: <https://orcid.org/0000-0003-1337-1946>

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1 Identifying the factors that influence species diversification is fundamental to our understanding
2 of the evolutionary processes underlying extant biodiversity. Behavioural innovation, coupled
3 with the social transmission of new behaviours, has been proposed to increase rates of
4 evolutionary diversification, as novel behaviours expose populations to new selective regimes.
5 Thus, it is believed that behavioural flexibility may play an important role in driving
6 evolutionary diversification across animals. We test this hypothesis within the primates, a
7 taxonomic group with considerable among-lineage variation in both species diversity and
8 behavioural flexibility. We employ a time cut-off in our phylogeny to help account for biases
9 associated with recent taxonomic reclassifications and compare three alternative measures of
10 diversification rate that consider different phylogenetic depths. We find that the presence of
11 behavioural innovation and social learning are positively correlated with diversification rates
12 among primate genera, but not at shallower phylogenetic depths. Given that we find stronger
13 associations when examining older rather than more recent diversification events, we suggest
14 that extinction resistance, as opposed to speciation, may be an important mechanism linking
15 behavioural flexibility and primate diversification. Our results contrast with work linking
16 behavioural flexibility with diversification of birds at various phylogenetic depths. We offer a
17 possible dispersal-mediated explanation for these conflicting patterns, such that the influence
18 behavioural flexibility plays in dictating evolutionary trajectories differs across clades. Our
19 results suggest that behavioural flexibility may act through several different pathways to shape
20 the evolutionary trajectories of lineages.

21

22

23 KEYWORDS: behavioural drive; behavioural flexibility; evolutionary diversification;
24 extinction; primates; speciation

25

26 Extant species diversity is remarkably variable across the Tree of Life (Willis, 1922; Williams,
27 1964). For clades of the same age, differences in net diversification rate (i.e. speciation rate
28 minus extinction rate) ultimately drive differences in clade size. Both the external environment
29 (e.g. Badgley, 2010; Kozak & Wiens, 2010; Frey, 2010) and intrinsic features of a lineage (e.g.
30 Raikow, 1986; Heard & Hauser, 1995) can influence net diversification. Despite ongoing study,
31 there remains considerable debate over the factors that lead to differences in diversification rate
32 among lineages, and their relative importance (e.g. Lewontin, 1983; West-Eberhard, 1989; Isaac,
33 et al., 2005; Rabosky, 2009; see review by Wiens, 2017).

34

35 Plasticity has been repeatedly proposed to play a major role in shaping evolutionary trajectories
36 in general, and speciation in particular (Baldwin, 1902; Lewontin, 1983; Bateson, 1988; Wcislo,
37 1989; Odling-Smee, et al., 2003; West-Eberhard, 2003; Pelletier, et al., 2009; also see review in
38 Pfennig, et al., 2010), and theoretical modelling supports its potential influence (e.g. Hinton &
39 Nowlan, 1987; Anderson, 1995; Behera & Nanjundiah, 1995; Ancel, 1999; 2000). Behavioural
40 development and expression often allow for more rapid responses than other forms of plasticity
41 such as induced morphological changes (Duckworth, 2009; Snell-Rood, 2013; West-Eberhard,
42 2003). Thus, plasticity of behaviour has been hypothesized to play a particularly important role
43 in influencing evolutionary trajectories of animal lineages (Wyles, et al., 1983; Wilson, 1985;
44 West-Eberhard, 2003). The propensity to adopt new behaviours can greatly and quickly alter
45 ecological niches, exposing populations to new selective regimes. This can lead to increased trait

46 disparity among populations (the "behavioural drive hypothesis"; Wyles, et al., 1983; Wilson,
47 1985); importantly, divergent selection can also lead to eventual speciation. As a result, it has
48 been suggested that behaviourally flexible taxa (i.e. those taxa exhibiting high propensities for
49 behavioural change due to, for example, learning or readiness to transition to new conditions; Sol
50 & Lefebvre, 2000; Audet & Lefebvre, 2017) may undergo faster rates of speciation, and thus
51 overall net rates of evolutionary diversification, compared to less flexible taxa (Sol, et al., 2005;
52 Grant & Grant, 2008; Price, 2008; Sol & Price, 2008; Tebbich, et al., 2010). However, despite
53 support from theoretical modelling (e.g. Price, et al., 2003; Lachlan & Servedio, 2004; Lapiedra,
54 et al., 2013), the idea that behavioural flexibility enhances diversification rates remains
55 contested. Some dispute the extent to which behaviour plays an active role in dictating animal
56 diversity (e.g. Scott-Phillips, et al., 2014). Meanwhile, an alternative hypothesis posits that
57 behavioural flexibility may inhibit, rather than enhance, species diversification: populations that
58 can utilize new resources or transition to new environments are shielding their genomes from
59 bouts of strong directional selection (Bogert, 1949; Huey, et al., 2003).

60

61 Duckworth (2009) suggests that behavioural flexibility could both dampen and promote
62 evolutionary rates depending on the time scale. Under this proposed framework, behavioural
63 flexibility inhibits evolution on short time scales by buffering against abrupt environmental
64 changes that may otherwise result in a population bottleneck or strong bouts of directional
65 selection. Over longer time scales, the same behavioural shift can lead to speciation, either by
66 setting the stage for allopatric speciation or by exposing the newly situated population to novel
67 selective regimes (Huey, et al., 2003; Losos, et al., 2004; Duckworth, 2009; see example in
68 Muñoz & Losos, 2018).

69

70 Previous studies have provided support for behavioural flexibility both driving (e.g. Yeh, 2004;
 71 Yeh & Price, 2004; Tebbich, et al., 2010, Riesch, et al., 2012; Foote, et al., 2016) and inhibiting
 72 (e.g. Losos, et al., 2004; Weber, et al., 2004; Shultz, et al., 2005; Gonzalez-Voyer, et al., 2016)
 73 evolution. However, many of these studies have primarily considered the effects of behavioural
 74 flexibility on microevolutionary change at short time scales (e.g. recent speciation events or
 75 population decline). One notable exception is in birds, where behavioural flexibility has been
 76 associated with multiple estimates of macroevolutionary lineage diversification (Nicolakakis, et
 77 al., 2003; Sol, et al., 2005 – also see Sol, 2003; Sayol, et al., 2019). These studies have employed
 78 two proposed correlates of behavioural flexibility: brain size relative to body size (a structural
 79 measure presumed and shown elsewhere to be associated with behavioural flexibility; e.g.
 80 Lefebvre, et al., 2004) and innovation rate (a behavioural measure) taken from literature surveys.
 81 Both large relative brain size and high innovation rates were associated with heightened
 82 diversification in birds (Nicolakakis, et al., 2003; Sol, et al., 2005; Sayol, et al., 2019), consistent
 83 with the idea that behavioural flexibility positively impacts diversification. Importantly, such
 84 tests have yet to be applied across other taxa, making it difficult to generalize the role of
 85 behaviour in shaping the Tree of Life.

86

87 Here, we explore the relationship between four proxies of behavioural flexibility and several
 88 measures of diversification rate in primates, a taxonomic group with considerable among-lineage
 89 variation in both behavioural flexibility (Reader & Laland, 2002; Reader, et al., 2011) and extant
 90 species diversity (Upham, et al., 2019a; 2019b). Variables associated with diversity of other taxa
 91 (e.g. geographic range size and latitude) have been shown to be poor predictors of primate

diversification (Arbour & Santana, 2017; Upham, et al., 2019a), leaving a great deal of what shapes extant primate diversity unexplained. We focus on two behavioural measures of behavioural flexibility, the presence or absence of published reports of innovation and of social learning, and two brain size measures widely thought to be associated with ability to exhibit flexible behaviours. Consistent with what has been reported for birds (Nicolakakis, et al., 2003; Sol, et al., 2005; Sayol, et al., 2019) and Duckworth (2009)'s proposal that behavioural flexibility promotes diversification events over longer evolutionary time scales, we predict that our separate measures of behavioural flexibility will covary positively with diversification rates across primate lineages. To examine how this association changes at different phylogenetic depths, we examine how behavioural flexibility correlates with diversification over both shallower and deeper time depths in our phylogeny. Understanding how behaviour and ecology may interact to shape evolutionary patterns provides a glimpse into some of the processes that have shaped primate biological diversity and could, in turn, dictate future diversity.

105

106 METHODS:

107 *Data*

108 *Diversification Rate*

Estimating diversification rates is challenging because it depends on an accurate assessment of both the taxonomic richness and divergence time of a given lineage. A previous study testing whether behavioural flexibility drives shallow divergences used subspecies per species as a measure of subspecific diversification in birds (Sol, et al., 2005). Using this subspecies metric could introduce considerable bias when applied in primates, however, as primate taxonomic

richness has changed drastically over recent decades (Tattersall, 2007; Groves, 2014; Rylands & Mittermeier, 2014), with much of this change attributed to application of the ‘phylogenetic species concept’ (PSC) and its tendency to raise former subspecies and variants to the full species rank (Tattersall, 2007). Importantly, it has been suggested that these elevations in subspecies status have been biased toward certain taxa (Isaac, et al., 2004), which would lead to inconsistent estimates of species versus subspecies richness across lineages. Studies using other estimates of primate diversification (i.e. diversification analyses using TreePar; Stadler, 2011) have been hindered by the applications of the PSC, particularly when it comes to accurately estimating shallow divergences (Springer, et al., 2012). Modern primate phylogenies are also not reflective of modern primate taxonomies, as they include some phylogenetic species and omit others, preventing us from using recently described evolutionary rate measures (see, e.g., Jetz, et al., 2012; Mitchell & Rabosky, 2017) that rely on a comprehensive phylogeny with consistent species designations among clades. Instead, we used well-resolved “lineages” that putatively reflect stable species complexes. We started with the most widely used, dated primate tree publicly available at the time of this study, the GenBank taxonomy consensus tree provided on the 10kTrees website (version 3) (Arnold, et al., 2010), containing 301 tips. We then created a time cut-off in the tree at the time when we determined a majority of robust biological species described in Honacki et al. (1982) had evolved (1.1mya). We chose Honacki et al. (1982) as it was the last major primate taxonomy published before the introduction of the PSC (Cracraft, 1983). After creating this time cut-off, we subsequently eliminated shallow divergences occurring after 1.1mya from the consensus tree (see Figure S1). Each branch in the tree that was extant at 1.1mya was retained in the tree and designated as a stable "lineage". We then additionally pruned species from this phylogeny that were no longer recognized by modern

137 taxonomies (IUCN/SSC Primate Specialist Group, 2018). This resulted in 241 identifiable
 138 lineages to compare in terms of taxonomic richness and divergence times. Using the most
 139 recently published primate species and subspecies list from the IUCN/SSC Primate Specialist
 140 Group (2018), we referenced taxonomic and phylogenetic works to assign each of the 705
 141 species and subspecies to one of these 241 lineages. This allowed us to assign each lineage an
 142 agnostic “taxon richness” score (i.e. the sum of all monotypic species and subspecies in a
 143 lineage; see Figure S1) that accounts for the discrepancies in subspecies elevations across
 144 lineages. Each species or subspecies listed by the IUCN/SSC Primate Specialist Group (2018)
 145 was also assigned to one of the 66 genera named in our 10kTrees phylogeny (Arnold, et al.,
 146 2010). After eliminating two individual species and one genus in our tree that could not be
 147 resolved using these methods (see supplementary material), our study considered 703 taxa
 148 (species or subspecies) assigned to 239 lineages and 65 genera.

149

150 To estimate lineage diversification rate we used the method-of-moments estimator (Magallon &
 151 Sanderson, 2001) that divides the natural log of “taxon richness” (species and subspecies) by
 152 lineage stem age to produce a ‘Taxa per Lineage Diversification Rate’ that should be less biased
 153 by recent subspecies elevations. This method was repeated at the genus-level where the natural
 154 log of “taxon richness” for each genus was divided by the stem age of that genus (hereafter
 155 ‘Taxa per Genus Diversification Rate’). We note that all log transformations referenced hereafter
 156 refer to natural log transformations ($\log_e$). Lastly, we created a second, and perhaps more
 157 conservative estimate of genus diversification rate where richness scores were generated using
 158 the number of lineages ($n=239$) per genus, rather than the number of taxa described by the
 159 IUCN/SSC Primate Specialist Group (2018), hereafter ‘Lineage per Genus Diversification Rate’.

160 A few genera were not monophyletic on our tree, and we considered these on a case-by-case
161 basis ultimately removing five from our genus-level analysis (see the supplementary material).

162

163 We illustrate these methods and present associated calculations using genus *Aotus* as an example
164 in the supplementary material to provide some considerations on the potential uses and
165 limitations of this approach.

166

167 *Behavioural Proxies of Behavioural Flexibility*

168 We focused on two key behaviours to infer behavioural flexibility: innovation and social
169 learning. Innovation and social learning are both important in determining the macroevolutionary
170 effects of behavioural flexibility because multiple individuals must acquire an innovation
171 through social learning or independent innovation to have population-level effects (Wyles, et al.,
172 1983; Wilson, 1985; Duckworth, 2009). In addition to facilitating the transmission of
173 innovations throughout a population, social learning can also be a valuable measure of
174 population-level behavioural flexibility on its own as it reflects the ability of individuals within a
175 population to pick up behaviours that are novel to them but not necessarily novel to the
176 population. We note that social learning and innovation are taxonomically widespread (Reader &
177 Biro, 2010; Snell-Rood, et al., 2015). However, we assume that species with no published
178 accounts of social learning or innovation are likely relying on these behaviours infrequently.
179 Moreover, the innovation and social learning data used here have been positively associated with
180 other measures of behavioural flexibility (e.g. brain size measures; Reader, et al., 2011;
181 Navarrete, et al., 2016). For innovation, we focus on technical innovations (classified as those

182 involving tool use following Navarrete, et al., 2016) because these more easily defined
 183 behaviours have been linked to complex cognition (Overington, et al., 2009), and reports of other
 184 classes of innovation (e.g. food type innovation) can be highly influenced by opportunistic
 185 events (Ducatez, et al., 2015). Combined with the fact that taxa with reports of technical
 186 innovation also tended to be those with evidence of other innovation types (see data in Navarrete,
 187 et al., 2016), this likely makes technical innovation a robust estimate of innovativeness across
 188 primates.

189

190 Counts of innovation and social learning per lineage came from Reader et al. (2011) and
 191 Navarrete et al. (2016). Reader et al. (2011) established this dataset through a survey of over
 192 4000 published articles for examples of social learning and behavioural innovation. Reader et al.
 193 (2011, p. 1018) define an innovation as the tendency to “discover novel solutions to
 194 environmental or social problems”. These data were later subdivided into different innovation
 195 categories by Navarrete et al. (2016), including ‘technical’ innovations, defined as innovations
 196 involving tool use. Reader et al. (2011, p. 1018) define social learning as the tendency to “learn
 197 skills and acquire information from others”, including instances of social learning from both kin
 198 and unrelated individuals. Social learning was often inferred from observational data in the
 199 original reports.

200

201 As an alternative to treating behavioural data as a binary metric (e.g. presence or absence of
 202 innovativeness in Ducatez, et al., 2020) some studies have used “rate” measures of behaviours:
 203 residuals from a log-log plot of the total number of recorded instances of a behaviour (e.g. social

learning) and an estimate of research effort (e.g. the number of papers published on that taxa; e.g. Sol, et al., 2005; Reader, et al., 2011; Navarrete, et al., 2016; Ducatez, et al., 2020). However, the choice of how to model the relationship between total number of recorded innovation or social learning instances and research effort matters considerably when creating these residual rate measures. For our data, the relationship between the total number of innovation or social learning instances and research effort was non-linear. This made the choice of model structure non-trivial, with different models proving difficult to justify over one another. Residuals from these models additionally showed further structural issues, including failure to meet assumptions about homoscedasticity. Thus, we opted to use binary measures, which allowed us to use data imputation methods to minimize biases caused by under-studied taxa, statistically account for potential biases associated with summarizing behavioural data at higher taxonomic levels, and run simulations to address the assumptions underlying our analyses. We therefore assigned each lineage or genus binary scores of 1 (presence of innovation or social learning) or 0 (absence of innovation or social learning). Further considerations regarding the use of literature-based estimates of behavioural flexibility can be found in the supplementary material.

219

220 *Structural Proxies of Behavioural Flexibility*

Literature-based evidence for behavioural flexibility across taxa has its limitations and so we chose to also consider structural correlates of behavioural flexibility. It is widely thought that particular brain regions are associated with flexible behaviour – particularly the neocortex (see, e.g., Keverne, et al., 1996; Mikhalevich, et al., 2017) and cerebellum (Vandervert, 2003; Vandervert, et al., 2007; Barton, 2012). Therefore, in addition to total brain size (relative to body mass), we considered the sum of neocortical and cerebellar volumes relative to rest of total brain

227 volume as another proxy for behavioural flexibility. Using both behavioural measures and
 228 structural correlates of behavioural flexibility, we were able to compare the consistency of results
 229 across different proxies for behavioural flexibility.

230

231 Lineage-level estimates for all brain measures were calculated by taking the geometric mean of
 232 taxon volumes for each lineage. Brain volume relative to body size (hereafter ‘relative brain
 233 volume’) was estimated by regressing lineage-level estimates of logarithmic endocranial volume,
 234 in cm³, (ECV) (Powell, et al., 2017) (hereafter ‘brain volume’) as a function of logarithmic body
 235 mass, in grams (Jones, et al., 2009), and retaining the residuals (Dunbar & Schultz, 2007).
 236 Notably, previous studies (e.g. Sayol, et al., 2019) have used phylogenetically corrected residuals
 237 to account for an effect of body size when using similar brain size measures. However, for our
 238 data, residuals obtained from phylogenetic models were skewed such that lineages with larger
 239 body mass consistently had larger residual brain volumes (see Figure S2), and thus we opted to
 240 use ordinary least square residuals that were more orthogonal to lineage body size. Consistent
 241 with relative brain volume, neocortex and cerebellum volume relative to rest-of-brain volume
 242 (hereafter ‘relative neocortex and cerebellum volume’) was estimated by taking the residuals
 243 from a log-log regression of the combined neocortex and cerebellum volumes on the rest-of-
 244 brain volumes (i.e. total brain volume minus neocortex and cerebellum volumes) taken from
 245 Navarrete et al. (2018) and the compilation in DeCasien & Higham (2019). Genus-level
 246 estimates for structural proxies of flexibility were calculated by taking the mean of the lineage
 247 estimates within each genus. Further details, and considerations regarding the use of structural
 248 proxies of behavioural flexibility, and residual brain measures can be found in the supplementary
 249 materials along with correlation coefficients for all predictor variables (Table S1).

250

251 Phylogenetic signal of all predictor and response variables are reported in the supplementary
252 material (Table S2).

253

254 *Analysis*

255 All analyses used R version 3.6.3 (R Core Team, 2020).

256

257 *Trait Imputation*

258 While we collected data for our predictor variables from the most comprehensive datasets and
259 compilations available, research biases and the persistent reassessment of primate taxonomy has
260 resulted in inconsistent data coverage across lineages, and there were still many lineages that
261 were missing data (see Figure S3). To maximize our evolutionary inferences on diversification
262 and allow for the inclusion of data-poor lineages, we chose to impute missing predictor variables
263 using phylogenetic imputation methods (see supplementary material for details and reports of
264 predictive accuracy from model cross-validation; Table S3 and Figure S4). Data on relative
265 neocortex and cerebellum volume were sparse and unevenly distributed across the phylogeny
266 (82.4% of lineages missing data; Table S3), making it infeasible to reliably impute missing
267 values. We thus only ran models of relative neocortex and cerebellum volume on the original,
268 non-imputed dataset. All of the regressions we report below were repeated for the original, non-
269 imputed datasets (see Results and the supplementary material Tables S4 to S6) and except as
270 noted gave similar results.

271

272 *Predictors of Diversification*

273 To assess the relationship between our measures of behavioural flexibility and diversification
 274 rate at the lineage-level (Taxa per Lineage Diversification Rate) we used phylogenetic
 275 generalized least squares (PGLS) regressions implemented using the “glS” function in the nlme
 276 package (Pinheiro, et al., 2020), including the 10kTrees consensus tree for our 239 defined
 277 lineages as the phylogenetic backbone. PGLS is a common regression method used to investigate
 278 evolutionary associations while accounting for the fact that closely-related lineages tend to be
 279 similar (e.g. in body size, life history and ecology; see Freckleton, et al., 2002). Continuous data
 280 were log-transformed, centred with respect to the mean, and scaled by 2 standard deviations in
 281 all models for both the lineage and genus-level analyses to make effect sizes comparable to those
 282 reported for binary variables (Gelman, 2008). After imputing missing values, our dataset
 283 contained 54 lineages scored as having evidence of social learning (scored as 1) and 28 lineages
 284 scored as having evidence of technical innovation (scored as 1). Wyles et al. (1983) predicted
 285 accelerated evolution in species with a dual capacity for innovation and social propagation of
 286 new behaviours, therefore, we also tested a combined measure of technical innovation and social
 287 learning. In this combined measure 26 lineages with the presence of both behaviours were scored
 288 as 1, and those exhibiting only one or neither behaviour were scored as 0.

289

290 To assess the relationship between our measures of behavioural flexibility and diversification
 291 rate deeper in the tree we repeated the same analysis at the genus-level using two different
 292 estimates of diversification rate: Taxa per Genus Diversification Rate and the more conservative

293 Lineage per Genus Diversification Rate. After imputing missing values, our dataset of 60 genera
 294 contained 21 genera scored as having evidence of social learning, 9 genera scored as having
 295 evidence of technical innovation and 8 genera with evidence of both behaviours.

296

297 Body mass and attendant life history traits have been predicted to impact diversification rates in
 298 some taxa, albeit with conflicting results (see, e.g., Cardillo, et al., 2003; Paradis, 2005;
 299 Fontanillas, et al., 2007; Thomas, et al., 2010), and body mass is closely correlated with many
 300 primate life history traits (e.g. age at first reproduction, maximum lifespan; Charnov & Berrigan,
 301 1993; Purvis, et al., 2003; Street, et al., 2017). To examine whether our results could stem from
 302 confounding effects of body mass and its correlates, we ran PGLS analyses to test body mass as
 303 an independent predictor of our diversification rate measures. Results from these tests were non-
 304 significant across all measures of diversification (see supplementary material Tables S4 to S6).

305

306 We re-ran all PGLS analyses reported above after eliminating the great apes, which are
 307 characterized by slow life histories, which may counteract the evolutionary effects of
 308 behavioural flexibility by slowing their evolutionary response time (Price, et al., 2003). For tests
 309 that proved significant, we then reran the same test 100 times over a sample of 1000 trees from
 310 the tree block available in 10kTrees (Arnold, et al., 2010) to confirm results were consistent after
 311 accounting for phylogenetic uncertainty.

312

313 *Genus-Level Simulations*

314 Genera were considered behaviourally flexible if any of their daughter lineages had evidence of
315 innovation or social learning, which potentially introduces a statistical bias if more lineage-rich
316 genera (which will generally have higher diversification rates) are more likely by chance to
317 include at least one lineage that expresses technical innovation or social learning. To account for
318 this possible bias, we simulated the neutral evolution of technical innovation and social learning
319 across the primate phylogeny 1000 times using the symmetrical rate Mk model of discrete trait
320 evolution (Lewis, 2001). We opted to model the evolution of these behaviours under a
321 symmetrical model of trait evolution since with smaller datasets such as ours, there is little power
322 to prefer asymmetric models (Mooers & Schluter, 1999). From these stochastic distributions of
323 the two traits, we repeated our analyses of diversification rate and created a distribution of
324 expected effect sizes under a null evolutionary scenario. More diverse genera may also be more
325 likely, by chance, to have well-studied lineages, which could create a bias toward observing the
326 presence of innovation or social learning in diverse genera (Ducatez & Lefebvre, 2014).
327 Although data did not suggest that lineage-rich clades were more likely to have intensely
328 investigated lineages in our dataset (see Figures S5 and S6), we nonetheless opted to take
329 research effort into account in our analysis and expanded upon our first simulation to consider a
330 scenario where the presence of technical innovation or social learning may go unobserved if
331 insufficient research effort was directed at a lineage. We took the 1000 simulations of neutral
332 evolution of technical innovation and social learning, and then randomly ‘evolved’ research
333 effort for each simulation, independently of the evolution of technical innovation and social
334 learning. We then converted the presence of these behaviours to absences in our simulated
335 datasets if a lineage’s ‘evolved’ research effort was below the minimum threshold of studies for
336 a lineage with observed technical innovation (as it contained the higher research effort threshold

than social learning; Figure S7). By repeating our analyses of diversification rate with these new simulated datasets where lineages with low research effort were assigned ‘hidden states’, we were able to see if a bias towards having better studied lineages in diverse genera could drive a positive association between behavioural proxies of flexibility and diversification rate by chance and independent of biological mechanisms. Importantly, this simulation makes the assumption that research effort and behavioural flexibility are independent; if this is not true such that behaviourally flexible lineages attract research effort (see discussion in the ‘Research Effort Bias’ section of the supplementary material) then the results of this simulation would actually be conservative. We detail both simulations, along with considerations about using research effort as a covariate in binary models (Ducatez, et al., 2020), in the supplementary material.

Ethical Note

This research was comparative and was based on data available in previously published literature.

RESULTS:

Lineage-Level Predictors of Diversification

We found no support for an association between behavioural flexibility and diversification rates when testing our measures of behavioural flexibility at the lineage-level (results summarized in Figures 1 and S8; Table S4). Social learning ($p=0.171$), technical innovation ($p=0.792$), the combined presence of technical innovation and social learning ($p=0.979$), relative brain volume

($p=0.215$), relative neocortex and cerebellum volume ($p=0.664$), and body mass ($p=0.764$; Table S4) did not exhibit noteworthy associations with Taxa per Lineage Diversification Rate in either direction.

Genus-Level Predictors of Diversification

Technical innovation ($p=0.577$), social learning ($p=0.442$), the combined presence of technical innovation and social learning ($p=0.411$), relative neocortex and cerebellum volume ($p=0.930$), and body mass ($p=0.204$) did not exhibit noteworthy associations with Taxa per Genus Diversification Rate (Figures 1 and S8; Table S5). Relative brain volume was insignificantly ($p=0.108$), but positively, related to diversification rate, and this relationship became significant when we considered the non-imputed dataset ($p=0.004$).

In contrast to the other diversification measures, Lineage per Genus Diversification Rate was positively associated with all three behavioural measures of behavioural flexibility (results summarized in Figures 1 and S8; Table S6). Genera with records of technical innovation were shown to have a faster mean Lineage per Genus Diversification Rate ($0.136 \text{ lineages my}^{-1}$) than those with no reports ($0.070 \text{ lineages my}^{-1}$; β [95% CI] = 0.066 [0.002 - 0.130]; $p=0.048$). Genera with records of social learning similarly exhibited a faster mean Lineage per Genus Diversification Rate ($0.137 \text{ lineages my}^{-1}$) than those without ($0.049 \text{ lineages my}^{-1}$; β [95% CI] = 0.088 [0.043 - 0.132]; $p<0.001$). Genera with reports of both technical innovation and social learning also exhibited a faster mean Lineage per Genus Diversification Rate ($0.153 \text{ lineages my}^{-1}$) compared to those with evidence for only one or neither behaviour ($0.068 \text{ lineages my}^{-1}$; β

380 [95% CI] =0.085 [0.018-0.151]; $p= 0.015$). These results were consistent with results run over a
 381 sample of 1000 trees from the posterior distribution, i.e. “tree block”, available from 10kTrees
 382 (Arnold, et al., 2010), indicating results were not biased by our choice of phylogeny (Figure S9).
 383 Based on our simulation testing for a lineage-richness sampling bias, we found that these effect
 384 sizes were unlikely to be due to chance alone for technical innovation ($p= 0.028$), social learning
 385 ($p= 0.002$) and the combined presence of both behaviours ($p= 0.008$) (see Figure S10 and
 386 supplementary results). After expanding our simulation to consider a research effort bias,
 387 significance of these effects remained for social learning ($p= 0.019$) and its combined presence
 388 with technical innovation ($p= 0.027$), but the effect of technical innovation alone was no longer
 389 nominally significant ($p= 0.109$) (see Figure S11 and supplementary results). No structural
 390 proxies of behavioural flexibility shared notable associations with Lineage per Genus
 391 Diversification Rate (Figures 1 and S8; Table S6).

392

393 Results of all PGLS analyses reported above were qualitatively consistent after removing great
 394 apes (see supplementary material Tables S7 to S9).

395

396

397 Figure 1: Results from PGLS analyses showing the association of proxies of behavioural

398 flexibility with Taxa per Lineage Diversification Rate (DR), Taxa per Genus Diversification

399 Rate and Lineage per Genus Diversification Rate across primates. 95% confidence intervals are

400 represented by horizontal lines around the associated value. Diamonds indicate diversification

401 rates estimated with species/subspecies richness, and squares indicate diversification rates

402 estimated with lineage richness. Results presented include imputed data when available and brain

403 measures were standardized (ln x/(2sd)). Significance indicated as: +P ≤ 0.1; *P ≤ 0.05; **P ≤ 0.01.

404

405 DISCUSSION:

406 We find little to no compelling support for an association between our proxy measures of
 407 behavioural flexibility and recent primate diversification rates of young species and subspecies,
 408 however, we do find some evidence supporting a positive association when looking at the
 409 diversification of older primate lineages. This pattern could be explained in several ways, and
 410 interpretation of these results depend on the assumptions one makes about our different measures
 411 of diversification rate.

412

413 One benefit of our study design is that it allowed us to consider taxa that are commonly
 414 overlooked (i.e. subspecies and species omitted from higher order phylogenies), many of which
 415 likely represent very recent splitting events. The weak associations with behavioural flexibility
 416 that we observed at shallower time scales could be explained in several ways. On one hand, this
 417 pattern could reflect biases in describing taxa (species and subspecies) among groups. While our
 418 time cut-off, and use of both species and subspecies, mitigates against biases associated with the
 419 elevation of subspecies under the PSC, if less flexible species are more likely to have a larger
 420 number of taxa described overall (e.g. based on regional biases in designating species or
 421 subspecies that covary with locations of inflexible clades) then this could obscure underlying
 422 biological patterns. If this is the case, then behavioural flexibility may indeed enhance
 423 diversification by acting on speciation, and we observe stronger associations when ignoring
 424 shallow splits because our diversification rate metric calculated using lineage-richness is less
 425 biased by this phenomenon. On the other hand, if we take our results at face value, a pattern of
 426 stronger associations deeper in the phylogeny could indicate that time plays an even larger role
 427 in the relationship between behavioural flexibility and diversification than previously suggested
 428 by Duckworth (2009).

429

430 Under Mayr's 'ephemeral speciation model' (Mayr, 1963; Rosenblum, et al., 2012) and the
 431 related 'ephemeral divergence hypothesis' (Futuyma, 1979; 2010), divergence can occur rapidly
 432 and often, but many newly diversifying lineages do not persist, instead being eradicated via
 433 extinction or 'reabsorption' by hybridization (see, e.g., Rosenblum, et al., 2012). It is possible
 434 that a number of the described species and subspecies used here (from the IUCN/SSC Primate
 435 Specialist Group, 2018) represent such ephemeral diversification events, especially considering
 436 that the PSC has facilitated the splitting of very closely related populations. If so, our results
 437 could be explained if behavioural flexibility buffers against extinction through behavioural shifts.
 438 Behavioural flexibility would then promote diversification through bolstering lineage persistence
 439 rather than the rate of splitting; and would be revealed when comparing the accumulation of
 440 lineages that have escaped extinction (i.e. looking deeper in the tree). This would be
 441 complementary to findings from Arbour & Santana (2017), who show that decreased extinction
 442 preceded a shift to increased evolutionary rates in the most speciose primate family
 443 (Cercopithecidae), and with evidence suggesting behavioural flexibility is beneficial for
 444 population persistence in birds (e.g. Shultz, et al., 2005; Rossmanith, et al., 2006; Sol, et al.,
 445 2007, Ducatez, et al., 2020). Under this scenario, the positive associations we find are not the
 446 result of behavioural flexibility enhancing evolutionary rates by facilitating divergence events,
 447 and instead indicate that extinction resistance may be an important mechanism linking
 448 behavioural flexibility and primate diversification. Our results stand in contrast with consistent
 449 reports of behavioural flexibility enhancing diversification of birds even at shallow phylogenetic
 450 depths (Nicolakakis, et al., 2003; Sol, et al., 2005; Sayol, et al., 2019).

451

452 A potential explanation for differing effects of behavioural flexibility in birds versus primates
 453 could be that the heightened dispersal capabilities (i.e. flight) of birds makes behavioural
 454 flexibility particularly beneficial for these taxa when it comes to establishing in new
 455 environments. This could cause behavioural flexibility to enhance bird speciation via increased
 456 success in dispersal events while also buffering against extinction – leading to the strong effects
 457 that have been observed on their net rates of evolution (Nicolakakis, et al., 2003; Sol, 2003; Sol,
 458 et al., 2005; Sayol, et al., 2019). Comparatively, primates have much more limited dispersal
 459 capabilities and thus behavioural flexibility may buffer against extinction while having little
 460 effect on promoting allopatric establishment and subsequent speciation. If true, it is possible that
 461 behavioural flexibility affects evolutionary trajectories via different mechanisms in these clades.
 462

463 Directly testing whether behavioural flexibility buffers against extinction may be difficult
 464 because measuring extinction rates at macroevolutionary scales is notoriously imprecise
 465 (Rabosky, 2010; Louca & Pennell, 2020). Future studies could test proxies of primate
 466 behavioural flexibility against estimates of contemporary extinction vulnerability (see, e.g.,
 467 Nicolakakis, et al., 2003; Ducatez, et al., 2020). Another prediction concerns the rate of genetic
 468 divergence within flexible versus less flexible, recent clades (e.g. subspecies within species): our
 469 conjecture would be that these would not be different, because flexibility does not lead to
 470 increased divergence over the short term.

471
 472 Notably, not all of our results are consistent with a significantly positive association between
 473 behavioural flexibility and diversification of older primate lineages. While the non-significant
 474 association between Lineage per Genus Diversification Rate and neocortex and cerebellum

475 volume might be explained by data limitations (discussed below), the non-significant association
 476 with relative brain volume illustrates that not all proxies of behavioural flexibility capture the
 477 same thing. While relative brain volume is a known structural correlate of measures of primate
 478 and avian behavioural flexibility (Lefebvre, et al., 2004), the brain has many functions and thus
 479 is a less direct measure of behavioural flexibility than behavioural measures. Measures of brain
 480 size have been linked to diversification rate in birds (Nicolakakis, et al., 2003; Sol, et al., 2005;
 481 Sayol, et al., 2019), but notably the sample for birds is much larger, and is likely to contain a
 482 broader range of variation, which would make it easier to detect a brain size effect. Additionally,
 483 results of our simulation accounting for potential research effort biases indicate that a positive
 484 association between technical innovation and diversification rate in primate genera could be
 485 driven by a research effort bias. However, this simulation assumes that research effort and
 486 behavioural flexibility are independent and, if instead research effort tends to be directed toward
 487 groups where innovation is expected, then this research bias may actually have a low
 488 contribution to the observed relationship between technical innovation and diversification rate.
 489 Thus, our results paint a complicated picture, and emphasize the need to compare methodologies
 490 and measures, and avoid a focus on single explanations for complex phenomena.

491

492 Our results provide some support for primate behavioural flexibility being associated with older
 493 as opposed to more recent diversification events, however, there are several caveats on the limits
 494 of our inferences. First, one measure thought to be associated with behavioural flexibility –
 495 neocortex and cerebellum volume – had very little data available for lineages reported as
 496 inflexible (e.g. among lemurs, tarsiers, titis and sakis). This meant our ability to test this measure
 497 as a driver of diversification was limited. Additionally, to examine the relationship between

different measures of behavioural flexibility and diversification rate, we had to run multiple tests, increasing the likelihood of observing Type I error. Our study is also limited by the lineages present in the phylogeny. Available primate phylogenies, (e.g. Arnold, et al., 2010; Upham, et al., 2019b) do not reflect the most recent taxon lists, and such limited taxonomic scope prevented us from using diversification rate estimates that require a fully-resolved tree (e.g. the DR measures from Jetz, et al., 2012). Lastly, many factors will contribute to true diversification, and although we test two (e.g. body mass and a "great ape effect"; see supplemental results), there are many biological and ecological factors (e.g. geographic discontinuities, habitat affiliations, or presence on islands) yet to be explored that could mediate any relationship between behavioural flexibility and primate diversification rate.

While our results provide some evidence for the hypothesis that behavioural flexibility drives diversification of primate lineages, they raise important questions about its underlying mechanisms. Importantly, our results are not consistent in supporting a significant association between behavioural flexibility and diversification rate, and depend on the proxy measures employed. The positive associations we do find may point to behavioural flexibility dampening extinction of young primate lineages, rather than accelerating diversification via splitting of behaviourally shifted individuals/populations. Thus, expanding tests of whether and how behavioural flexibility is associated with diversification to other taxa may help us interpret the results we report here.

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527

528 Data and code will be made available through Dryad or a similar repository.

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