DETERMINANTS OF PRIMATE DIVERSITY WITH IMPLICATIONS FOR COMPARATIVE BIOLOGY AND CONSERVATION

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ABSTRACT

Variation in species diversity across the Tree of Life has long been of interest to biologists. Despite this interest, a great deal of variation in species richness across the Tree of Life remains unexplained. Species are used as an important unit of comparison across many areas of biology, making it important to further our understanding of the processes by which species originate. In this thesis I explore determinants of species diversity across primates – one of the more species rich and rapidly evolving groups of mammals, with over 500 described species. I address two major determinants of extant species diversity across higher taxa: (i) evolutionary processes; (ii) the application of species concepts leading to the formal recognition of species by scientists – and explore hypotheses related to each. In Chapter 2, I investigate the role of evolutionary processes in shaping primate diversity. Specifically, I test the hypothesis that behavioural flexibility leads to higher rates of speciation, thereby increasing rates of evolutionary diversification in behaviourally flexible clades. I test the relationship between multiple measures of behavioural flexibility and primate diversification rate, and find that behavioural flexibility does not seem to be driving recent, shallow divergences, in contrast to findings in other taxa (i.e. subspecific diversification of birds). I do, however, find positive associations deeper in the tree which may support a role for behavioural flexibility enhancing lineage persistence, as opposed to driving speciation events. When testing this hypothesis, taxonomic instability and rapid inflation in species numbers complicated estimates of primate diversification rate – requiring me to produce a method of accounting for biases associated with applications of the 'phylogenetic species concept' (PSC) in primate taxonomy. Thus, in Chapter 3, I opted to further investigate the role of systematic biases in determining extant species richness across primate clades. More specifically, I explore predictors of taxonomic inflation under the PSC. I also investigate whether the PSC is influencing trends in conservation by testing whether taxonomic inflation is associated with primate threat scores. I find that neither biological processes (i.e. diversification rate) nor estimates of human imposed bias (i.e. measures of research effort) are significant predictors of inflation among primate genera. However, when testing whether the PSC influences trends in primate conservation, I find an association between inflation and genus threat score that is region specific, where highly inflated genera are perceived as the most at risk in some regions, but the least at risk in others. I suggest that this could be a result of other factors (e.g. the total geographic range size of genera) influencing how inflation impacts threat score. Together, these chapters improve our

understanding of species diversity and have implications for how species are used across many disciplines of biology that rely on species as an important unit of comparison.

RÉSUMÉ

La variation de la diversité en espèces à travers l'Arbre de Vie intéresse depuis longtemps les biologistes. Malgré cet intérêt, une grande partie de la variation de la richesse en espèces de l'Arbre de Vie reste inexpliquée. Les espèces sont utilisées comme une unité de comparaison importante dans de nombreux domaines de la biologie, ce qui montre l'importance de comprendre les processus déterminants de l'origine des espèces. Dans cette thèse, j'explore les facteurs de diversité des espèces chez les primates - l'un des groupes de mammifères les plus riches en espèces et en évolution rapide, avec plus de 500 espèces décrites. J'aborde deux facteurs majeurs de la diversité des espèces existantes dans les taxons supérieurs: (i) les processus évolutifs; (ii) l'application des concepts d'espèces conduisant à la reconnaissance formelle des espèces par les scientifiques – et j'explore plusieurs hypothèses liées a chacun des facteurs. Au deuxième chapitre, j'étudie le rôle des processus évolutifs dans la formation de la diversité des primates. Plus précisément, je teste l'hypothèse selon laquelle la flexibilité comportementale entraîne des taux de spéciation plus élevés, augmentant ainsi les taux de diversification évolutive dans les groupes à flexibilité comportementale. Je teste la relation entre plusieurs mesures de flexibilité comportementale et le taux de diversification des primates et détecte que la flexibilité comportementale ne semble pas être à l'origine de divergences récentes et peu profondes contrairement à ce qui a été démontré dans d'autres taxons (c.-à-d. Diversification sous-spécifique des oiseaux). Cependant, je trouve des associations à un niveau plus profond de l'arbre qui supportent l'idée que la flexibilité comportementale améliorerait la persistance de la lignée au lieu de générer des générer des événements de spéciation. Au cours de ces analyses, j'ai détecté que l'instabilité taxonomique et l'inflation rapide des espèces compliquent les estimations du taux de diversification des primates - m'obligeant à utiliser une méthode de comptabilisation des biais associés aux applications du «concept d'espèce phylogénétique» (CEP) dans la taxonomie des primates. Ainsi, dans le troisième chapitre, j'ai choisi d'étudier plus en détail le rôle des biais systématiques dans la détermination de la richesse des espèces existantes à travers les clades de primates. Plus précisément, j'explore les prédicteurs de l'inflation taxonomique dans le cadre du CEP. J'étudie également si le CEP influence les tendances de conservation des primates en testant si l'inflation taxonomique est associée au score de menace des primates. Je détecte que ni les processus biologiques (c'est-à-dire le taux de diversification) ni les estimations du biais imposé par l'homme (c'est-à-dire les mesures de l'effort de recherche) ne sont des prédicteurs significatifs de l'inflation parmi les genres de primates.

Cependant, les analyses visant à tester l’influence du CEP sur les tendances de conservation des primates révèlent qu’il existe une association spécifique aux régions entre l’inflation taxonomique et le score de menace. C’est-à-dire, les genres pour lesquels il y a une forte inflation sont perçus comme étant les plus à risque dans certaines régions, mais dans d’autres régions sont perçus comme étant les moins à risque. Je suggère que cela pourrait être le résultat d'autres facteurs (par exemple, la taille de l'aire géographique totale d'un genre) qui pourraient influencer la façon dont l’inflation affecte le score de menace du genre. Ensemble, ces chapitres approfondissent notre compréhension de la diversité des espèces et ont des implications sur la façon dont la notion d’espèces est utilisée dans les disciplines de la biologie qui se basent sur les espèces comme unité de comparaison importante.

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CONTRIBUTION TO ORIGINAL KNOWLEDGE

The present thesis is manuscript based. All chapters herein contain original work and contributions to knowledge. In Chapter 2, I provide evidence for behavioural flexibility mediating net rates of evolution across primates. Although behavioural flexibility has often been suggested to influence rates of evolution, to the best of my knowledge this is the first large-scale comparative study to test this hypothesis in primates. Patterns in my results suggest that the association between proxies of behavioural flexibility and diversification rate observed in my study may be a product of behavioural flexibility buffering against extinction, rather than enhancing speciation as previously suggested. In Chapter 3, I explore the role of taxonomic inflation and its associated biases in dictating species richness across primate clades. My results do not suggest that a strong biological nor a strong interest-driven mechanism is responsible for variation in observed inflation across primate genera. I do, however, find an association between inflation and threat score that is region specific, where highly inflated genera are considered most at risk in some regions, but least at risk in others. This could indicate that other factors (e.g. total geographic range size) impact how inflation influences a genera's perceived extinction risk. These findings add to our understanding of the causes and consequences of taxonomic inflation.

CONTRIBUTION OF AUTHORS

Chapter 1: General introduction

Maria J.A. Creighton wrote the chapter with feedback from Simon M. Reader.

Chapter 2: The role of behavioural flexibility in primate diversification

Maria J.A. Creighton, Arne Ø. Mooers and Simon M. Reader designed the study. Maria J.A. Creighton collected the data. Maria J.A. Creighton and Dan A. Greenberg analysed the data with input from Arne Ø. Mooers. Maria J.A. Creighton wrote the manuscript with input from Arne Ø. Mooers, Dan A. Greenberg and Simon M. Reader. All authors approve the submission of this manuscript as part of the present thesis. Manuscript in review at Animal Behaviour.

Chapter 3: Predictors of taxonomic inflation and its role in primate conservation

Maria J.A. Creighton designed the study. Maria J.A. Creighton collected and analysed the data with input from Arne Ø. Mooers. Maria J.A. Creighton wrote the manuscript with input from Arne Ø. Mooers and Simon M. Reader. All authors approve the submission of this manuscript as part of the present thesis.

Chapter 4: General discussion

Maria J.A. Creighton wrote the chapter with feedback from Simon M. Reader.

CHAPTER 1: GENERAL INTRODUCTION

SPECIES AND SPECIES DIVERSITY:

Biologists have long been fascinated by the incredible range of biological diversity exhibited by organisms across the Tree of Life. In nature, variation in organism diversity is not continuous, thereby allowing scientists to group them together based on distinctive traits (e.g. morphology, behaviour, karyotype) (Ereshefsky, 1992; Schemske, 2000). 'Species' were employed as the lowest level of biological unity by Carl Linnaeus (Linnaeus, 1753; Svenson, 1953) and provide biologists with a means of categorizing the natural world. Species are intended to reflect organism diversity and, as a result, species diversity (most simply estimated by counting species – i.e. species richness; MacArthur, 1965) is often used to estimate biological diversity (Clarke, 1975; Wilson, 1988). Species richness and thus perceived biological diversity is shown to be extremely variable across the Tree of Life.

Animal phyla can contain one (e.g. Micrognathozoa) to upwards of 1.3 million (e.g. Arthropoda) described species and show considerable within phyla variance in species richness (Zhang, 2013; Scholl & Wiens, 2016). At large phylogenetic scales (i.e. across higher taxa), variation in species richness among taxa is suggested to be driven by a range of intricate and mutually dependant biological, historical and geographic factors (Rabosky, et al., 2012). Evolutionary biologists and ecologists have done considerable work to elucidate the factors shaping species richness (e.g. Coyne & Orr, 2004; Futuyma, 2009). Still, much variation remains unexplained and many putative drivers of variation in species richness have yet to be empirically explored. Identifying the sources of this variation is important since biologists rely on species as the fundamental unit of comparison across many sub-disciplines of biology (Zink & McKitrick, 1995; De Queiroz, 2005). As a result, understanding what determines species richness across the Tree of Life has implications for both fundamental and applied areas of biology.

"Because the species is one of, if not the most significant of, the units of evolution, of systematics, of ecology, and of ethology, the species is as important a unit of biology as is the cell at a lower level of integration."
— Ernst Mayr (1982, pp. 296–297)

Species serve many purposes across different sub-disciplines of biology. For instance, in studies of behaviour, anatomy and physiology, studies of sample populations are often taken as being reflective of the species as a whole (Mayr, 1982). Species are also used as the primary unit of conservation, with species lists being used to determine which biological units should receive conservation attention (Mace, 2004). Meanwhile, species are widely regarded as the principal unit of evolution, with evolutionary biologists using species as a measure of evolutionary relationships and distinctiveness (Mayr, 1969; Mayr, 1982; Mayr, 1996). Notably, the term 'species' can be used to describe two biological entities that are linked to one another by necessity: the species category (a rank in the Linnaean hierarchy) and the species taxon (which includes taxonomic groups at the level of the species category following the application of the species category in systematics) (Mayr, 1982). Species taxa are recognized with help of explicit definitions detailed by various species concepts. Henceforth, I will use the term 'species' in reference to species taxa rather than the species category.

As biologists, it is essential that we have a thorough understanding of the processes involved in determining the species we rely on in our respective areas of study. Across many fields, species are considered a result of biological and evolutionary processes, however, the role of scientists in naming and defining species inevitably plays a role in determining species lists. Here, I discuss two distinct determinants of extant species diversity: (i) evolutionary processes; (ii) the application of systematic processes leading to the formal recognition of species by scientists. I explore some notable ways in which each of these factors has been suggested to drive described species diversity, and go on to empirically test these supposed associations in Chapters 2 and 3.

EVOLUTION AS A DETERMINANT OF SPECIES DIVERSITY – WITH A FOCUS ON BEHAVIOUR:

Famously regarded as the 'mystery of mysteries' by Charles Darwin, the processes leading to the emergence of new species remain largely unresolved (Darwin, 1859; Coyne & Orr, 2004). When considering the determinants of species diversity across the Tree of Life one typically thinks of the evolutionary processes involved. This is because evolutionary processes are directly responsible for the addition of new species (through speciation) and the subtraction of existing species (through extinction), thereby controlling the number of species within clades through time

(Scholl & Wiens, 2016). Historically, much work has been done to identify the determinants of geographical species diversity (e.g. the latitudinal gradient hypothesis; Pianka, 1966; Rohde, 1992), but less focus has been put on identifying the causes of differences in diversity across clades (Scholl & Wiens, 2016). Some extrinsic factors and intrinsic features of lineages have been proposed to influence diversity across taxa (Sayol, et al., 2019). Empirical tests have provided support for several of these factors indeed influencing diversity. For instance, recent evidence has shown that metamorphosis may drive extant species diversity across insects (Rainford, et al., 2014), impressive species diversity in African cichlid fishes has been attributed to key innovations (McGee, et al., 2016), and urbanization has been shown to be negatively associated with diversity across bird clades (Sol, et al., 2017). Meanwhile, factors previously thought to influence variation in species numbers across taxa have now been shown to play a lesser role than previously suggested. For example, sexual selection has been repeatedly suggested to drive diversity across clades (see references in Panhuis, et al., 2001). However, measures of sexual selection (sexual size dimorphism and degree of polyandry) have now been shown to share no association with species richness across mammals, butterflies or spiders (Gage, et al., 2002). Thus, more work is needed to identify the macroevolutionary processes that drive species diversity across clades.

Behaviour has long been thought to have particularly consequential impacts on evolution (see Wcislo, 1989 for an overview). For brevity, I here mention some notable contributions. Lamarck made many biological contributions during the early nineteenth century, a majority of which have since been refuted. However, Lamarck did advocate that species and genera exhibit special and diverse adaptations rather than a linear sequence toward perfection because animals must remain in harmony with their environment (Lamarck, 1809; Mayr, 1982). Although he never suggested an explicit process, Lamarck did suggest that it is an animals' behaviour that reestablishes this harmony when it becomes disturbed (Lamarck, 1809; Mayr, 1982). Thus, while many of his theories have been discredited, Lamarck was correct in emphasizing that behaviour plays an important role in changing the form of an organism (Wcislo, 1989). The turn of the twentieth century marked the proposal of an explicit hypothesis describing the origins of organism adaptation. This hypothesis emphasized a role for behaviour in influencing organism adaptation, and – due to the important role adaptation plays in evolution – this hypothesis was influential for views on animal behaviour and its role in evolutionary processes. In this hypothesis, later termed ‘the Baldwin effect’, behavioural adaptability and other non-heritable modifications are suggested to impact an organism’s ability to persist in an ecological niche, with the ability to acquire new behaviours impacting the reproductive success of an organism, thus affecting the genetic makeup of a species (Osborn, 1896; Morgan, 1896; Baldwin, 1902; Simpson, 1958). For instance, if a new predator is introduced in an organism’s external environment, individuals who adopt new behaviours to avoid predation will increase their chances of survival, opening the door for natural selection to act. While some assumptions made by the Baldwin effect have been criticized (e.g. Mayr, 1963), the idea that behaviour influences evolution has remained widely advocated.

Due to its supposed role in influencing evolutionary processes, behaviour is also thought to be an important driver of biological diversity. Specifically, behavioural flexibility (also known as behavioural plasticity – i.e. the ability of an organism to change their behaviour in response to their internal or external environment) has been suggested to lead to evolved increases in trait disparity (the "behavioural drive hypothesis"; Wyles, et al., 1983; Wilson, 1985). Divergent selection can also drive speciation events and thus, it has been suggested that behaviourally flexible taxa may undergo faster rates of speciation, and eventual evolutionary diversification, compared to less flexible taxa (Nicolakakis, et al., 2003; Sol, et al., 2005). If behavioural flexibility influences evolution by increasing diversification events as suggested, this would make behaviour partially responsible for determining species diversity across lineages. The relationship between behavioural flexibility and species diversification has been tested with some support for behavioural flexibility increasing net rates of diversification (e.g. Nicolakakis, et al., 2003; Sol, et al., 2005). However, conflicting reports on the way in which behaviour is suggested to influence evolution (e.g. evidence for behavioural flexibility inhibiting evolutionary rates over short time scales; Huey, et al., 2003; Duckworth, 2009; Scott-Phillips, et al., 2014) and the fact that large macroevolutionary studies have been limited to one class (Aves), makes it important to continue investigating the role of behavioural flexibility in influencing diversity across the Tree of Life.

SYSTEMATICS AS A DETERMINANT OF SPECIES DIVERSITY – WITH A FOCUS ON TAXONOMIC INFLATION:

"The so-called species problem in biology can be reduced to a simple choice between two alternatives: Are species realities of nature or are they simply theoretical constructs of the human mind?"

— Ernst Mayr (1982, pp. 285)

While evolution is often thought of as the primary driver of species diversity, the role of biologists in naming and defining species plays a role in determining species richness and thus perceived diversity across taxa. In its broadest form, the term ‘species’ refers to “the unknown element of a distant act of creation” (Darwin, 1859, pp. 42), and is associated with more explicit definitions detailed by various species concepts. Biologists’ interpretation of species has changed drastically through time, with many influential naturalists including Darwin, Mayr and Simpson working toward a common definition of ‘species’ that satisfies our understanding of biological diversity while allowing us to identify them accurately and agreeably (Hey, 2001). Despite this work, biologists have failed to reach a consensus on what constitutes a ‘species’ and how it should be defined. Some argue that species represent divisions of nature made for human convenience, and are consequently completely subjective (Coyne & Orr, 2004). As suggested by Cracraft (1987), species are vital across biology but species concepts serve two masters: taxonomy and evolutionary theory. This is because taxonomists must be able to operationalize a given species concept and apply it across many groups of organisms while the resulting species taxa are often expected to reflect distinct and comparable evolutionarily units. Changing definitions of species have led to fluctuations in species numbers over time (Coyne & Orr, 2004; Tattersall, 2007), thereby influencing perceived biological diversity.

The inherent instability of species lists makes it so that when considering the determinants of species diversity across the Tree of Life, one must consider the role of taxonomy and systematics in addition to evolutionary processes. While the previously widely used ‘biological species concept’ (BSC) put emphasis on reproductive barriers as the defining characteristic of species (Mayr, 1963), the ‘phylogenetic species concept’ (PSC) defines species as the smallest population or meta-population that is distinct in heritable differences from other populations or meta-populations (Cracraft, 1983; Groves & Grubb, 2011; Groves, 2014). Recent applications of the PSC have led to a dramatic increase in species numbers across many taxa as a result of its tendency to split taxa into a greater number of less inclusive units in comparison to the BSC (Agapow, et al., 2004) – a phenomena which has now been referred to as 'taxonomic inflation'. This trend has made applications of the PSC extremely controversial. Taxonomic inflation has been widely criticized for introducing potential biases in how 'species' are defined across lineages (Agapow, et al., 2004; Zachos, et al., 2013; Zachos & Lovari, 2013). As a result, discrepancies in present-day species richness across taxa has been suggested to be partially driven by biases associated with applications of the PSC, rather than biological processes (Agapow, et al., 2004; Zachos, et al., 2013; Zachos & Lovari, 2013). Some have argued that the PSC, while causing some increase in species numbers, is still the best method of recognizing species and that criticisms of bias are in many cases unfounded (Groves, 2013). Others have argued that observed inflation is artificial and reflects shortcomings of the PSC and reliance on insufficient data (Zachos, et al., 2013; Zachos & Lovari, 2013). Much of the aforementioned contention stems from the fact that little work has been done to empirically test trends in inflation or validate supposed biases. The reliance on species as a fundamental unit of comparison across many biological sub-disciplines makes it of vital importance to determine if and how changes in taxonomic practices (e.g. applications of the PSC) bias variability in species numbers across taxa which might otherwise be interpreted as being representative of some underlying biological reality. This could have implications for how scientists choose to use species in disciplines like evolutionary biology, where units of comparison must be comparable across taxa.

PRIMATE SPECIES DIVERSITY:

Primates are one of the most species rich (over 500 species; IUCN/SSC Primate Specialist Group, 2018) and rapidly diversifying (Upham, et al., 2019a) mammal clades. Similar to patterns noted in other taxonomic groups (e.g. birds; Nicolakakis, et al., 2003), primates exhibit a great deal of asymmetry in species richness among higher taxa (Upham, et al., 2019a; 2019b). For example, primate families like Cercopithecidae are incredibly species rich (comprising approximately 155 species; IUCN/SSC Primate Specialist Group, 2018; see Figure 1.1). Meanwhile, other families like Daubentoniidae are depauperate (comprising a single species; IUCN/SSC Primate Specialist

Group, 2018; see Figure 1.1) – illustrating a clear imbalance in species diversity across primate clades.

Primates serve as a particularly interesting model system for studying asymmetry in described species diversity because they are one of the more highly studied groups of organisms (Nunn, et al., 2004; 2010) and have, therefore, undergone persistent reassessment of species richness since the 1960s (Rylands & Mittermeier, 2014). As a result, there are few gaps in our knowledge of primate taxonomy compared to lesser studied taxa where new discoveries are being made regularly and lineage relationships are considerably unresolved (e.g. invertebrates – see Kur, et al., 2016). This research charisma has resulted in the relatively comprehensive application of multiple species concepts in primate taxonomy through time including the BSC (e.g. Honacki, et al., 1982) and the PSC (e.g. Groves, 2001 to present day International Union for Conservation of Nature (IUCN) species lists). Primates additionally present considerable among-lineage variation in traits suggested to drive speciation (e.g. behavioural flexibility), and have large amounts of available data on many aspects of their behaviour, ecology and life history. This make them a good study system for large comparative studies of macroevolutionary trends. In primates, a few variables have been positively associated with increased species diversity across higher taxa including diversification rate shifts (Arbour & Santana, 2017; Upham, et al., 2019a), parasitism (Nunn, et al., 2004) and taxonomic reevaluation of particular groups (e.g. increase in species numbers across the Neotropical primates; Isaac & Purvis, 2004). However, the mechanisms underlying these associations remain undiscovered and many suggested determinants of described species diversity have yet to be empirically explored.

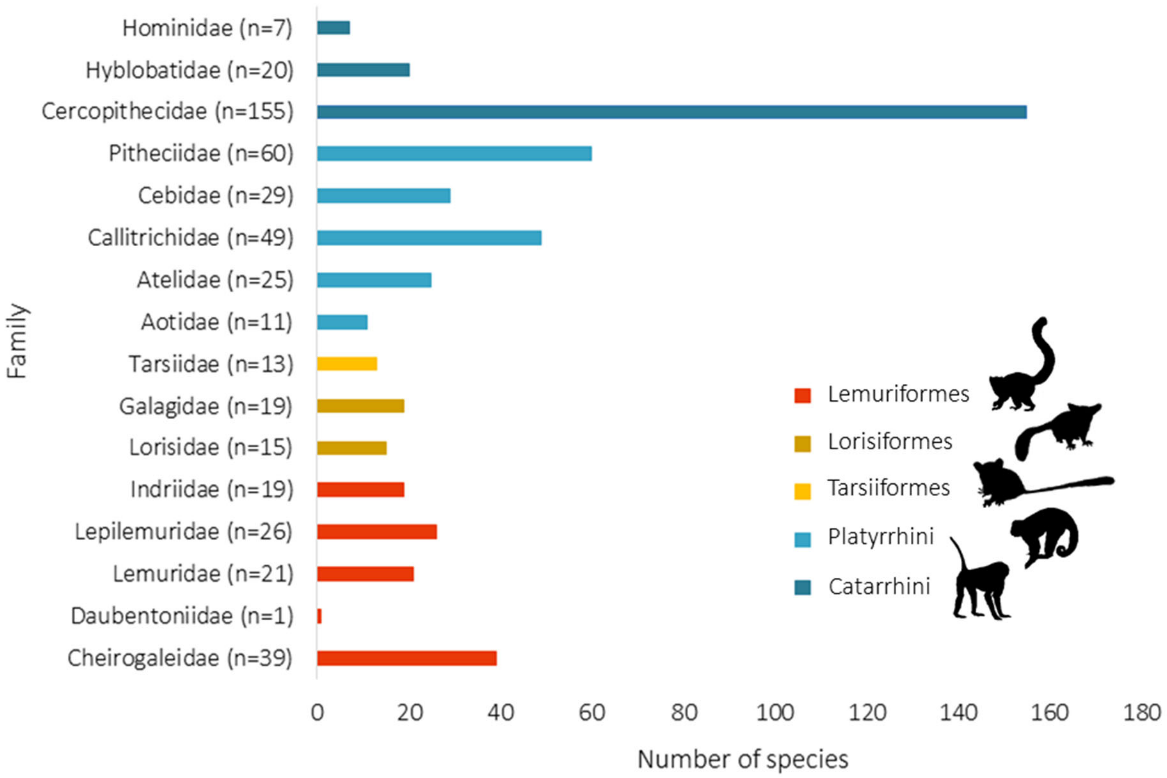

Figure 1.1: Bar graph illustrating variation in species richness among primate families according to the IUCN/SSC Primate Specialist Group (2018) where 'n' equals the total number of species in each family. Legend colours denote primate parvorder/infraorder.

THESIS OVERVIEW:

Here, I have introduced the two major determinants of species diversity across taxa: evolutionary processes and systematic practices involved in classifying species. In this thesis I explore how these two factors influence species diversity across primates. In Chapter 2, I explore the role of evolutionary processes in driving species diversity across primate clades by testing how behavioural flexibility influences primate diversification. The 'behavioural drive hypothesis' posits that behavioural flexibility increases rates of evolution and diversification, as novel behaviours expose individuals to new selection regimes (Wyles, et al., 1983; Wilson, 1985). As a result one would expect that behaviourally flexible taxa diversify more quickly and thus undergo speciation more rapidly in comparison to less behaviourally flexible taxa. I use comparative techniques to explore the relationship between multiple proxies of behavioural flexibility and diversification rate in primates. In doing so I present a new method to help account for biases associated with recent taxonomic reclassifications when generating classic estimates of diversification rate. This approach allows me to consider the diversification of recently evolved lineages (e.g. subspecies), often omitted from higher-order phylogenies (i.e. species trees) and thus often not considered by alternative diversification rate metrics (e.g. the DR measure from Jetz, et al., 2012). Using these methods I show that some measures of behavioural flexibility share a positive association with primate diversification rate – consistent with the idea that behavioural flexibility drives evolutionary diversification. However, I find these associations when examining the diversification of well-established and persistent lineages, in comparison to diversification metrics incorporating more recently evolved lineages. Given that I find associations between behavioural flexibility and diversification rate when examining older as opposed to newer diversification events even after controlling for potential sampling biases, I suggest that extinction resistance, rather than speciation, may be an important mechanism linking behavioural flexibility and diversification rate in primates.

In Chapter 3 I explore the role of systematic practices in driving species richness and thus perceived diversity across primate clades. More specifically I explore predictors of taxonomic inflation under the PSC – a phenomena that presented complications requiring new approaches for estimating lineage diversification rate in Chapter 2 due to its disparate effects across primate taxa. I find that neither research effort in fields suggested to be associated with inflation (i.e. molecular genetics and conservation) nor the rate at which lineages evolve explain inflation across primate genera. In addition to complicating evolutionary measures as discussed in Chapter 2, inflation has also been suggested to have implications in applied fields of biology – most notably conservation. It has been suggested that inflation may result in a greater number of threatened species and more imperilled threat statuses for species that are already listed (Agapow, et al., 2004; Isaac, et al., 2007). As a consequence, rare but poorly-defined taxa may be prioritized over well-defined and perhaps biologically more distinctive taxa (Pillon & Chase, 2007). Therefore, I go on to explore whether taxonomic inflation contributes to driving threat score across primate genera. I find that associations between inflation and threat score vary by region, sharing a positive association in Africa and Asia, no association in Madagascar, and a negative association in the Neotropics. I suggest these differences may indicate that other factors (e.g. the total geographic range size of genera) influence how inflation affects threat score. Regardless, I suggest that organizations involved in conservation (e.g. the IUCN) may benefit from adopting their own species criteria or shifting more resources toward regional management efforts that are less likely to be impacted by changing species designations. Overall, my thesis contributes new insights into the mechanisms suggested to drive species diversity across primate clades and provides considerations for sub-disciplines of biology relying on species as a fundamental unit of comparison.

CHAPTER 2: THE ROLE OF BEHAVIOURAL FLEXIBILITY IN PRIMATE DIVERSIFICATION

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

In review at Animal Behaviour

ABSTRACT:

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

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

INTRODUCTION:

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

Plasticity has been repeatedly proposed to play a major role in shaping evolutionary trajectories in general, and speciation in particular (Baldwin, 1902; Lewontin, 1983; Bateson, 1988; Wcislo, 1989; Odling-Smee, et al., 2003; West-Eberhard, 2003; Pelletier, et al., 2009), and theoretical modelling supports its potential influence (e.g. Hinton & Nowlan, 1987; Anderson, 1995; Behera & Nanjundiah, 1995; Ancel, 1999; 2000). Behavioural development and expression often allow for more rapid responses than other forms of plasticity such as induced morphological changes (Duckworth, 2009; Snell-Rood, 2013; West-Eberhard, 2003). Thus, plasticity of behaviour has been hypothesized to play a particularly important role in influencing evolutionary trajectories of animal lineages (Wyles, et al., 1983; Wilson, 1985; West-Eberhard, 2003). The propensity to adopt new behaviours can greatly and quickly alter ecological niches for populations, exposing those populations to new and potentially divergent selective regimes. This can lead to increased trait disparity (the "behavioural drive hypothesis"; Wyles, et al., 1983; Wilson, 1985); and importantly, divergent selection also drives speciation events. As a result, it has been suggested that behaviourally flexible taxa (i.e. those taxa exhibiting high propensities for behavioural change due to, for example, learning or readiness to transition to new conditions; Sol & Lefebvre, 2000; Audet & Lefebvre, 2017) may undergo faster rates of speciation, and eventual evolutionary diversification, compared to less flexible taxa (Sol, et al., 2005; Grant & Grant, 2008; Price, 2008; Sol & Price, 2008; Tebbich, et al., 2010). However, despite support from theoretical modelling (e.g. Price, et al., 2003; Lachlan & Servedio, 2004; Lapiedra, et al., 2013), the idea that behavioural flexibility enhances diversification rates remains contested. Some dispute the extent to which behaviour plays an active role in dictating animal diversity (e.g. Scott-Phillips, et al., 2014).

Meanwhile, an alternative hypothesis posits that behavioural flexibility may inhibit, rather than enhance, species diversification: populations that can utilize new resources or transition to new environments are shielding their genomes from bouts of strong directional selection (Bogert, 1949; Huey, et al., 2003).

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

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

Here, we explore the relationship between four proxies of behavioural flexibility and several measures of diversification rate in primates, a taxonomic group with considerable among-lineage variation in both behavioural flexibility (Reader & Laland, 2002; Reader, et al., 2011) and extant species diversity (Upham, et al., 2019a; 2019b). Variables associated with diversity of other taxa (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 shallow and deep 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.

METHODS:

Data

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 (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, including some phylogenetic species and omitting others, preventing us from using recently described evolutionary rate measures (e.g. Jetz, et al., 2012; Mitchell & Rabosky, 2017) that rely on a comprehensive phylogeny with consistent species estimates 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 S2.1). 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 taxonomies (IUCN/SSC Primate Specialist Group, 2018). This resulted in 241 identifiable lineages to compare in terms of taxonomic richness and divergence times. Using the most recently published primate species and subspecies list from the IUCN/SSC Primate Specialist Group (2018), we referenced taxonomic and phylogenetic works to assign each of the 705 species and subspecies to one of these 241 lineages. This allowed us to assign each lineage an agnostic "taxon richness" score (i.e. the sum of all monotypic species and subspecies in a lineage; see Figure S2.1) that accounts for the discrepancies in subspecies elevations across lineages. Each species or subspecies listed by the IUCN/SSC Primate Specialist Group (2018) was also assigned to one of the 66 genera named in our 10kTrees phylogeny (Arnold, et al., 2010). After eliminating two individual species and one genus in our tree that could not be resolved using these methods (see supplementary material), our study considered 703 taxa (species or subspecies) assigned to 239 lineages and 65 genera.

To estimate lineage diversification rate we used the method-of-moments estimator (Magallon & Sanderson, 2001) that divides the natural log of "taxon richness" (species and subspecies) by lineage stem age to produce a 'Taxa per Lineage Diversification Rate' that should be less biased by recent subspecies elevations. This method was repeated at the genus level where the natural log of "taxon richness" for each genus was divided by the stem age of that genus (hereafter 'Taxa per Genus Diversification Rate'). We note that all log transformations referenced hereafter refer to natural log transformations ($\log_e$). Lastly, we created a second, and perhaps more conservative estimate of genus diversification rate where richness scores were generated using the number of lineages (n=239) per genus, rather than the number of taxa described by the IUCN/SSC Primate Specialist Group (2018), hereafter 'Lineage per Genus Diversification Rate'. A few genera were not monophyletic on our tree, and we considered these on a case by case basis (see the supplementary material).

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

Behavioural Proxies of Behavioural Flexibility

We focused on two key behaviours to infer behavioural flexibility: innovation and social learning. Innovation and social learning are both important in determining the macroevolutionary effects of behavioural flexibility because multiple individuals must acquire an innovation through social learning or independent innovation to have population-level effects (Wyles, et al., 1983; Wilson, 1985; Duckworth, 2009). In addition to facilitating the transmission of innovations throughout a population, social learning can also be a valuable measure of population-level behavioural flexibility on its own as it reflects the ability of individuals within a population to pick up behaviours that are novel to them but not necessarily novel to the population. We note that social learning and innovation are taxonomically widespread (Reader & Biro, 2010; Snell-Rood, et al., 2015). However, we assume that species with no published accounts of social learning or innovation are likely relying on these behaviours infrequently. Moreover, the innovation and social learning data used here have been positively associated with other measures of behavioural flexibility (e.g. brain size measures; Reader, et al., 2011; Navarrete, et al., 2016). For innovation, we focus on technical innovations (classified as those involving tool use following Navarrete, et al., 2016) because these more easily defined behaviours have been linked to complex cognition (Overington, et al., 2009), and reports of other classes of innovation (e.g. food type innovation) can be highly influenced by opportunistic events (Ducatez, et al., 2015). Combined with the fact that taxa with reports of technical innovation also tended to be those with evidence of other innovation types (see data in Navarrete, et al., 2016), this likely makes technical innovation a robust estimate of innovativeness across primates.

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

As an alternative to treating behavioural data as a binary metric (e.g. innovativeness in Ducatez, et al., 2020) some studies have used "rate" measures of behaviours: 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.

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

Lineage-level estimates for all brain measures were calculated by taking the geometric mean of taxon volumes for each lineage. Brain volume relative to body size (hereafter 'relative brain volume') was estimated by regressing lineage-level estimates of logarithmic endocranial volume, in cm^3, (ECV) (Powell, et al., 2017) (hereafter 'brain volume') as a function of logarithmic body mass, in grams (Jones, et al., 2009), and retaining the residuals (Dunbar & Schultz, 2007). While some recent studies have used phylogenetically correct residuals to model relative brain volume (e.g. Sayol, et al., 2019), heteroscedasticity among residuals obtained from phylogenetic models led us to prefer our ordinary least squares residuals. Importantly, these residuals were analysed downstream in a phylogenetic framework where a phylogenetic autocorrelation was incorporated in the diversification analyses. Similar to relative brain volume, neocortex and cerebellum volume relative to rest-of-brain volume (hereafter 'relative neocortex and cerebellum volume') was estimated by taking the residuals from a log-log regression of the combined neocortex and cerebellum volumes on the rest-of-brain volumes (i.e. total brain volume minus neocortex and cerebellum volumes) taken from Navarrete et al. (2018) and the compilation in DeCasien &

Higham (2019). Genus-level estimates for structural proxies of flexibility were calculated by taking the geometric mean of the lineage estimates within each genus. Further details, and considerations regarding the use of structural proxies of behavioural flexibility, and residual brain measures can be found in the supplementary materials along with correlation coefficients for all predictor variables (Table S2.1).

Phylogenetic signal of all predictor and response variables are reported in the supplementary material (Table S2.2).

Analysis

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

Trait Imputation

While we collected data for brain size, body mass, and behavioural flexibility from the most comprehensive datasets and compilations available, research biases and the persistent reassessment of primate taxonomy has resulted in inconsistent data coverage across lineages, and there were still many lineages that were missing data (see Figure S2.2). To maximize our evolutionary inferences on diversification and allow for the inclusion of data-poor lineages, we chose to impute missing predictor variables using phylogenetic imputation methods (see supplementary material for details and reports of predictive accuracy from model cross-validation; Table S2.3 and Figure S2.3). Data on relative neocortex and cerebellum volume were sparse and unevenly distributed across the phylogeny (82.4% of lineages missing data; Table S2.3), making it infeasible to reliably impute missing values. We thus only ran models of relative neocortex and cerebellum volume on the original, non-imputed dataset. All of the regressions we report below were repeated for the original, non-imputed datasets (see Results and the supplementary material Tables S2.4, S2.5 and S2.6) and except as noted gave a similar pattern of results.

Predictors of Diversification

To assess the relationship between our measures of behavioural flexibility and diversification rate at the lineage-level (Taxa per Lineage Diversification Rate) we used phylogenetic generalized least squares (PGLS) regressions implemented using the nlme package (Pinheiro, et al., 2020) with the

10kTrees consensus tree including our 239 defined lineages. PGLS is a common regression method used to investigate evolutionary associations while accounting for the fact that closely-related lineages tend to be similar (e.g. in body size, life history and ecology; see Freckleton, et al., 2002). Continuous data were log-transformed and scaled by 2 standard deviations in all models for both the lineage and genus-level analyses to make effect sizes comparable to those reported for binary variables (Gelman, 2008). After imputing missing values, our dataset contained 54 lineages scored as having evidence of social learning (scored as 1) and 28 lineages scored as having evidence of technical innovation (scored as 1). Wyles et al. (1983) predicted accelerated evolution in species with a dual capacity for innovation and social propagation of new behaviours, therefore, we also tested a combined measure of technical innovation and social learning. In this combined measure 26 lineages with the presence of both behaviours were scored as 1, and those exhibiting only one or neither behaviour were scored as 0.

To assess the relationship between our measures of behavioural flexibility and diversification rate deeper in the tree we repeated the same analysis at the genus-level using two different estimates of diversification rate: Taxa per Genus Diversification Rate and the more conservative Lineage per Genus Diversification Rate. After imputing missing values, our dataset of 60 genera contained 21 genera scored as having evidence of social learning, 9 genera scored as having evidence of technical innovation and 8 genera with evidence of both behaviours.

Body mass and attendant life history traits have been predicted to impact diversification rates in some taxa, albeit with conflicting results (e.g. Cardillo, et al., 2003; Paradis, 2005; Fontanillas, et al., 2007; Thomas, et al., 2010), and body mass is closely correlated with many primate life history traits (e.g. age at first reproduction, maximum lifespan; Charnov & Berrigan, 1993; Purvis, et al., 2003; Street, et al., 2017). To examine whether our results could stem from confounding effects of body mass and its correlates, we ran PGLS analyses to test body mass as an independent predictor of our diversification rate measures. Results from these tests were non-significant across all measures of diversification (see supplementary material Tables S2.4 to S2.6).

Genus-Level Simulations

Genera were considered behaviourally flexible if any of their daughter lineages had evidence of innovation or social learning, which potentially introduces a statistical bias if more lineage-rich genera (which will generally have higher diversification rates) are more likely by chance to include at least one lineage that expresses technical innovation or social learning. To account for this possible bias, we simulated the neutral evolution of technical innovation and social learning across the primate phylogeny 1000 times using the Mk model of discrete trait evolution (Lewis, 2001). We opted to model the evolution of these behaviours under a symmetrical model of trait evolution since with smaller datasets such as ours, there is no power to prefer asymmetric models (Mooers & Schluter, 1999). From these stochastic distributions of the two traits, we repeated our analyses of diversification rate and created a distribution of expected effect sizes under a null evolutionary scenario. More diverse genera may also be more likely, by chance, to have well-studied lineages, which could create a bias toward observing the presence of innovation or social learning in diverse genera (Ducatez & Lefebvre, 2014). Although data did not suggest that lineage-rich clades were more likely to have intensely investigated lineages in our dataset (see Figures S2.4 and S2.5), we nonetheless opted to take research effort into account in our analysis and expanded upon our first simulation to consider a scenario where the presence of technical innovation or social learning may go unobserved if insufficient research effort was directed at a lineage. We took the 1000 simulations of neutral evolution of technical innovation and social learning, and then randomly 'evolved' research effort on each, independently of the evolution of technical innovation and social learning. We then converted the presence of these behaviours to absences in our simulated datasets if a lineage's 'evolved' research effort was below the minimum threshold of studies for a lineage with observed technical innovation (as it contained the higher research effort threshold than social learning; Figure S2.6). 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, and if this is not true (i.e. if behaviourally flexible lineages attract research effort; we discuss this possibility in the 'Research Effort Bias' section of 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 2.1 and S7; Table S2.4). 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 S2.4) 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 2.1 and S2.7; Table S2.5). Relative brain volume was insignificantly (p= 0.108), but positively, related to diversification rate, and this positive relationship was significant and positive in 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 2.1 and S2.7; Table S2.6). Genera with records of technical innovation were shown to have a faster mean Lineage per Genus Diversification Rate (0.136 lineages my^{-1}) than those with no reports (0.070 lineages my^{-1}; ß [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 lineages my^{-1}) than those without (0.049 lineages my^{-1}; ß [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 lineages my^{-1}) compared to those with evidence for only one or neither behaviour (0.068 lineages my^{-1}; ß [95% CI] =0.085 [0.018-0.151]; p= 0.015). Based on our simulation testing for a lineage-richness sampling bias, we found that these effect sizes were unlikely to be due to chance alone for technical innovation (p= 0.028), social learning (p= 0.002) and the combined presence of both behaviours (p= 0.008) (see Figure S2.8 and supplementary results). After expanding our simulation to consider a research effort bias, significance of these effects remained for social learning (p= 0.019) and its combined presence with technical innovation (p= 0.027), but the effect of technical innovation alone was no longer nominally significant (p= 0.109) (see Figure S2.9 and supplementary results). No structural proxies of behavioural flexibility shared notable associations with Lineage per Genus Diversification Rate (Figures 2.1 and S2.7; Table S2.6).

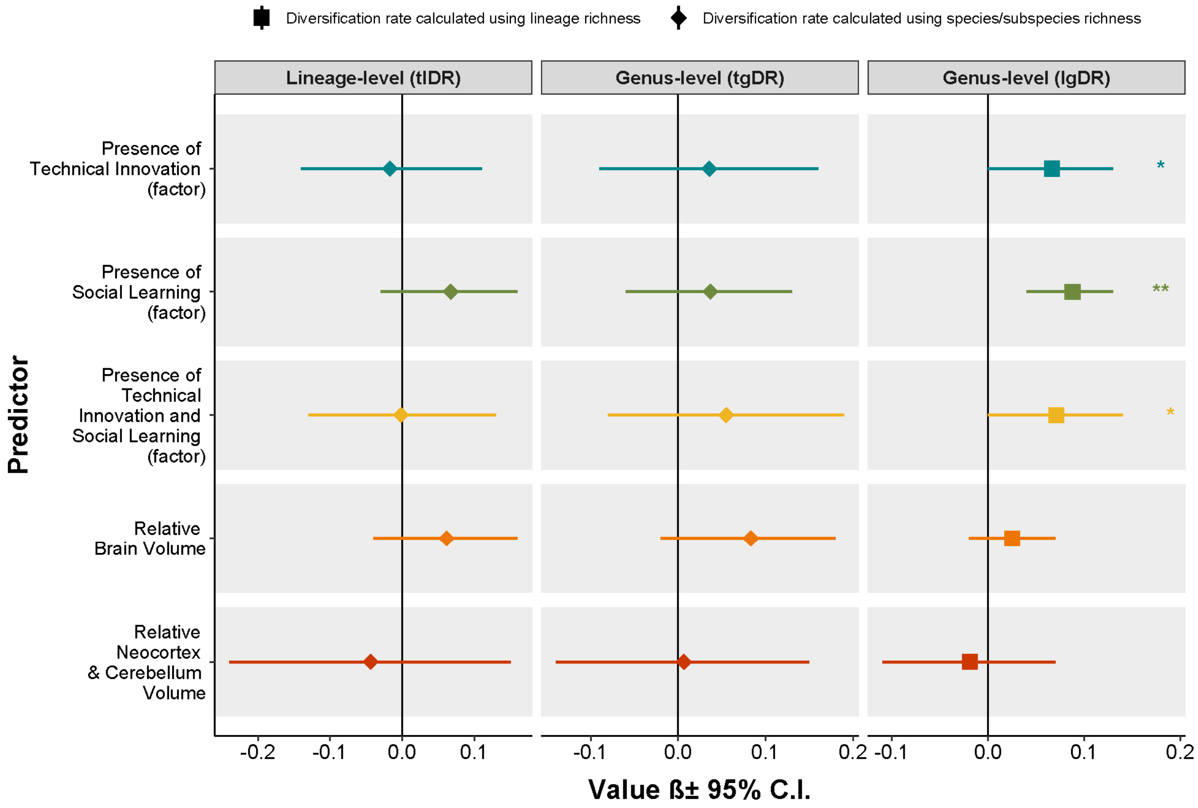

Figure 2.1: Results from PGLS analyses showing the association of proxies of behavioural flexibility with Taxa per Lineage Diversification Rate (DR), Taxa per Genus Diversification Rate and Lineage per Genus Diversification Rate across primates. 95% confidence intervals are represented by horizontal lines around the associated value. Diamonds indicate diversification rates estimated with species/subspecies richness, and squares indicate diversification rates estimated with lineage richness. Results presented include imputed data when available and brain measures were standardized (ln x/(2sd)). Significance indicated as: +P≤0.1; *P≤0.05; **P≤0.01.

DISCUSSION:

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

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

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

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

Directly testing whether behavioural flexibility buffers against extinction may be difficult, because measuring extinction rates at macroevolutionary scales is notoriously imprecise (Rabosky et al., 2017; Louca and Pennell 2020). Future studies could test proxies of primate behavioural flexibility against estimates of extinction vulnerability (see, e.g., Nicolakakis, et al., 2003; Ducatez, et al., 2020). Another prediction concerns the rate of genetic divergence within flexible versus less flexible, recent clades (e.g. subspecies within species): our conjecture would be that these would not be different, because flexibility does not lead to increased divergence over the short term.

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

Although our results do not support a role for behavioural flexibility in recent primate diversification, there are several caveats on the limits of our inferences. First, one measure thought to be associated with behavioural flexibility – neocortex and cerebellum volume – had very little data available for lineages reported as inflexible (e.g. among lemurs, tarsiers, titis and sakis). This meant our ability to test this measure 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 for an effect of body mass, 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 largely upon 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 as previously suggested (Wilson, 1985). 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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“The role of behavioural flexibility in primate diversification” — Supplementary Material

SUPPLEMENTARY METHODS:

Diversification Rate

When assigning species and subspecies listed by the IUCN/SSC Primate Specialist Group (2018) to each lineage >1.1my old in the 10kTrees consensus phylogeny (Arnold, et al., 2010), there were two species that could not be assigned to any of our lineages, and were removed as a result: *Galagoides kumbirensis* (Svensson, et al., 2017) and *Callithrix humilis* (van Roosmalen, et al., 1998). In addition, one genus, *Presbytis* (comprising the surilis), was so unresolved that lineage richness was impossible to estimate given the lineages available in 10kTrees. This genus and its comprised species were also removed prior to analyses.

We estimated ‘Taxa per Lineage Diversification Rate’ using the method-of-moments estimator based on stem age, i.e. the natural log of richness divided by the stem age of that lineage (see Figure S2.1) (Magallon & Sanderson, 2001). Notably, all log transformations referenced in this document and in the main text refer to natural log transformations ($\log_e$). In the example in Figure S2.1B, Taxa per Lineage Diversification Rate for the *Aotus azarai* lineage would be log(3)/1.29 taxa per my. For genus-level diversification rates we delineated genera in our phylogeny and extracted stem ages for each genus, and subsequently used the method-of-moments approach for two estimates of diversification rate. For the first estimate (hereafter ‘Taxa per Genus Diversification Rate’) richness score was estimated based on assignments of the same 705 taxa method-of-moments estimates. ‘Taxa per Genus Diversification Rate’ thus is based on “taxon richness” (so, for *Aotus* in Figure S2.1, Taxa per Genus Diversification Rate=log(13)/19.49 taxa per my, where 19.49my is the stem age of genus *Aotus*, and 13 is the number of species and subspecies in the genus). For the second estimate, ‘Lineage per Genus Diversification Rate’, richness was equal to the sum of >1.1 million-year old lineages from our tree (so, for *Aotus* in Figure S2.1, Lineage per Genus Diversification Rate=log(5)/19.49 lineages per my).

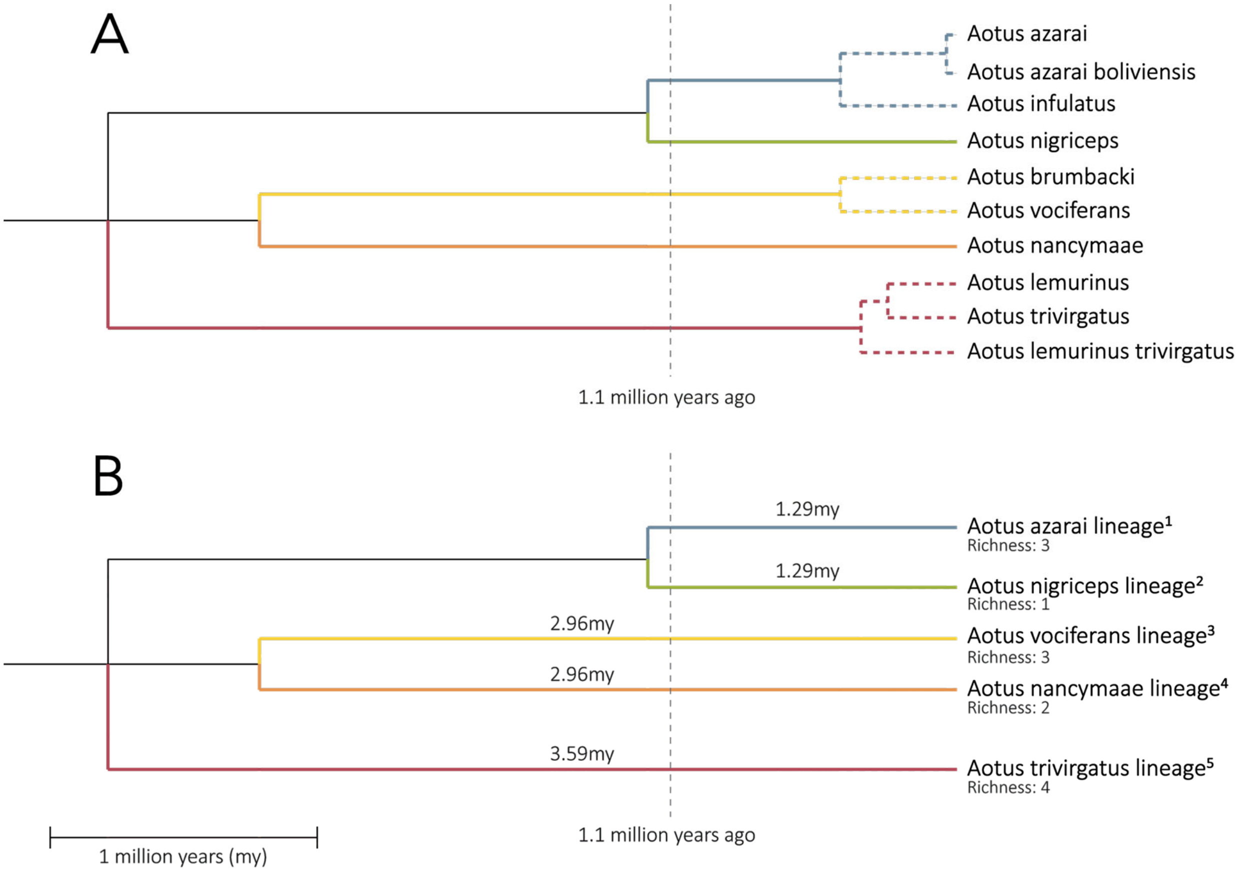


Figure S2.1: Illustration of the method used to estimate diversification rate at the lineage-level using genus *Aotus* as an example. (A): the 10kTrees consensus phylogeny for *Aotus* where splitting events in the tree occurring more recently than 1.1 million-years ago are represented by dotted lines. (B): the revised phylogeny after collapsing taxa diverging after the 1.1 million-year time cut-off to their corresponding 5 lineages, and appending the taxon richness (total species and subspecies) from the 2018 IUCN taxonomy. Branch lengths (=stem age) are labelled in million years (my). The stem genus age for *Aotus* is 19.49 my (not shown). Species and subspecies listed by the IUCN/SSC Primate Specialist Group (2018) were assigned to lineages to create taxon richness estimates: [1]*Aotus azarae azarae*, *Aotus azarae boliviensis*, *Aotus azarae infulatus*; [2]*Aotus nigriceps*; [3]*Aotus vociferans*, *Aotus brumbacki*, *Aotus jorgehernandezi*; [4]*Aotus nancymaae*, *Aotus miconax*; [5]*Aotus trivirgatus*, *Aotus lemurinus*, *Aotus griseimembra*, *Aotus zonalis* (nomenclature here follows IUCN/SSC Primate Specialist Group, 2018).

We found that there were several instances of non-monophyletic genera within the phylogeny (*Galagoides*, *Otolemur*, *Galago* and *Euoticus*). As such, we elected to retain these lineages in our lineage-level tree (as their unresolved nature may simply be due to taxonomic issues; Masters, et al., 2017), but removed these genera from genus-level analysis as it is unclear how to assign a stem age to these clades. We additionally removed the genus *Semnopithecus*, which comprised a single lineage nested within the genus *Trachypithecus*. Thus, while our lineage-level dataset contained lineages from 65 genera, our genus-level analysis considered only 60 genera. Lineages of *Cercopithecus* were also resolved as polyphyletic in the phylogeny, with a small fraction of lineages forming a clade sister to *Erythrocebus*. Since a majority of *Cercopithecus* lineages were resolved as monophyletic, we opted to assign *Cercopithecus* the divergence date that separates it from the clade of *Chlorocebus* and *Erythrocebus*; we note that removing *Cercopithecus* in its entirety did not qualitatively change the results we report here.

We note that this approach to measuring diversification rate does have its limitations, specifically that it can result in a loss of relevant information (i.e. phylogenetic distances between closely related species). This method additionally relies on taxonomic assignments that inherently carry some subjectivity since what is considered a subspecies, species or genera is ultimately determined by taxonomists who must make decisions based on whatever e.g. genetic, morphological, and geographical information that is available for a given population. However, this method allowed us to readily incorporate shallow divergences (in terms of both species and subspecies) since current primate phylogenies do not contain comparable species numbers across clades. Applications of the phylogenetic species concept (PSC) have favoured elevations of subspecies to the full species status non-uniformly across the primate tree. As a result, relying on diversification estimates that only consider species would result in disproportionally high diversification rate estimates being assigned to lineages where elevations of subspecies to the full species status have been favoured (e.g. strepsirrhines and platyrrhines; Isaac, et al., 2004).

Structural Proxies of Behavioural Flexibility

In addition to behavioural measures, we used brain volume measures as a proxy of behavioural flexibility. We note that while brains perform many functions, and the link between volume and function is not well established (e.g. Healy & Rowe, 2007; Logan, et al., 2018), behavioural flexibility measures such as innovation rate, social learning rate and learning performance in the laboratory do correlate with brain volume measures across species (Reader, 2003; Lefebvre, et al., 2004; Reader, et al., 2011). This suggests that primate brain volume measures are useful secondary proxies of behavioural flexibility. While direct measures of behavioural flexibility under standardized testing conditions would be valuable, such measures are not available for the large-scale comparative tests we conduct here. We can however compare the consistency of results across different proxies for behavioural flexibility.

Data on brain size, estimated as endocranial volume (ECV) in cm^3 (hereafter 'brain volume'), were obtained from Powell et al. (2017) (a compilation containing data from Isler, et al., 2008 and van Woerden, et al., 2010; 2012; 2014). Powell et al. (2017) calculated species means for endocranial volume (ECV) across males and females for species that were not considered sexually dimorphic. For sexually dimorphic species (size difference > 10%), Powell et al. (2017) used only female measures of ECV to create means. When assigning these values to species and subspecies in our own dataset, one species, *Semnopithecus dussumieri*, was no longer considered to be a valid taxon (Roos, et al., 2014), and was omitted from our dataset.

Data for neocortex, cerebellum and rest-of-brain volume were obtained from the compilation in DeCasien & Higham (2019) and Navarrete et al. (2018). Navarrete et al. (2018) obtained data through measurements of MRI scans. The DeCasien & Higham (2019) compilation includes data from the prior Reader & Macdonald (2003) compilation and contains brain component volumes (mm^3) from multiple studies, including data from both MRI and serial section measurements: Stephan et al. (1970); Stephan et al. (1981); Frahm et al. (1984); Stephan et al. (1988); Rilling & Insel (1998); Rilling & Insel (1999); MacLeod et al. (2003); Bush & Allman (2004a); Bush & Allman (2004b); Sherwood et al. (2004); Sherwood et al. (2005); Barger et al. (2007); De Sousa et al. (2010); Barger et al. (2014); Barks et al. (2015); Bauernfeind et al. (2013); Stimpson et al. (2016). Where necessary, DeCasien & Higham (2019) converted brain component masses to volumetric measurements by dividing mass by the density of fresh tissue (1.036 grams per cubic centimeter). DeCasien & Higham (2019) apply the dataset corrections detailed in Reader & Macdonald (2003).

We only included data on neocortex, cerebellum and rest-of-brain volumes from either source when all these measures were made on the same individuals. We were interested in the underlying neural activity that contributes to behavioural flexibility – often attributed to neuron density (see references in Mikhalevich, et al., 2017) – thus we opted to use only neocortical grey matter volume (regions containing neural cell bodies). In some cases volume estimates were reported as means for multiple individuals (n >1 individuals); estimates from each source were therefore multiplied by their respective n values to ensure each individual brain was weighted equally. These values were then summarized across taxa by summing the individual estimates (previously multiplied by n) and then dividing by the total n value for that species/subspecies across studies prior to creating lineage and genus-level estimates. Brain size and behavioural measures of flexibility (e.g. innovation rate) are often summarized at the genus level (e.g. Riska & Atchley, 1985; Barton, 2006; Deaner, et al., 2007; Lefebvre, 2013). However, there is considerable variation in species' propensity to exhibit flexible behaviour within many primate families and subfamilies (e.g. subfamily Cercopithecinae contains genus *Macaca* – a highly flexible genus, and genus *Theropithecus* – a relatively low scoring genus in terms of flexible behaviour and brain size correlates; see Figure S2.2), thus we opted to not summarize any of our data beyond the genus level.

We used residuals from log-log regressions to estimate brain volume relative to body mass, and neocortex and cerebellum volume relative to rest of brain volume at the lineage-level. These lineage-level residuals were then averaged to get genus-level estimates (see 'Methods' section of main text). We are limited to averaging data among taxa (subspecies and species) at the lineage level because our phylogenetic imputation of missing brain volume and body mass data relied on a phylogeny, and thus had to be done at the lineage level. However, we note that our lineages are typically equivalent to the species for which brain data are available. Past studies using comparable primate brain volume residuals have relied on much more conservative species taxonomies (e.g. Reader & Laland, 2002) which are comparable to our 239 species-complexes (i.e. lineages). Thus, averaging brain volume and body mass estimates at the lineage-level before taking the residuals is the equivalent of calculating residuals at the species level for most comparative studies of primates. Residual analyses may lead to an inflation of Type II error as it is a very conservative method of controlling for body size (Darlington & Smulders, 2001). However, including both variables in a multiple regression as suggested by some (e.g. Freckleton, 2002) caused errors in parameter estimation in the PGLS models due to the very high correlation between brain volume and body mass resulting in exceptionally large and opposing effect sizes. As a result, we opted to use the more conservative approach based on residual brain volume where subsequent parameter estimates were similarly conservative.

Behavioural Proxies of Behavioural Flexibility

We matched behavioural data from Reader et al. (2011) to our own species and subspecies list provided by the IUCN/SSC Primate Specialist Group (2018). One species used by Reader et al. (2011), *Aotus hershkovitzi*, has since been reclassified as a junior synonym of species *Aotus lemurinus* (Defler & Bueno, 2007), and was thus omitted from our analysis. Some species in the Reader et al. (2011) dataset were reported to have zero accounts of technical innovation and social learning with no recorded measure of research effort or a research effort of zero papers. Data from these species were also omitted from our dataset. Technical innovation data for species used by Reader et al. (2011), but not Navarrete et al. (2016), were supplemented by examining and categorizing innovation reports provided by Reader et al. (2011). Reader et al. (2011) additionally provide a measure of research effort for each species, recorded as the number of published articles per species published in a survey of the Zoological Record. Research effort from Reader et al. (2011) was also summarized at both the lineage and genus levels as a sum of the total number of published articles recorded for each species or subspecies assigned to the given lineage or genus to inform imputation models on the reliability of our observed trait values and to test possible data collection biases associated with research effort.

Experimental data on behavioural innovations and social learning would be preferred to observational data from the literature (Reader & Biro, 2010), but these data are not available for the wide taxonomic spread of our study. The innovation and social learning accounts from literature sources provide quantitative comparative data for a large number of species, typically from observations in the wild. Despite acknowledged weaknesses of such observational data (discussed in Lefebvre, et al., 1997; Laland & Reader, 1999; Reader, 2003; Reader & MacDonald, 2003; Reader, et al., 2011), the taxonomic spread allows for tests of large-scale macroevolutionary trends that can then be followed up by targeted experimental approaches.

Correlation of Predictors

Correlation between predictor variables varied greatly (Table S2.1). Powell et al. (2017) provide their own body mass data from previous compilations, which were highly correlated with body mass estimates from PanTHERIA (Jones, et al., 2009; Table S2.1). Therefore, we chose to use the more extensive body mass data provided by PanTHERIA in analyses.

Phylogenetic Patterns

To visualize phylogenetic patterns in our measures of innovation, social learning, brain size, and diversification rate we painted our 10kTrees consensus tree with these data using the “plotBranchbyTrait” function in the R package phytools (Revell, 2012; 2014), which implements an ancestral-state reconstruction based on symmetric models under maximum likelihood. We also used geiger (Harmon, et al., 2008) to estimate the symmetrical transition rate for the gain and loss of innovation and social learning at the lineage level, needed to produce the null distribution of lineages with innovation and social learning through simulations. We also estimated the phylogenetic signal for all variables of interest. For continuous variables phylogenetic signal was estimated using Pagel’s λ (Freckleton, et al., 2002), where a λ value nearing 1 denotes stronger signal, using the “phylosig” function in phytools. For discrete variables, we used Fritz and Purvis's (2010) D statistic, where a D approaching 0 denotes stronger signal. Results are in Table S2.2.

Distribution of Behavioural Flexibility Measures

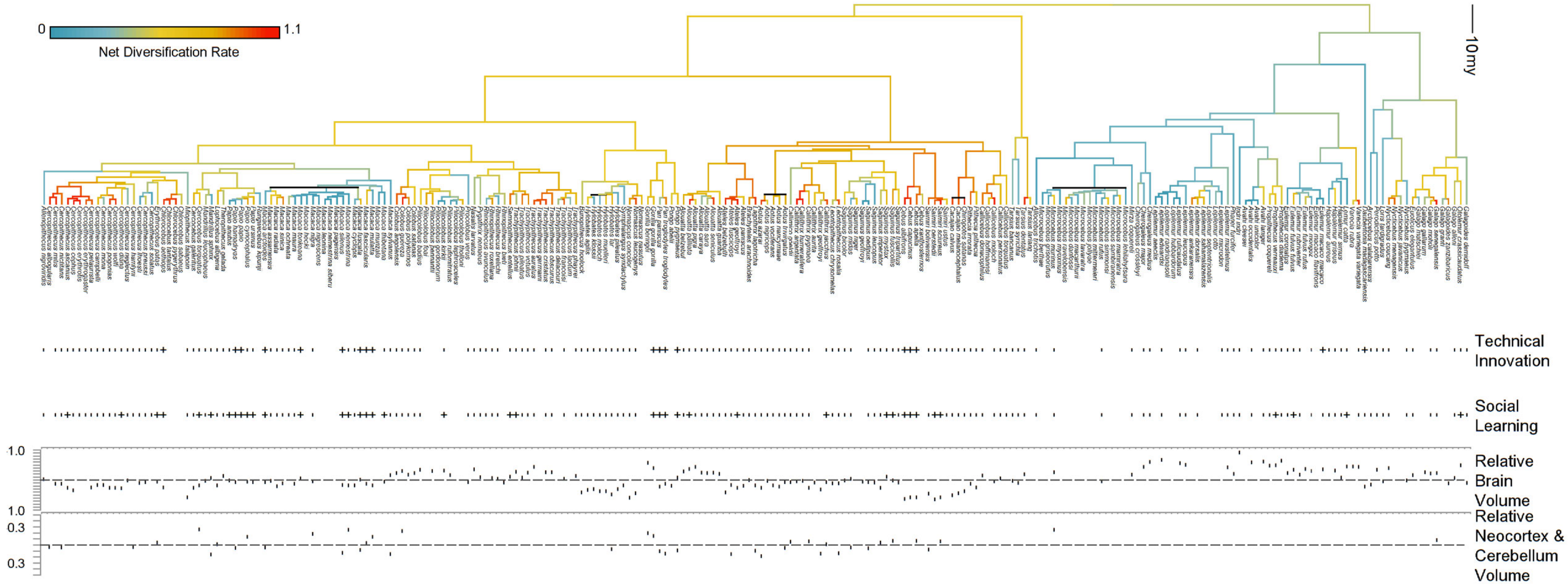


Figure S2.2: Lineage-level phylogeny painted by Taxa per Lineage Diversification Rate with qualifiers of proxies for behavioural flexibility among non-imputed data. For binary variables (technical innovation and social learning) (+) indicates presence and (–) indicates absence.

Phylogenetic Imputations of Behavioural Flexibility Measures

For many of the lineages in our dataset, we were missing data for our different measures and co-variates. Brain data and body mass data are not available for some lineages, while technical innovation and social learning data were collected under a different taxonomy than the one used in this study, meaning that some lineages were not represented in the search done by Reader et al. (2011) due to changes in naming conventions. Additionally, some species searched for by Reader et al. (2011) had no published papers, in which case we considered them to be missing data points. The proportion of missing data varied greatly among variables with body mass (n=196; 82.0%) and relative brain volume (n=186; 77.8%) having the most available data, technical innovation (n=176; 73.6%) and social learning (n=176; 73.6%) having fewer data, and our measures of neocortex, cerebellum and brain volume (n=42; 17.6%) having the least available data (Table S2.3). Many of the predictors that we examined exhibited strong phylogenetic patterns (Table S2.2), allowing us to use phylogenetically-informed prediction to estimate the missing traits for these lineages (Pagel, 1999; Guénard, et al., 2013; Swenson, 2014; Penone, et al., 2014). We created a phylogenetic variance-covariance matrix of our pruned 10kTrees phylogeny using the MCMCglmm package (Hadfield, 2010) in R. We decomposed this phylogenetic variance-covariance matrix into 238 eigenvectors using the "PVRdecomp" function from the R package PVR (Santos, et al., 2013), where each eigenvector represents a node in the phylogeny following the order of bifurcation from root to tips. We built phylogenetic models for each proxy of behavioural flexibility (relative brain volume, technical innovation and social learning), using forward model selection to determine the phylogenetic eigenvectors (and covariates) that had the best support for inclusion based on Akaike Information Criterion (AIC_c) scores. We implemented this stepwise model selection for phylogenetic models of each covariate using the "stepAIC" function from the MASS R package (Venables & Ripley, 2002).

Our goal for phylogenetic imputation was to maximize the predictive accuracy in our models using phylogenetic position and other covariates to estimate missing data. We ordered our imputation of traits so that we could use imputed information to inform subsequent model fits – for example, body mass is required to estimate brain size. Although there may be concern that this introduces circularity to the analyses, the correlation structure of these covariates is already present in the observed data (Table S2.1) and imputing with these covariates merely propagates the already present correlations. We first performed model selection on the missing body masses (18.2% of the data) using ordinary least squares regression (on the natural log of body mass) of the first 50 phylogenetic eigenvectors (corresponding to the 50 deepest splits in the tree). We then used the phylogenetic eigenvectors with logarithmic body mass as a covariate to estimate brain volume (natural log transformed) with an ordinary least squares regression. We used generalized linear models, with a Bernoulli error distribution, for the presence (1) or absence (0) of technical innovation and social learning, with observations weighted by the square-root of research effort. Weighting by research effort, i.e. the number of published articles per species published in the Zoological Record documented by Reader et al. (2011), informs the model about the strength of evidence for a given lineage exhibiting either of these measures of behavioural flexibility: higher research effort indicates a higher certainty that a lineage does or does not display a given behaviour. Innovation and social learning are moderately correlated ($r = 0.533$; Table S2.1), so we first modelled technical innovation and then used this as a predictive covariate for social learning. The coefficients used in each model can be found in Table S2.3. We used a larger number of eigenvectors (50; see Table S2.3) to impute data for variables with high phylogenetic signal and less missing data (e.g. body mass and brain volume) to potentially capture variation presenting itself in shallower splits in the phylogeny. In cases where phylogenetic signal was lower (e.g. technical innovation and social learning) and we had less observed data, we opted to use a lesser number of eigenvectors (40; see Table S2.3) to avoid problems of overfitting.

We performed a leave-one-out cross-validation to assess the performance of all models. This procedure involved serially removing each species' data and using the remaining dataset to replicate our same model-building procedure and predicting that now "missing" species' data from the best-fit model. The resulting estimate can then be compared to each species observed value to evaluate how closely we are able to recreate observed data from the models. We evaluated this for continuous variables (body mass and brain volume) based on each model's predictive accuracy (p^2):

Equation S1:

$$p^2 = 1 - \sqrt{\frac{\mathrm{mean}(\hat{y} - y)}{\mathrm{variance}(y)}}$$

where ŷ is the predicted value and y is the observed trait value (Greenberg, et al., 2017). Predictive accuracy was high (approaching $p^2=1$) in all cases (Table S2.3). For our binary variables, technical innovation and social learning, we instead used an approach that quantified whether models could discriminate the presence or absence of these behaviours based on phylogenetic position and covariates. To do this, we constructed receiver operating characteristic curves that compare the true positive and false positive rate across different model predicted probability thresholds for classifying the presence or absence of each behaviour in a species. An accurate model will have a high rate of true positives and negatives, relative to false positives and negatives. The overall model performance (across thresholds) can be assessed by taking the integral of the receiver operating curve: the area under the curve (AUC). The AUC was taken as a measure of classifier performance for binary data. The AUC describes how accurately a given model can predict binary outcomes, and is scored between 1 (describing a perfect fit; model predictions are all correct) and 0 (model predictions are all incorrect), with a score of 0.5 describing chance performance (Bradley, 1997). Receiver operating characteristic curves and AUC values were calculated using the ROCR package (Sing, et al., 2005) (Figure S2.3). For these binary traits, the AUC was moderate to high (Table S2.3), indicating good model performance. For prediction of missing data, we had to choose a predicted threshold as a cut-off for binary classification of each behaviour, we chose this threshold by comparing the accuracy (the ratio of true positives + true negatives: false positives + false negatives) of each probability threshold value in the receiver operating characteristic curve and selecting the cut-off associated with optimal accuracy. The genus *Tarsius* consisted of two pairs of sister lineages that were very distantly related to all other primates. Due to their phylogenetic distance from all other lineages it is expected that phylogenetic imputation will perform poorly. As the missing data was generally clustered in species with close relatives we removed genus *Tarsius* from our cross-validation tests to obtain a more representative estimate of model performance for the species that were missing data.

Lineage-Richness Sampling Bias

To test whether lineage-rich genera are more likely by chance to have reports of technical innovation or social learning, and to quantify this sampling effect, we simulated the evolution of these traits on our tree independently of diversification rate and tested whether observed correlations depart from this expectation. We simulated the evolution of lineage-specific technical innovation and social learning on the phylogeny over 1000 iterations using the symmetrical rate Mk model of discrete trait evolution (Lewis, 2001) implemented through the geiger package (Harmon, et al., 2008). We parameterized the transition rates for the simulation with the Mk model based on the observed presence and absence of both behaviours across the primate phylogeny. We included imputed data for estimating transition rates of these behaviours, noting that removal of these points did not meaningfully influence estimated transition rates. After simulating the random evolution of technical innovation and social learning across the primate phylogeny 1000 times, we repeated genus-level PGLS analyses over the resulting datasets. From these analyses on the simulated datasets, we obtained a distribution of null effect sizes and compared our estimated effect sizes from the real data to calculate the probability of randomly observing an effect size of that magnitude.

Research Effort Bias

Research effort varies considerably across primate lineages, and there is the potential that unknown innovative behaviours exist in currently data-limited species. If well-studied lineages are more likely to have reports of technical innovation or social learning then it is possible that genera containing a greater number of lineages could be more likely to include a well-studied lineage by chance. If true, this could create a bias towards these diverse genera displaying technical innovation or social learning and in turn erroneously suggest that the presence of these behaviours increase diversification rate. Though our data did not suggest a bias toward clades with higher taxonomic richness having lineages with higher research effort (Figures S2.4 and S2.5), we also wanted to take research effort into account in our analysis. Previous studies have controlled the total number of innovation or social learning instances recorded for a given lineage by research effort, however, this was not possible in our case (for rationale, see Methods section of main text) and we thus used binary data. When testing binary measures of innovation against diversification rate, others have accounted for research effort by including it as a covariate in the model (Ducatez, et al., 2020). However, we found a similar approach problematic for primates. Large-brained and innovative primates are extensively studied due to their complex behaviour and, in some cases, perhaps of their close relationship to humans (e.g. primates that exhibit habitual tool use are studied to elucidate the origins of human and animal material culture; McGrew, 1992; Visalberghi, 1994; van Schaik, et al., 1999; van Schaik, et al., 2003; Koops, et al., 2014). Thus, some part of research effort on a given species may be driven by such work, making it difficult to disentangle research effort and behavioural flexibility measures. Inspection of residuals from models including research effort as a covariate alongside our binary behavioural measures additionally revealed that this approach resulted in numerous irregularities in terms of which lineages are considered better innovators or social learners given a typical level of research effort (i.e. positive residuals). Well-studied primates such as chimpanzees have hundreds of reports of innovation and social learning, as well as hundreds of publications in the Zoological Record survey used to estimate research effort. The binary measure effectively caps these behaviours at 1, meaning that accounting for research effort with a binary technical innovation or social learning measure will unfairly penalize well-studied but ‘truly’ innovative species, making it appear that their propensity to innovate is falsely low. Therefore, we instead extended our simulation to consider whether 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.

In this second simulation we “evolved” research effort onto the phylogeny over 1000 iterations in tandem, but independently, of the evolution of technical innovation or social learning. We assume research effort (on the log-scale, bounding it above zero) would change across the tree according to a Brownian motion model, with the rate of change (σ) and ancestral state being estimated from the distribution of the natural log of research effort in our lineage dataset. Of course, the research effort directed by scientists is not a trait that evolves, but certainly there are a number of lineage characteristics and traits that are likely to attract research effort (e.g. geographic location, diurnality, social group size and behaviour) and we can expect many of these characteristics to be shaped by common descent and share phylogenetic inertia. Based on our empirical dataset, we defined a minimum threshold of 8 studies (or log(research effort) = 2.07) to observe social learning or technical innovation, based on the least-studied species with a record of technical innovation (as it contained the higher threshold; Figure S2.6). In our simulation we then changed evolved data points for any lineages that had evolved the presence of social learning and technical innovation, turning these lineages into non-innovators, if that lineage’s independently simulated research effort was below 8 studies. With these lineages assigned ‘hidden states’, we then repeated our genus-level analyses testing behavioural proxies of behavioural flexibility against diversification rate over these simulated datasets to get a distribution of expected neutral effect sizes that also include this potential research effort bias. This simulation was designed to mimic the effect false negatives (i.e. understudied innovators or social learners) may have on our results, illustrating whether having better studied lineages in diverse genera by chance could drive a positive association between the presence of technical innovation or social learning and diversification rate independent of biological mechanisms.

SUPPLEMENTARY RESULTS:

Phylogenetic Patterns

At the lineage-level relative brain volume showed high phylogenetic signal (λ=0.989; where λ closer to 1 indicates strong phylogenetic signal), with a moderate signal for technical innovation (D=0.187; where D closer to 0 indicates strong phylogenetic signal), and a modest signal for social learning (D=0.521), and none for relative neocortex and cerebellum volume (λ<0.001) as has previously been described when testing other relative measures of neocortex volume (possibly as a result of limited power; Shultz & Dunbar, 2006). Taxa per Lineage Diversification Rate also had a very low phylogenetic signal (λ=0.179) (see Figure S2.2; Table S2.2).

At the genus-level relative brain volume again showed high phylogenetic signal (λ=0.827). Technical innovation (D=0.438) and social learning (D=0.486) showed modest phylogenetic correlations, while relative neocortex and cerebellum volume (λ<0.001) showed almost no relationship with phylogeny. Taxa per Genus Diversification Rate again had a relatively low phylogenetic signal (λ=0.293) while Lineage per Genus Diversification Rate showed almost no phylogenetic signal (λ<0.001) (Table S2.2).

Table S2.1: Correlation matrix of predictor variables.

	Technical innovation (factor)	Social learning (factor)	Body mass^1	Body mass^2	Brain volume	Relative brain volume	Neocortex & cerebellum volume	Rest of total brain volume	Relative neocortex & cerebellum volume
Technical innovation (factor)	----	0.533	0.418	0.427	0.452	0.162	0.618	0.592	0.148
Social learning (factor)		----	0.337	0.343	0.381	0.113	0.481	0.484	-0.127
Body mass^1			----	0.985	0.869	-0.140	0.839	0.918	-0.186
Body mass^2				----	0.916	-0.122	0.880	0.942	-0.149
Brain volume					----	0.106	0.988	0.992	-0.042
Relative brain volume (residuals)						----	-0.378	-0.453	0.302
Neocortex & cerebellum volume							----	0.979	0.024
Rest of total brain volume								----	-0.112
Relative neocortex & cerebellum volume (residuals)									----

Technical innovation and social learning predictors represented by 0/1 integers and coefficients are thus not comparable to coefficients of continuous predictors

Data sources: ^{1}PanTHERIA; ^{2}Powell et al., 2017

Relative brain volume data obtained by retaining residuals from a log-log regression of brain volume as a function of body mass^1

Relative neocortex & cerebellum volume data obtained by retaining residuals from a log-log regression of neocortex & cerebellum volume as a function of rest of total brain volume

Table S2.2: Phylogenetic signal of predictor variables and diversification rate recorded as Pagel's λ (for continuous variables; where λ closer to 1 indicates signal) or the D-statistic (for binary variables; where D closer to 0 indicates signal).

Variable (Units)	**Lineage-level Pagel's λ or D-statistic**	**Genus-level Pagel's λ or D-statistic**
Technical innovation (factor)	D= 0.187	D= 0.438
Social learning (factor)	D= 0.521	D= 0.486
Brain volume (cm^3)	λ= 1.000	λ= 1.000
Body mass (g)	λ= 1.000	λ= 0.818
Relative brain volume (residuals)	λ= 0.989	λ= 0.827
Neocortex & cerebellum volume (mm^3)	λ= 1.000	λ= 1.000
Rest of brain volume (mm^3)	λ= 1.000	λ= 1.000
Relative neocortex & cerebellum volume (residuals)	λ< 0.001	λ< 0.001
Taxa per Lineage Diversification Rate	λ= 0.179	----
Taxa per Genus Diversification Rate	----	λ= 0.293
Lineage per Genus Diversification Rate	----	λ< 0.001

Table S2.3: Available data (%), predictive accuracy (p^2) and AUC scores for predictors across the lineage-level dataset (239 lineages), with selected coefficients and the number of eigenvectors included in imputation models. N/A: not applicable since imputation was not attempted.

Variable (Units)	**# Lineages with available data (%)**	**Selected coefficients (including # of eigenvectors selected by model from the phylogeny)**	**# of eigenvectors**	**Predictive accuracy (p^2) or area under the ROC curve (AUC)**
Body mass (g)	196 (82.0%)	10KTrees consensus phylogeny (27 eigenvectors)	50	p^2=0.999
ECV (brain volume) (cm^3)	186 (77.8%)	Body Mass + 10KTrees consensus phylogeny (32 eigenvectors)	50	p^2=0.990
Technical innovation (factor)	176 (73.6%)	ECV + 10KTrees consensus phylogeny (9 eigenvectors)	40	AUC= 0.928
Social learning (factor)	176 (73.6%)	Technical innovation + ECV + 10KTrees consensus phylogeny (21 eigenvectors)	40	AUC= 0.699
Neocortex & cerebellum volume (mm^3)	42 (17.6%)	N/A	N/A	N/A
Rest of total brain volume (mm^3)	42 (17.6%)	N/A	N/A	N/A

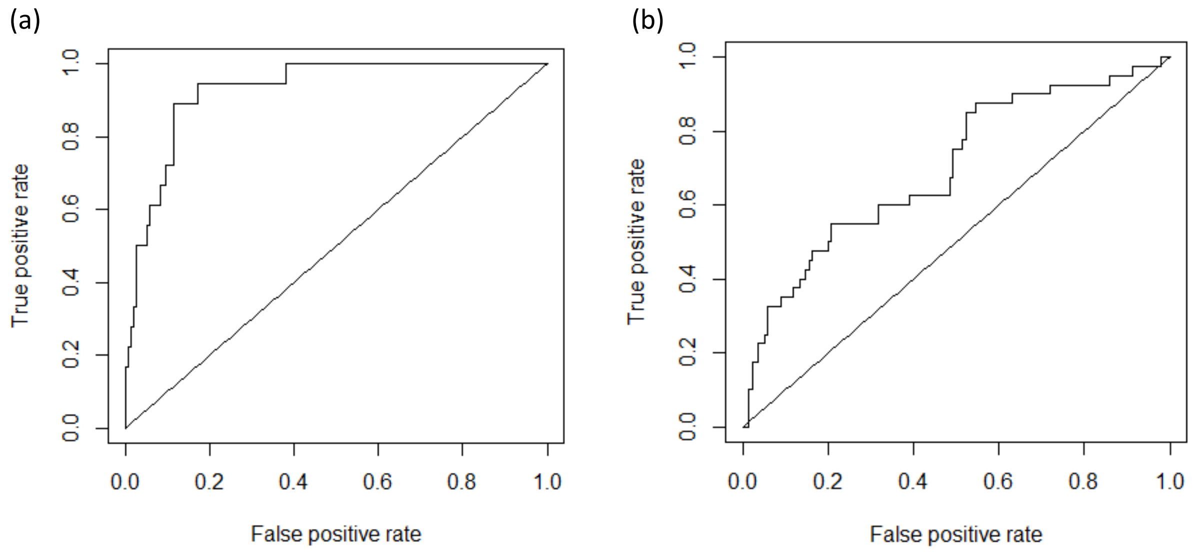


Figure S2.3: Receiver operating characteristic curves from leave-one-out cross-validation models for predicting the presence or absence of: (a) technical innovation (maximum accuracy=0.926; AUC=0.928) and (b) social learning (maximum accuracy=0.801; AUC=0.699) imputations.

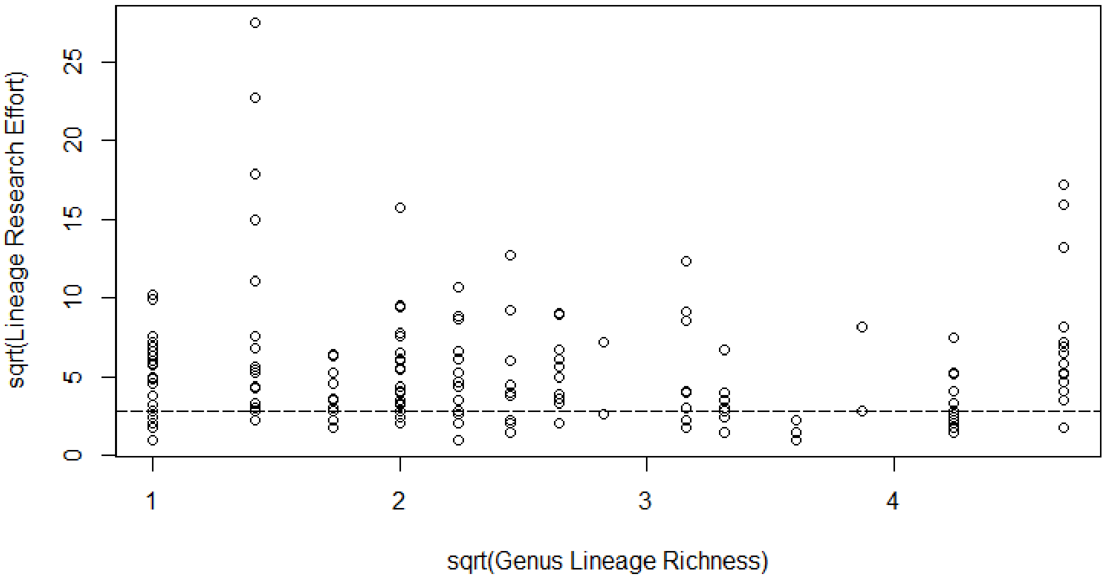


Figure S2.4: Square-root of lineage per genus richness versus the square-root of lineage-level research effort. The dotted line represents the fewest number of papers in the research effort survey for an observation of technical innovation to be made in a lineage (log(research effort) = 2.07; see Figure S2.6). There was no trend between lineage research effort and the richness of its genus (ß=-0.239; p=0.343).

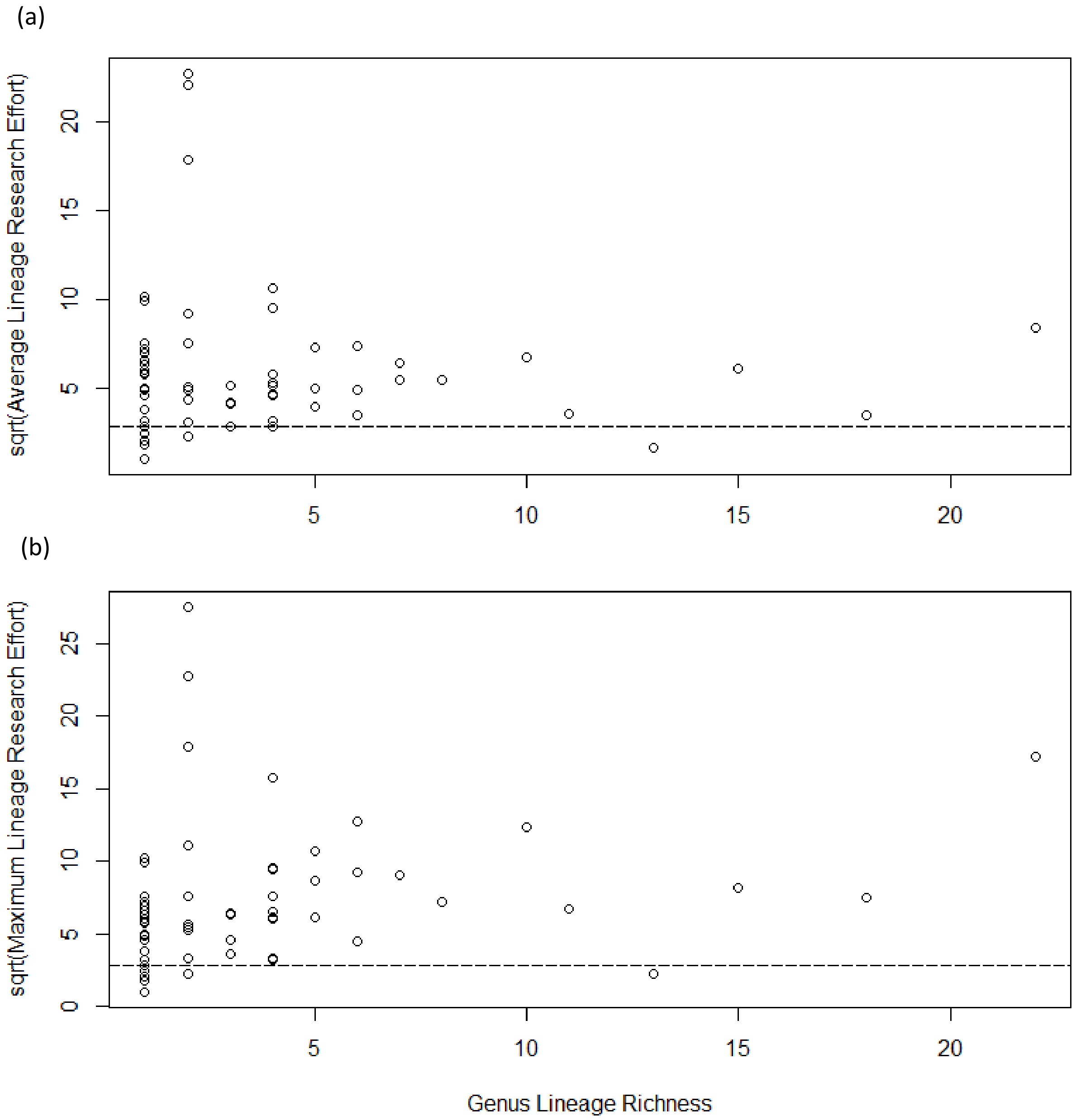


Figure S2.5: Lineage per genus richness versus (a) the square-root of the average research effort per lineage in each genus, and (b) the square-root of the maximum research effort per lineage in each genus. The dotted line represents the fewest number of papers in the research effort survey for an observation of technical innovation to be made in a lineage (log(research effort) = 2.07; see Figure S2.6).

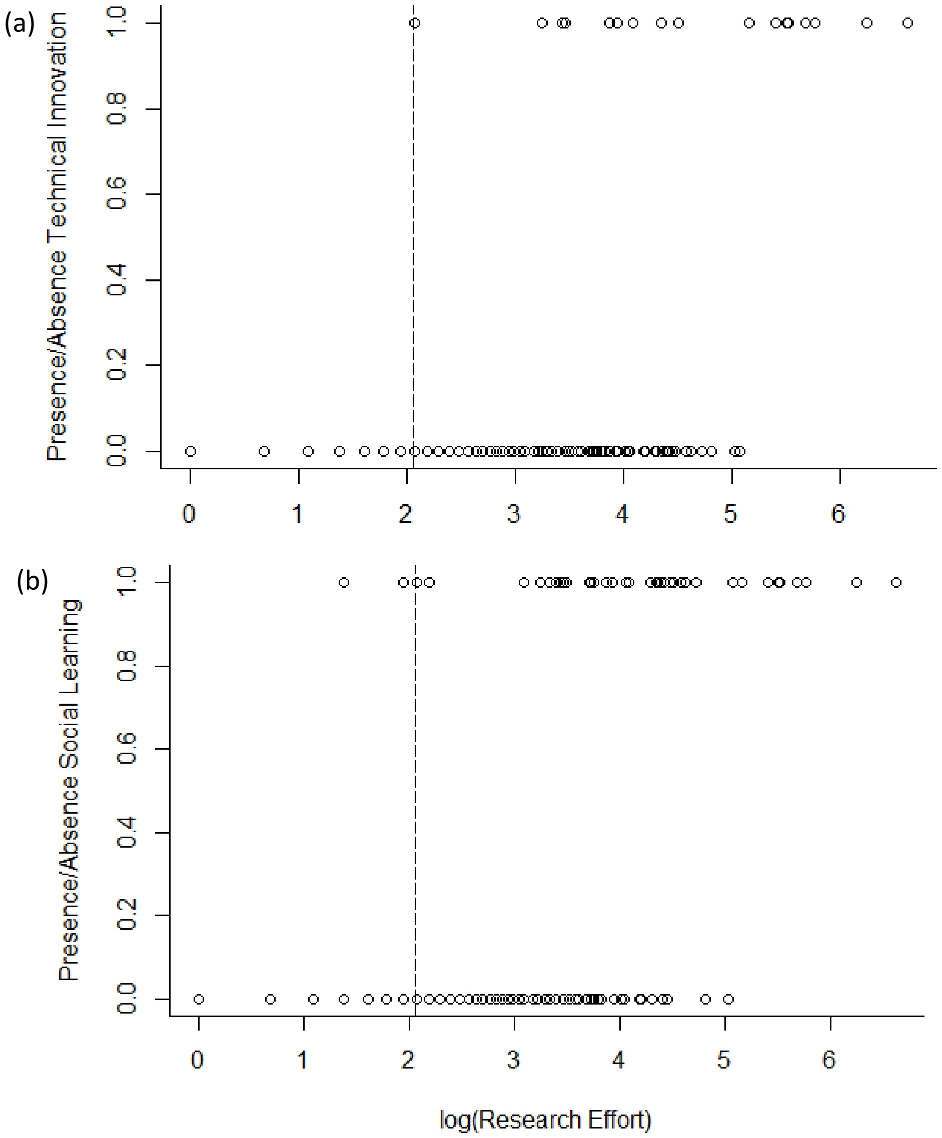


Figure S2.6: Presence and absence of (a) technical innovation and (b) social learning versus research effort per lineage. The dotted line represents the fewest number of papers in the research effort survey for an observation of technical innovation to be made in a lineage (log(research effort) = 2.07).

Table S2.4: Results of lineage-level analyses using Taxa per Lineage Diversification Rate from all imputed and non-imputed models +P≤0.1; *P≤0.05; **P≤0.01. Each row represents a separate analysis.

Variable (Units)	**Imputed**						**Non-imputed**					
	Min 95%CI	Max 95%CI	ß	SE	t	p	Min 95%CI	Max 95%CI	ß	SE	t	p
Technical innovation (factor)	-0.143	0.109	-0.017	0.064	-0.264	0.792	-0.166	0.149	-0.009	0.080	-0.110	0.912
Social learning (factor)	-0.029	0.163	0.067	0.049	1.374	0.171	-0.020	0.205	0.092	0.057	1.605	0.110
Technical innovation and social learning (factor)	-0.133	0.130	-0.002	0.067	-0.026	0.979	-0.151	0.185	0.017	0.086	0.200	0.841
Relative brain volume*	-0.036	0.159	0.062	0.050	1.243	0.215	-0.007	0.218	0.106	0.057	1.844	0.067+
Relative neocortex & cerebellum volume*							-0.240	0.152	-0.044	0.100	-0.437	0.664
Body mass*	-0.107	0.145	0.019	0.064	0.300	0.764	-0.111	0.147	0.018	0.066	0.270	0.787

* = $\log_e$-transformed and scaled by 2 standard deviation

<u>Table S2.5:</u> Results of genus-level analyses using Taxa per Genus Diversification Rate from all imputed and non-imputed models

+P≤0.1; *P≤0.05; **P≤0.01. Each row represents a separate analysis.

Variable (Units)	Imputed						Non-imputed					
	Min 95%CI	Max 95%CI	ß	SE	t	p	Min 95%CI	Max 95%CI	ß	SE	t	p
Technical innovation (factor)	-0.089	0.160	0.036	0.064	0.562	0.577	-0.093	0.154	0.031	0.063	0.486	0.629
Social learning (factor)	-0.057	0.130	0.037	0.048	0.774	0.442	-0.065	0.121	0.028	0.048	0.589	0.558
Technical innovation and social learning (factor)	-0.075	0.185	0.055	0.066	0.828	0.411	-0.081	0.177	0.048	0.066	0.733	0.467
Relative brain volume*	-0.017	0.183	0.083	0.051	1.635	0.108	0.049	0.228	0.138	0.046	3.020	0.004**
Relative neocortex & cerebellum volume*							-0.141	0.154	0.007	0.075	0.089	0.930
Body mass*	-0.039	0.186	0.074	0.057	1.285	0.204	-0.034	0.194	0.080	0.058	1.379	0.173

* = $\log_e$-transformed and scaled by 2 standard deviation

Table S2.6: Results of genus-level analyses using Lineage per Genus Diversification Rate from all imputed and non-imputed models +P≤0.1; *P≤0.05; **P≤0.01. Each row represents a separate analysis.

Variable (Units)	**Imputed**						**Non-imputed**					
	Min 95%CI	Max 95%CI	ß	SE	t	p	Min 95%CI	Max 95%CI	ß	SE	t	p
Technical innovation (factor)	0.002	0.130	0.066	0.033	2.025	0.048*	0.000	0.129	0.065	0.033	1.973	0.053+
Social learning (factor)	0.043	0.132	0.088	0.023	3.884	< 0.001**	0.042	0.131	0.086	0.023	3.789	< 0.001**
Technical innovation and social learning (factor)	0.018	0.151	0.085	0.034	2.504	0.015*	0.017	0.150	0.083	0.034	2.452	0.017*
Relative brain volume*	-0.022	0.072	0.025	0.024	1.037	0.304	-0.019	0.078	0.030	0.025	1.203	0.234
Relative neocortex & cerebellum volume*							-0.112	0.074	-0.019	0.047	-0.400	0.693
Body mass*	-0.020	0.074	0.027	0.024	1.118	0.268	-0.017	0.078	0.030	0.024	1.247	0.218

* = $\log_e$-transformed and scaled by 2 standard deviation

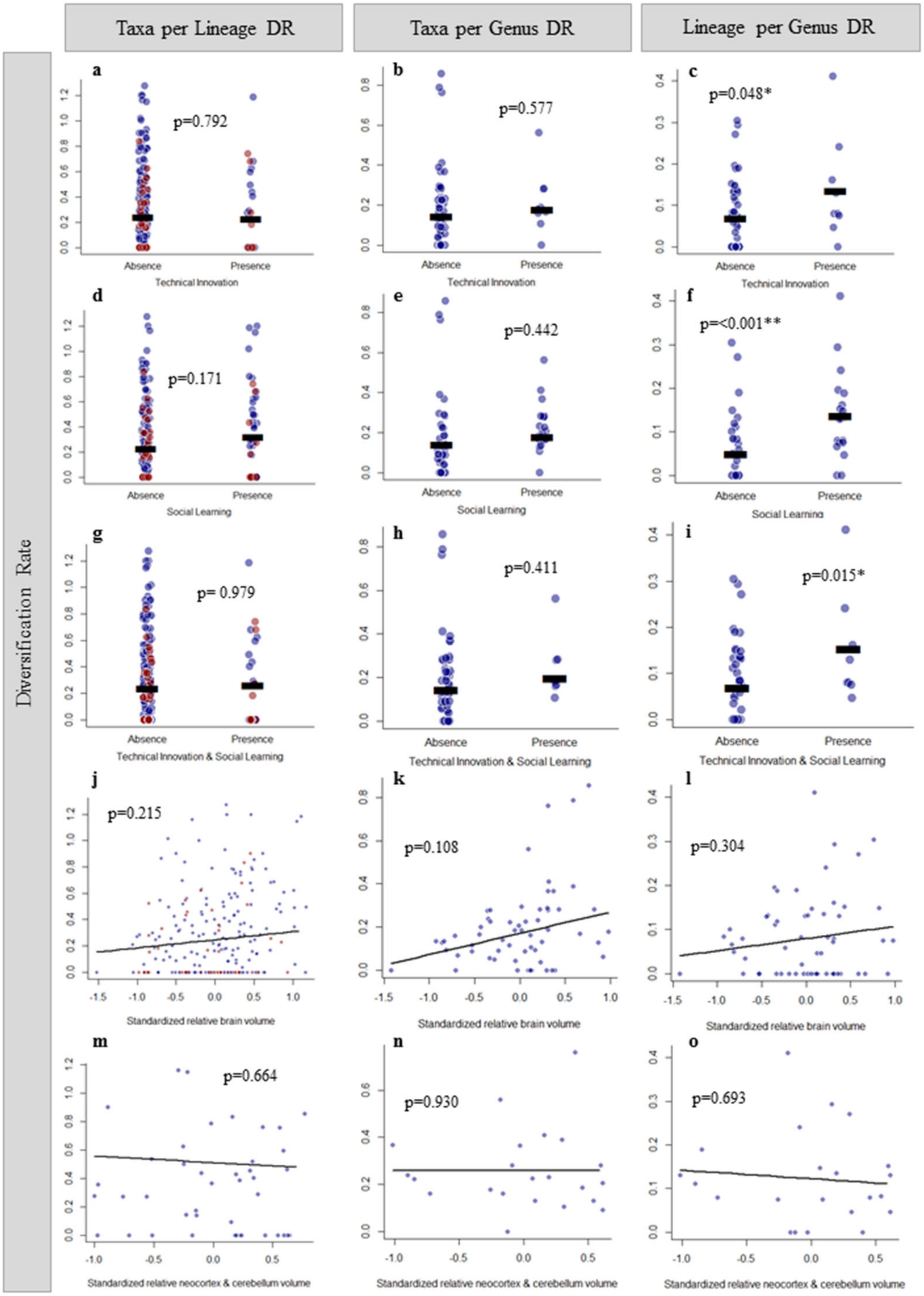
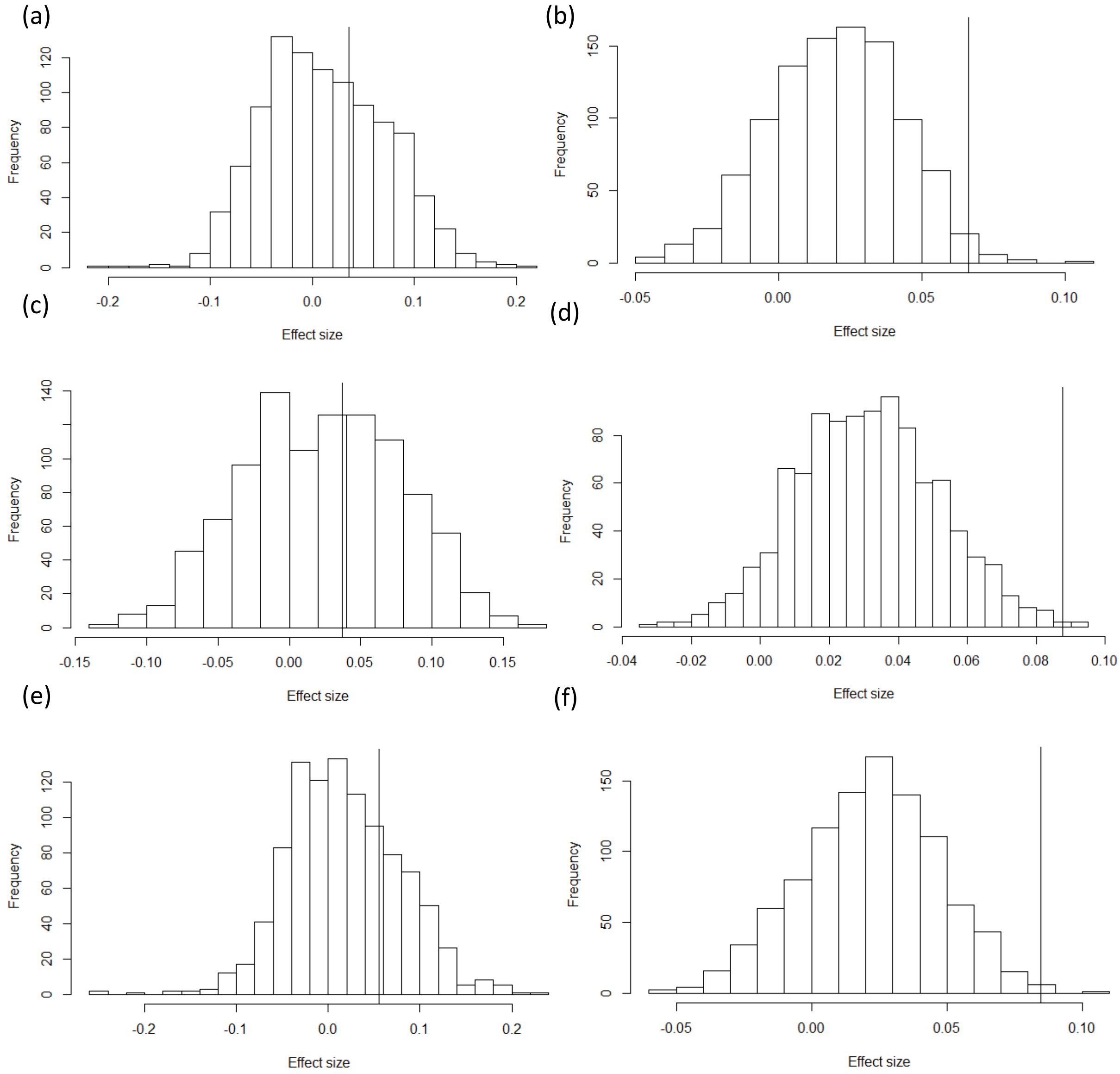


Figure S2.7: Relationships between technical innovation (a-c), social learning (d-f), combined technical innovation and social learning (g-i), relative brain volume (j-l) (all including imputed data) and relative neocortex & cerebellum volume (m-o) (non-imputed) on three measures of primate diversification rate. Imputed lineage-level data points are indicated in red. Horizontal bars indicate group means. Significance indicated as: +P≤0.1; *P≤0.05; **P≤0.01.

Lineage-Richness Sampling Bias

From our simulations, we confirmed that there is a bias towards a positive relationship between diversification rate and the presence of each behavioural flexibility measure (Figure S2.8). For Taxa per Genus Diversification Rate, the probabilities of the observed effect sizes (ß) occurring by chance were p=0.392 for presence of technical innovation, p=0.420 for presence of social learning, and p=0.260 for combined presence of technical innovation and social learning. For Lineage per Genus Diversification Rate, the probabilities of the observed effect sizes (ß) occurring by chance were p=0.028 for presence of technical innovation, p=0.002 for presence of social learning, and p=0.008 for combined presence of technical innovation and social learning. That is, the effect sizes generated by this bias for the association with Lineage per Genus Diversification Rate were considerably lower than the observed effect size from the empirical data.



<u>Figure S2.8:</u> Distribution of effect sizes (ß) from PGLS tests on 1000 simulations of the random evolution of technical innovation and social learning. The neutral effect sizes for technical innovation on (a) Taxa per Genus Diversification Rate (DR) (median ß=0.009) and (b) Lineage per Genus DR (median ß=0.020); effect sizes for social learning on (c) Taxa per Genus DR (median ß=0.025) and (d) Lineage per Genus DR (median ß=0.031); Effect sizes for the combined presence of technical innovation and social learning on (e) Taxa per Genus DR (median ß=0.012) and (f) Lineage per Genus DR (median ß=0.023). Vertical line indicates the observed effect size for each predictor.

Research Effort Bias

Positive correlations between our measures of behavioural flexibility and genus-level estimates of diversification rate could also be further biased by asymmetry in research effort. If many understudied lineages scored as zero are truly technical innovators or social learners (i.e. false negatives), and these lineages tend to be in depauperate clades, then heightened observation of behavioural flexibility in diverse clades could bias our results. Testing this potential bias with a simulation where observed behaviours were hidden based on simulated research effort, we found that this scenario generated a slightly greater bias towards a positive relationship between diversification rate and the presence of each behavioural flexibility measure (Figure S2.9). Our results for Taxa per Genus Diversification Rate remained non-significant, and for Lineage per Genus Diversification Rate remained significant except for technical innovation. For Taxa per Genus Diversification Rate, the probabilities of the observed effect sizes (ß) occurring by chance were $p=0.408$ for presence of technical innovation, $p=0.439$ for presence of social learning, and $p=0.281$ for combined presence of technical innovation and social learning. For Lineage per Genus Diversification Rate, the probabilities of the observed effect sizes (ß) occurring by chance were $p=0.109$ for presence of technical innovation, $p=0.019$ for presence of social learning, and $p=0.027$ for combined presence of technical innovation and social learning.

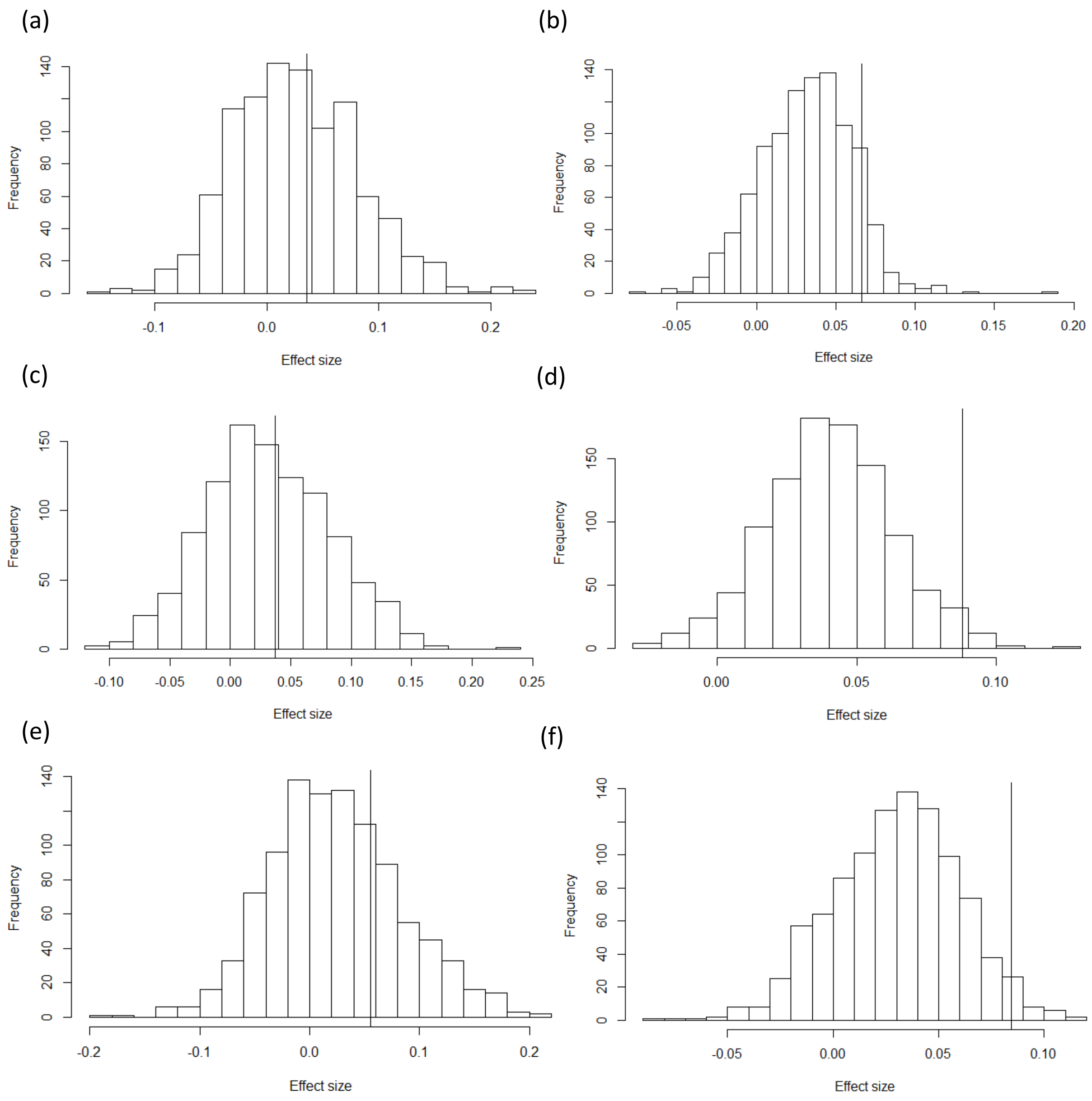


Figure S2.9: Null distribution of effect sizes (ß) from PGLS tests on 1000 simulated technical innovation/social learning datasets censoring the presence of these behaviours when a lineage has a simulated research effort < 8 papers, testing the effect of technical innovation on (a) Taxa per Genus Diversification Rate (DR) (median ß=0.023) and (b) Lineage per Genus DR (median ß=0.033); social learning on (c) Taxa per Genus DR (median ß=0.028) and (d) Lineage per Genus DR (median ß=0.040); and the combined presence of technical innovation and social learning on (e) Taxa per Genus DR (median ß=0.020) and (f) Lineage per Genus DR (median ß=0.032). Vertical line indicates the observed effect size.

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LINKING STATEMENT

One of the main obstacles I encountered when attempting to measure diversification rate in Chapter 2 was the unreliable estimate of species and subspecies richness across primate lineages ascribable to recent applications of the ‘phylogenetic species concept’ (PSC). In particular, the PSC has a tendency of splitting lineages into a greater number of less inclusive units in comparison to previous species concepts. As a result, there has been an observable “inflation” in the number of species listed in many primate groups since the introduction of the PSC in 1983. This phenomena has now been referred to as ‘taxonomic inflation’ and has been criticized for being heterogeneous and biased toward certain clades. Taxonomic inflation has complicated evolutionary measures as discussed in Chapter 2, however, inflation has also been suggested to have implications in applied fields of biology – most notably conservation. Therefore, in Chapter 3 I explore the predictors of taxonomic inflation across primate taxa and its role in conservation.

CHAPTER 3: PREDICTORS OF TAXONOMIC INFLATION AND ITS ROLE IN PRIMATE CONSERVATION

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Unpublished manuscript

ABSTRACT:

Species are the main unit used to measure biodiversity but different preferred diagnostic criteria can lead to very different delineations. For instance, named primate species have more than doubled since 1982. Such increases have been termed "taxonomic inflation" and have been attributed to the widespread adoption of the ‘phylogenetic species concept’ (PSC) in preference to the previously popular ‘biological species concept’ (BSC). Criticisms of the PSC have suggested taxonomic inflation may be biased toward particular taxa and pose unpropitious consequences for conservation. Here, we explore predictors of taxonomic inflation across primate taxa since the initial application of the PSC nearly 40 years ago. We do not find evidence that diversification rate, the rate of lineage formation over evolutionary time, is linked to inflation, contrary to expectations if the PSC identifies incipient species. Research effort in fields suggested to be associated with inflation also exhibited no significant association with increases in species numbers among genera. To test the suggestion that splitting groups is likely to increase their threat score, we additionally examined whether genera that have undergone more inflation are more at risk. We find that associations between inflation and threat score vary by region, with a positive association in Asia and Africa, no significant association in Madagascar, and a negative association in the Neotropics. We suggest these differences may indicate that other factors (e.g. total geographic range size of a genus) impact how inflation affects threat score. Regardless, we echo warnings that it is unwise for conservation to be reliant on taxonomic stability. Species (however defined) are not independent from one another, and thus monitoring and managing them as such may not meet the overarching goal of conserving biodiversity.

KEYWORDS: species; phylogenetic species concept; primates; taxonomic inflation; conservation

INTRODUCTION:

“Species” are an integral unit of biodiversity used across many sub-disciplines of biology, yet how scientists define species has been subject to change. As of 2004, over 24 different species definitions were recorded in the scientific literature (Coyne & Orr, 2004; Tattersall, 2007). New species definitions have led to dramatic shifts in the number of species listed in many taxonomic groups throughout time. Notably, in the last 40 years, the widespread popularization of the phylogenetic or ‘diagnostic’ species concept (PSC) (Cracraft, 1983; Isaac, et al., 2004; Cotton, et al., 2016) has led to large increases in species numbers across many taxa (Agapow, et al., 2004).

Groves (2014) provides a brief overview of popular species definitions employed by taxonomists through the late nineteenth to twentieth century. One notable phenomenon is the considerable decrease in diagnosed species following the rapid adoption of the polytypic species concept from the 1890’s onward. The polytypic species concept emphasizes that species should be inclusive and that one should delineate taxa that resemble one another as subspecies (Groves, 2014). The popularization of the polytypic species concept was eventually accompanied by the widespread adoption of the ‘biological species concept’ (BSC) beginning in the early 1960’s (Groves, 2014). The BSC, proposed by Theodosius Dobzhansky and Ernst Mayr (Mayr, 1963), states that species are populations/meta-populations that do not interbreed with other populations/meta-populations under natural conditions (Mayr, 1963; Groves, 2014). While this definition has been subject to revisions, the central premise of the BSC is that reproductive barriers are key to diagnosing species (Groves, 2014). The BSC was widely accepted and layered onto the pre-existing polytypic species concept, creating a period of relative taxonomic stability for vertebrates from the 1960’s to 1980’s (Isaac, et al., 2004). However, various criticisms of the BSC did emerge, the most notable being the practical difficulty of diagnosing species under the BSC because of the need for information on reproductive barriers. Closely related lineages sharing parapatric (i.e. separate but contiguous) distributions are especially difficult to diagnose under the BSC (Tattersall, 2007). In many instances limited records of potential mating interactions or of hybrid forms do not provide researchers with enough information to confirm whether parapatric populations belong to a single species. In these cases, genetic evidence is required to show that gene pools are still actively reintegrating after being geographically separated (Tattersall, 2007). Collecting such evidence in every case of parapatry would be a daunting task, and these critiques suggested the need for a species concept with higher diagnostic power.

In the last 40 years the ‘phylogenetic’ or ‘diagnostic’ species concept (Cracraft, 1983; Isaac, et al., 2004) has been widely popularized in vertebrate taxonomy due to its diagnosable advantages over the BSC. Under the phylogenetic species concept (PSC), a species is diagnosed as the smallest population or meta-population that is distinct in heritable differences from other populations or meta-populations (Cracraft, 1983; Groves & Grubb, 2011; Groves, 2014). According to its proponents, the emphasis on more easily diagnosable evidence under the PSC creates a scientific proposition that can be tested. As a result, the PSC began being used almost immediately after its inception, with influential taxonomists quickly advocating for its use over the BSC (see, e.g. Donoghue, 1985).

Although the PSC offers diagnostic advantages over the BSC, it has also been subject to criticism. Notably, the PSC has been criticized for its tendency of splitting species into a range of less-inclusive units compared to previous species concepts (Agapow, et al., 2004; Zachos, et al., 2013; Zachos & Lovari, 2013). Under the PSC many populations previously recognized as subspecies or morphological variants have been elevated to full species status, resulting in a large increase in the number of listed species. For instance, 181 species of primates were listed by Honacki et al. (1982), one year prior to Cracraft’s proposal of the PSC (Cracraft, 1983). Today the IUCN (International Union for Conservation of Nature)/SSC (Species Survival Commission) Primate Specialist Group lists over 500 distinct primate species (IUCN/SSC Primate Specialist Group, 2018). Figure 3.1 illustrates the increase in species numbers among primate families listed by Honacki et al. (1982) over time. Some families (e.g. Cheirogaleidae and Indriidae) have more than tripled in species numbers since the introduction of the PSC. While some of these species have been added as a result of new discoveries, a majority are populations previously identified at a lower taxonomic level that have since been elevated to species status following the application of the PSC. For instance, 391 of the 509 primate species listed by the IUCN as of 2018 (IUCN/SSC Primate Specialist Group, 2018) have names and discovery dates that pre-date the publication of Honacki et al. (1982). This means at least 210 are populations previously considered to be subspecies or morphological variants of other species under the BSC that have since been elevated to full species status under the PSC. Of course, populations need not be identified as formal subspecies or variants prior to being split from an already recognized species, making 210 a conservative estimate of the number of populations that have been elevated to full species status under the PSC. This trend of the PSC increasing species numbers by raising taxonomic statuses has now been referred to as 'taxonomic inflation' (Rylands & Mittermeier, 2014). Inflation is certainly heterogeneous across primate families (Figure 3.1), and the application of the PSC has been criticized for being non-random, and biased toward certain taxonomic groups (Isaac, et al., 2004).

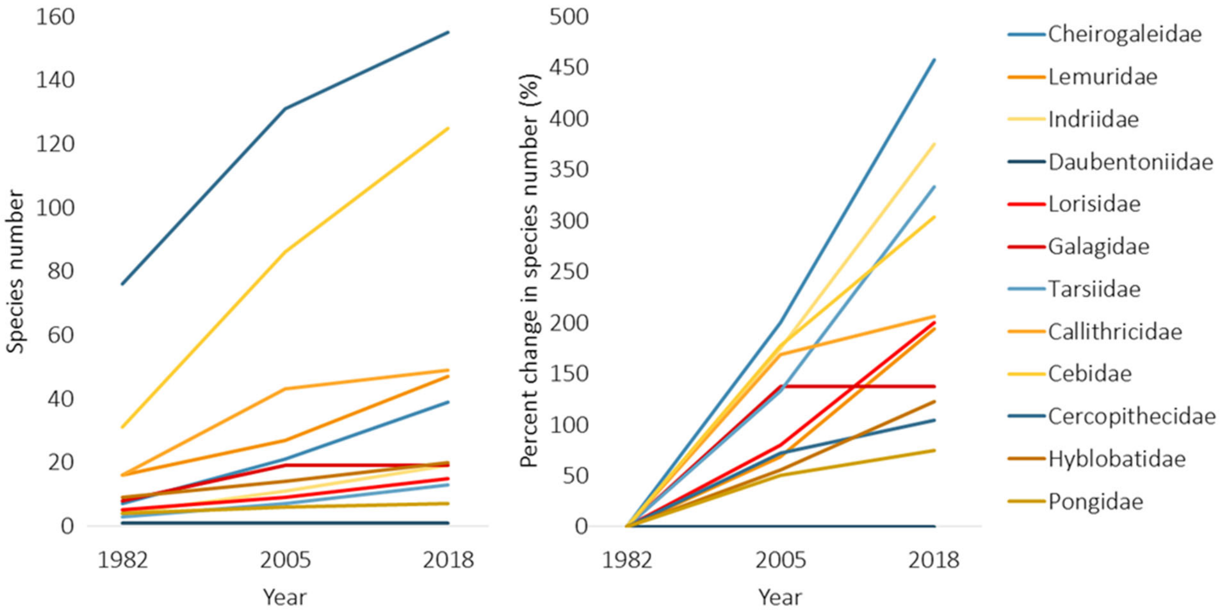

Figure 3.1: Species numbers and percentage change in species numbers for historic primate families recorded at three time points by Honacki et al. (1982), Wilson & Reeder (2005) and the IUCN/SSC Primate Specialist Group (2018).

What motivates disproportional splitting among certain taxonomic groups relative to others has been poorly explored. Of course, variation in the number of new species described under the PSC across taxa could be driven by variation in the rate at which lineages evolve, e.g. if genetic variation is revealing cryptic diversity or incipient species formation among rapidly evolving taxa. In this case, new species listed under the PSC might point to situations where there is a discordance between patterns of genetic change and the evolution of gross morphological changes used by traditional taxonomists. This could be due to ecology – if some lineages are diversifying along ecological axes that we do not notice, or due to demographics – if some lineages have ecologies and/or histories that lead to faster local genetic coalescent times and so diagnosability. Under either of these scenarios, inflation would not lead to a bias *per se*, but simply reflect underlying biological reality. However, it is also possible that splitting is driven by other factors that may indeed be prone to bias. Many have argued that most of the inflation among groups is artificial, simply reflecting major shortcomings of applying the PSC and reliance on insufficient data (Zachos, et al., 2013; Zachos & Lovari, 2013). Zachos et al. (2013) provides some evidence suggesting unwarranted splitting in select cases, advocating that the PSC has been taken to the "molecular extreme". In one cited example, Sumatran tigers (previously *Panthera tigris sumatrae*, raised to *Panthera sumatrae*) were split by Cracraft et al. (1998) and further split by Mazák & Groves (2006), based on diagnosable mitochondrial and craniometrics differences, respectively. Zachos et al. (2013) argues that if such fine diagnosable distinctions were applied to groups like domestic dogs, or even humans one could just as well advocate for their splitting. By this logic, groups may continue to be split as an increasing amount of molecular work supports more splitting (i.e. we are likely to find more PSC species the more we look for them).

It has additionally been suggested that conservation interest in particular groups may motivate splitting. Funding for conservation research is increasingly focused on 'biodiversity hotspots' and it has been suggested that – due to the limited supply of conservation resources – researchers could have a vested interest in declaring taxa in these regions as endemic species (Karl & Bowen, 1999; Isaac, et al., 2004). There is indeed evidence among well-studied and charismatic taxa for species receiving more conservation attention and funding when comprised of multiple, small and taxonomically distinct populations (e.g. African apes; Stanford, 2001; Oates, 2006; Gippoliti & Amori, 2007). This is because species lists are often used to determine which groups should receive conservation attention (Mace, 2004) and changing the way we define species can also change which groups receive action. This has led to another major criticism of the PSC which suggests that it may create a burden on conservation efforts (Agapow, et al., 2004; Mace, 2004; Isaac, et al., 2004; Frankham, et al., 2012; Zachos, et al., 2013; Zachos, 2015).

Along with being potentially biased toward certain groups, splitting under the PSC has been suggested to result in populations that are considered to be more imperilled (Agapow, et al., 2004;

Isaac, et al., 2004; Morrison, et al., 2009; Robuchon, et al., 2019). One criterion used by the IUCN to classify “Vulnerable” species is that fewer than 1000 mature individuals should be found in the wild. Species identified as “Endangered” should have fewer than 250 mature individuals left in the wild (Agapow, et al., 2004; Frankham, et al., 2012). Thus splitting an already vulnerable species into several new species may result in one or more receiving a more imperilled status, in addition to generally increasing the number of recognized threatened species (Agapow, et al., 2004; Isaac, et al., 2007). This could also lead to seemingly rare but poorly-defined species being prioritized over well-defined and perhaps biologically more distinctive species (Pillon & Chase, 2007). Criticisms of the PSC have sparked division across many fields of biology, with many still advocating that the PSC is the best method of defining species (e.g. Groves, 2013).

Here, we set out to better understand taxonomic inflation in primates by exploring predictors of taxonomic inflation across primate genera and testing how inflation interacts with risk status across primate genera. We test to determine (i) whether taxonomic inflation is associated with the amount of research being done in fields suggested to motivate splitting, or whether it is associated with a lineage's underlying diversification rate, and, (ii) whether rates of inflation dictate which groups are considered to be most imperilled.

We consider whether biological factors or measures of human-induced bias explain increases in species numbers among primate taxa. To test potential human-induced biases in splitting, we consider estimates of research effort for each taxon, and predict that more research done on a given taxon may increase splitting. We examine research effort in two fields: molecular genetics (since molecular work could cause species to be split continuously as finer molecular distinctions are made) and conservation (since splitting has been suggested to be motivated by conservation interests: Karl & Bowen, 1999; Isaac, et al., 2004). To explore possible biological explanations for inflation trends, we test to see if inflation is explained by diversification rate, using a diversification measure designed to be uncoupled from changes in species naming conventions (see Methods). Lineages with high past diversification rates are expected to contain more incipient or cryptic species than lineages diversifying at a lower rate, such that diversification rate would be expected to correlate positively with PSC-induced taxonomic inflation.

To explore our second question linking inflation and risk, we would ideally test for an association between inflation per genus and changes in genus-level risk status between 1982 and 2016. However, Red List criteria for threat categories have changed considerably over time (e.g. see criteria and statuses in IUCN Conservation Monitoring Centre, 1986) and an ever-increasing number of species have now been evaluated (Collen, et al., 2016). Additionally, prior to the 1990s Red Lists were determined based upon nominations by experts in the field, rather than any systematic review process (Mace, et al., 1992; Mace & Collar, 1995). Therefore, changes in risk status between 1982 and 2016 could well reflect adjustments in listing criteria and a general improvement in assessments for many taxa (particularly those which were previously understudied). As a result, we instead specifically test whether inflation is associated with which taxa are considered to be at the greatest risk today. We test this using a genus-level estimate of threat score (hereafter "threat score"), estimated based on a modified version of the Red List Index (RLI) (a compound measures of IUCN Red List Status; IUCN Red List of Threatened Species, 2019) equation provided in Butchart et al. (2007) and Bubb et al. (2009). In our adjusted measure, high threat score (approaching 1) indicates high risk taxa and low threat score (approaching 0) indicates low risk taxa. We ask whether genera with species that have been split more frequently following the implementation of the PSC have higher threat scores compared to genera with species that have been split less frequently. If splitting drives which taxa are considered to be at the greatest risk, we predict that we should observe a positive association between inflation and threat score after accounting for other know predictors of genus-level threat scores (e.g. region).

METHODS:

Data

To measure the number of primate species before the introduction of the PSC, we used the last pre-PSC taxonomy, that of Honacki et al. (1982). This taxonomy contains 181 species, and is considered a reliable estimate of the number of species thought to exist during the popularity of the BSC (see Rylands & Mittermeier, 2014). This taxonomy was contrasted with the IUCN taxonomy from 2016 and attendant data documented in Estrada et al. (2017), which lists 503 species. For each of these 503 species we noted their taxonomic placement (genus and family), threat status (LC=Least Concern, NT=Near Threatened, VU=Vulnerable, EN=Endangered, CR=Critically Endangered, EX=Extinct, NE = no evaluation exists or DD = data deficient), biogeographic region, and assigned them a corresponding threat level score (LC=0, NT=1, VU=2, EN=3, CR=4, EX=5, NE=NA or DD=NA) following Butchart et al. (2007) and Bubb et al. (2009). For each other species described by the IUCN in 2016 that was not listed in Honacki et al. (1982), we scored whether the species was a "*de novo*" species description (Burgin, et al., 2018). *De novo* species descriptions included 40 cases where a new species had not been previously formally identified as a subspecies or subpopulation of another species prior to splitting.

We compiled all the species listed by the IUCN in 2016 into the 12 families and 50 genera they corresponded with in Honacki et al. (1982). Family "Callimiconidae" in Honacki et al. (1982) was not used as this taxon has since been recognized as a genus of the larger family "Callitrichidae" (Wilson & Reeder, 2005). Species *Rungwecebus kipunji* was removed from IUCN species list from 2016 as it represents a newly discovered genus and as such, does not collapse into any of the genera provided by Honacki et al. (1982). Total threat scores were calculated for each genus by summing the threat scores of all species assigned that genus. A maximum possible threat score was also assigned to each genus (assuming all species are EX) as 5 times the number of species in that genus. The 34 NE and 23 DD species (which have no status weight) were not included in calculations of maximum possible score (following Butchart, et al., 2007).

Research effort in the fields of molecular genetics and conservation were estimated for each genus through a literature review of publications in the Web of Science Core Collection published between 1983 (the year the PSC was first proposed) and 2016. To obtain papers in the field of conservation we searched the genus name AND "conservation" (hereafter 'conservation research effort'). To obtain papers in the field of molecular genetics we searched the same combination of genus name AND the following terms: "mitochondrial DNA" OR "barcoding" OR "bar-coding" OR "cytochrome b" OR "phylogeography" OR "microsatellites" OR "micro-satellites" OR "population genetics" OR (species AND genetics) OR (taxonomy AND genetics) OR "SNP" (hereafter 'molecular genetics research effort'). All hits from these searches were reviewed and irrelevant papers were eliminated (see supplementary materials; Tables S3.1 and S3.2). In this study we used the genera listed in Honacki, et al. (1982) (n=50), many of which have since been further separated into multiple genera. Thus, when appropriate we included new genera names in addition to those listed by Honacki, et al. (1982) in the literature search (see Table S3.3). The supplementary material describes how searches were conducted and how changes in nomenclature and ambiguous genera names were accounted for.

Diversification rate was estimated per the method-of-moments approach described in Magallon & Sanderson (2001) (i.e. ln(taxa richness)/stem age). Diversification rate estimates generated using this method often rely on species numbers as their estimate of taxa richness, meaning that diversification rate estimates are inherently biased by the inflation phenomenon we are studying (i.e. highly inflated genera will receive disproportionally high diversification rates). Therefore, richness scores for our diversification rate calculations were determined as the counts of the well-resolved "lineages" described in Creighton et al. (2020). These lineages were determined by creating a time cut-off in the 10kTrees consensus primate phylogeny (Arnold, et al., 2010) in an attempt to eliminate very young PSC species descriptions and obtain a consistent (unbiased) estimate of diversity across clades. These lineages were assigned to each of the 50 genera described in Honacki, et al. (1982). Diversification rate was then estimated by taking the natural log lineage richness for each genus and dividing by the stem age of that genus (Magallon & Sanderson, 2001). We note that all log transformations referenced hereafter refer to natural log transformations ($\log_e$). Stem ages for each genus were extracted from the 10kTrees consensus phylogeny (version 3) (Arnold, et al., 2010) trimmed to contain a single branch representing each genus. During this process, there were several instances where genera described in Honacki et al. (1982) were non-monophyletic within the more recent primate phylogeny we used (Arnold, et al., 2010), making it unclear how to assign a divergence date for these clades. We therefore removed eight genera from analyses where diversification rate was a variable of interest: *Presbytis*, *Lemur*, *Galago*, *Cebuella*, *Cercocebus*, *Cercopithecus*, *Papio*, and *Pygathrix*. This left 42 genera for subsequent analyses. Data were analysed using R version 3.6.3 (R Core Team, 2020).

Analysis

Predictors of Inflation

To determine if measures of potential human bias (i.e. research effort) or diversification rate explain discrepancies in inflation across taxa, we tested to see if these variables were significantly associated with the number of species added to primate genera since the introduction of the PSC while controlling for the original number of described species (i.e. species number prior to the

PSC) and region. We fit three general linear mixed effects models with Poisson distributions using the lme4 package in R (Bates, et al., 2014), and obtained p-values using the lmerTest package (Kuznetsova, et al., 2017). Inflation is likely to be phylogenetically clustered, meaning that phylogenetic relationships are likely to account for some of the variation in inflation across genera. Phylogenetic models could be used to account for this influence of phylogeny, however, we used the genera listed by Honacki et al. (1982) as our level of observation. These genera are very conservative and do not always match up with recently described phylogenetic patterns. This means that there are several instances where genera described in Honacki et al. (1982) are non-monophyletic (see 'Methods' on diversification rate calculations above), making it unclear how to designate them a single branch in modern phylogenies. Notably, a majority of the phylogenetic clustering in inflation is determined by differences in inflation rates among Madagascar, the Neotropics, and Asia and mainland Africa. Thus, we instead opted to use GLMMs where the effect of both region and family was considered to account for an influence of phylogeny, cognizant that some third-variable covariation may not be fully accounted for. In these models the response variable was the number of species assigned to a given genus by the IUCN in 2016 that had not been previously described by Honacki et al. (1982). Each model had either conservation research effort, molecular genetics research effort or diversification rate included as a fixed effect, as well as region and the number of species in the genus per Honacki et al. (1982) to control for their effects on inflation. The number of species listed for each genera in Honacki et al. (1982) was included as a logarithmic value, and was represented with both a linear and a quadratic term following inspection of raw plots and plots against scaled residuals from the simulation output. A square-root transformation was used on molecular genetics research effort to decrease the impact of outliers on model fit. To assist with model stability and convergence, we scaled all continuous variables in the model to have a mean of zero and standard deviation of one (Becker, et al., 1988). Asia and mainland Africa (hereafter Asia and Africa) were grouped together and served as the baseline region in our models based on previous studies that have shown that the taxonomy of primates from these regions has been relatively stable compared to Madagascar and the Neotropics (e.g. Isaac & Purvis, 2004; Isaac, et al., 2004; Tattersall, 2007). We also chose to group Asia and Africa together because one genus (*Macaca*) is found in both regions. Observation ID (a unique ID assigned to each genus) was included as a random effect in these models to correct for overdispersion. Family (nested within region) was originally included as a random effect but contributed very little to model fit and created issues with convergence due to overfitting, and thus was dropped from the final models. We tested potential interaction terms with all variables and region to test for regional effects, but none were significant and so these terms were also dropped from the final models. We ran all models a second time after removing species with no evidence of previously being a subspecies or subpopulation of another species in our dataset (i.e. *de novo* species descriptions) from our response (Tables S3.4, S3.5 and S3.6). We checked model assumptions and fit by plotting residuals versus the fitted values and versus each covariate in the model. Residual plots and analyses with the Diagnostics for Hierarchical Regression Models (DHARMa) R package (Hartig, 2017) indicated acceptable model fits.

Inflation and Threat Score

To test whether inflation is associated with higher risk levels across genera today, we fit a general linear mixed effects model with a binomial distribution using the lme4 package in R (Bates, et al., 2014), and obtained p-values using the lmerTest package (Kuznetsova, et al., 2017). As with inflation, phylogenetic relationships are likely to account for some of the variation in risk status across primate genera. However, as with inflation, phylogenetic patterns in risk status are largely mediated by geography. Thus, for reasons noted above, we opted to use GLMMs where family and biogeography were considered as explicit covariates to probe these patterns and account for an influence of phylogeny. The response variable was the threat score estimated based on the equation provided in Butchart et al. (2007) which returns a proportional overall extinction risk for taxa between 0 and 1. Therefore, we modeled threat score using a proportional count model, where the sum of the actual threat scores for species in a given genus were regarded as the number of 'successes' and the number of 'fails' were calculated as the total possible threat score minus the successes. Importantly, we note that equation provided in Butchart et al. (2007) scales RLI from 1 (all least concern) whereas our model estimating threat score using successes and fails did not. Thus, a model estimate of 1 using our measure denotes all species in a genus are extinct and an estimate of 0 indicates all evaluated species qualify as least concern. The standardized proportional change in species within each genus (# of new species in the IUCN species list from 2016 / original # of species in Honacki et al. (1982)) (our measure of "inflation") and region were entered as fixed effects. We chose to use proportional change in species numbers as our estimate of inflation since splitting occurs at the species level, and thus, each species listed prior to the PSC should present an opportunity for splitting to occur. In other words, our inflation variable modelled the number of new species listed in a primate genus for every one species that existed prior to the PSC, accounting for the fact that there is an increased opportunity for splitting in originally speciose genera. We were also interested in assessing whether there would be regional differences in the association between inflation and threat score, therefore, an inflation × region interaction term was included in the final model. We dummy coded region and releveled the baseline in order to test if the conditional effect of inflation was significantly different from zero for each region. Family was nested within region and entered in the model as a random effect to control for relatedness among genera, and behaved well. We repeated these analyses after removing taxa with *de novo* species descriptions that may represent novel discoveries from our inflation estimate and present these results in the supplementary materials (Table S3.7). We checked model assumptions and fit by plotting residuals versus the fitted values and versus each covariate in the model. Residual plots and analyses with the DHARMa R package (Hartig, 2017) indicated acceptable model fits.

RESULTS:

Predictors of Inflation

None of our measures – conservation research effort ($\beta = -0.220$; $p = 0.180$; Table 3.1), molecular genetics research effort ($\beta= -0.188$; $p= 0.212$; Table 3.2) nor diversification rate ($\beta= 0.132$; $p= 0.477$; Table 3.3) – were significantly associated with taxonomic inflation of primate genera. Notably, the quadratic term added for the original number of species in 1982 was significant in the model with diversification rate sharing a downwardly concave association with inflation ($\beta= -1.890$; $p= 0.042$; Table 3.3) and approached significance in models including conservation and molecular genetics research effort as predictors ($\beta= -1.529$; $p= 0.072$; Table 3.1 and $\beta= -1.626$; $p= 0.057$; Table 3.2), illustrating that number of species added to genera since the introduction of the PSC is not completely proportional to the original number of species listed in genera in 1982 after accounting for other predictors of inflation (see Figure S3.1). Removing *de novo* species did not impact this pattern of results (Tables S3.4, S3.5 and S3.6).

Table 3.1: Results of a general linear effects model testing the effect of conservation research effort on inflation. Model set-up: number of species added to primate genera since 1982 (dependent variable) vs. original number of species in each genus in 1982 (included as a linear (^{1}) and quadratic (^{2}) term), conservation research effort and region using Asia/Africa as the baseline (all independent variables), with observation ID included as a random effect. +P≤0.1; * P<0.05; ** P<0.01.

Effect	**Estimate**	**SE**	**z**	**p**
(Intercept)	0.904	0.220	4.107	<0.001**
Conservation research effort	-0.220	0.164	-1.342	0.180
Region Madagascar	0.581	0.338	1.721	0.085+
Region Neotropics	0.559	0.301	1.859	0.063+
log(# of species in 1982)^1	7.647	1.057	7.234	<0.001**
log(# of species in 1982)^2	-1.529	0.849	-1.802	0.072+

Continuous variables scaled to have a mean of zero and standard deviation of one

Table 3.2: Results of a general linear effects model testing the effect of genetics research effort on inflation. Model set up: the number of species added to primate genera since 1982 (dependent variable) vs. original number of species in each genus in 1982 (included as a linear (^{1}) and quadratic (^{2}) term), molecular genetics research effort and region using Asia/Africa as the baseline (all independent variables) where observation ID included as a random effect. +P≤0.1; * P<0.05; ** P<0.01.

Effect	**Estimate**	**SE**	**z**	**p**
(Intercept)	0.889	0.222	4.012	<0.001**
sqrt(Molecular genetics research effort)	-0.188	0.151	-1.247	0.212
Region Madagascar	0.646	0.334	1.932	0.053+
Region Neotropics	0.550	0.305	1.806	0.071+
log(# of species in 1982)^1	7.613	1.066	7.145	<0.001**
log(# of species in 1982)^2	-1.626	0.854	-1.904	0.057+

Continuous variables scaled to have a mean of zero and standard deviation of one

Table 3.3: Results of a general linear effects model testing the effect of diversification rate on inflation. Model set up: the number of species added to primate genera since 1982 (dependent variable) vs. original number of species in each genus in 1982 (included as a linear (^{1}) and quadratic (^{2}) term), diversification rate and region using Asia/Africa as the baseline (all independent variables) where observation ID included as a random effect. +P≤0.1; * P<0.05; ** P<0.01.

Effect	**Estimate**	**SE**	**z**	**p**
(Intercept)	0.623	0.288	2.166	0.030*
Diversification rate	0.132	0.186	0.712	0.477
Region Madagascar	0.819	0.398	2.056	0.040*
Region Neotropics	0.648	0.375	1.729	0.084+
log(# of species in 1982)^1	5.303	1.186	4.469	<0.001**
log(# of species in 1982)^2	-1.890	0.931	-2.030	0.042*

Continuous variables scaled to have a mean of zero and standard deviation of one

Inflation and Threat Score

We found some evidence for an association between inflation and threat score, where region and inflation interacted to predict threat scores for primate genera. For the baseline region Asia/Africa, genus-level threat score increased with inflation (β= 0.328; p= 0.005), and the associations between inflation and threat score in Madagascar and the Neotropics were significantly different from the association observed in the baseline region of Asia and Africa (β= -0.374; p= 0.004 and β= -0.402; p= 0.001, respectively; Table 3.4; Figure 3.2). Inflation was negatively associated with threat score in the Neotropics (β= -0.074; p= 0.004) while there was no significant association between inflation and threat score in Madagascar (β= -0.045; p= 0.422). Removing *de novo* species impacted this pattern of results in that the relationship observed in Madagascar no longer differed significantly from the baseline region (Table S3.7; Figure S3.2).

Table 3.4: Results of general linear effects model comparing genus threat score (dependent) to inflation (the proportional increase in species between 1982 and 2016), region using Asia/Africa as the baseline and inflation × region interaction term (independent) where family (nested within region) is a random effect. +P≤0.1; * P<0.05; ** P<0.01.

Effect	**Estimate**	**SE**	**z**	**p**
(Intercept)	-0.973	0.366	-2.656	0.008**
Inflation	0.328	0.117	2.812	0.005**
Region Madagascar	1.474	0.590	2.498	0.012*
Region Neotropics	0.060	0.646	0.093	0.926
Inflation: Region Madagascar	-0.374	0.130	-2.879	0.004**
Inflation: Region Neotropics	-0.402	0.120	-3.362	0.001**

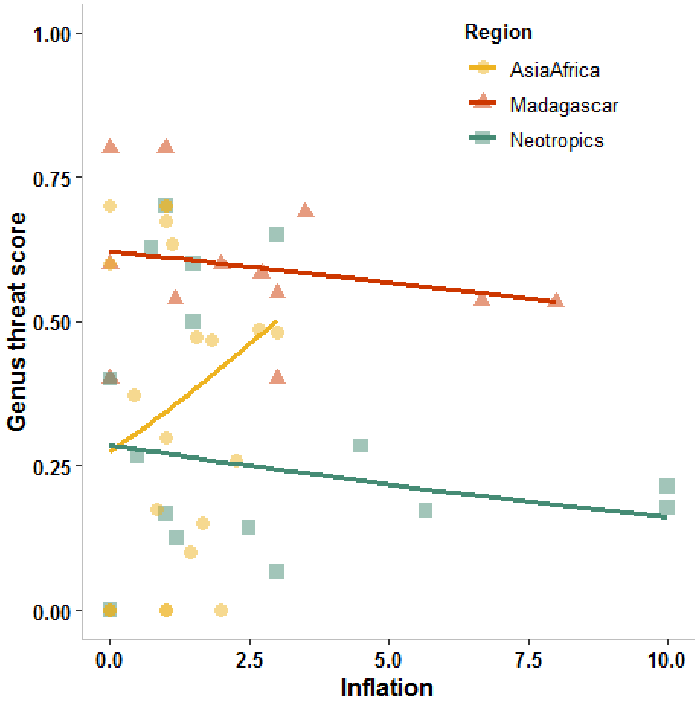

Figure 3.2: The interaction between inflation and region on threat score for genera of primates. Threat score approaching 1 denotes high risk of extinction and threat score approaching 0 denotes low risk. Points represent raw values with trend-lines estimated from a general linear mixed effects model. Points are transparent with darker values corresponding to overlapping points.

DISCUSSION:

Our results support neither a strong biological nor a strong interest-driven mechanism for variation in species designations across primate genera. If inflation captures true incipient speciation, we predicted that diversification rate might predict inflation. However, we found no evidence for this as diversification rate was not a significant predictor of inflation in our models. We also tested the prediction that splitting is motivated by conservation interest (Karl & Bowen, 1999; Isaac, et al., 2004) or by increasing molecular research within certain taxa, with for example more new species designations arising as finer molecular distinctions are made (Zachos, et al., 2013; Zachos & Lovari, 2013). However, we found no evidence that research effort in either of these areas was associated with inflation across taxa. We did find that the number of species originally listed in primate genera in 1982 shared a downward concave quadratic relationship with inflation in most models. This could indicate that inflation is being driven by something not captured by our models. Therefore, future studies could aim to elucidate the origins of this decelerating association.

We found that associations between inflation and threat score varied by region. Inflation among genera in Asia and Africa shared a positive association with threat score, while a negative association was observed in the Neotropics and no significant association was found for Madagascar. In regions like Madagascar where a large number of species have imperilled statuses, we might have expected a different relationship between threat score and inflation in comparison to Asia and Africa which contain fewer at risk species. Threatened species often have a small number of mature individuals left in the wild (Agapow, et al., 2004; Frankham, et al., 2012). Species that were already greatly imperilled prior to applications of the PSC might be less likely to present genetic or morphological variations among populations that are typically used as evidence to justify species-level splitting under the PSC (Zachos, et al., 2013). As a result, it is possible that genera already containing a very large number of threatened species prior to the PSC might not observe high rates of inflation due to their (already) small population sizes. We also observed that the trend in Madagascar was no longer significantly different from the baseline region if we removed *de novo* species descriptions. Figure S3.2 shows that the removal of *de novo* species greatly reduces estimates of inflation for Malagasy genera represented as being most inflated in Figure 3.2. This could indicate that primate diversity was previously underestimated in the most inflated Malagasy genera in Honacki et al. (1982)'s application of the BSC (perhaps as a result of being previously understudied). If so, some increases in species numbers across these genera may be a result of taxonomy of these genera catching up to other (perhaps better studied) primate clades. *De novo* species descriptions would likely capture these new discoveries, and these new species may not contribute to heightened threat status because they are not products of over-splitting. However, neither of the aforementioned explanations of regional differences would explain why inflation and threat score are negatively related across Neotropical genera.

An alternative explanation is that some distinguishing aspect of the biology of taxa from these regions influences the association between inflation and threat score. Neotropical primate genera listed by Honacki et al. (1982) that have undergone the greatest increase in species numbers under the PSC are *Callithrix*, *Callicebus* and *Aotus* (represented by the rightmost blue data points in Figure 3.2). Despite being split frequently these genera have relatively low threat scores, and these drive the observed negative association between inflation and threat score. Prior to applications of the PSC these genera contained few species (three, three and one, respectively; Honacki, et al., 1982) with geographic ranges spanning large portions of Central and South America. Conversely, genera with the highest inflation in Asia and Africa: *Tarsius*, *Nycticebus* and *Cercocebus* (represented by the rightmost yellow data points in Figure 3.2) – are geographically less widespread. Splitting of species in these genera may be expected to have a larger resulting effect on criteria considered in conservation listing (i.e. geographic range size and number of mature individuals left in the wild; Agapow, et al., 2004; Frankham, et al., 2012). Thus, splitting of large and geographically widespread genera (as has been the case in the Neotropics) may not lead to more imperilled statuses if resulting species still support large ranges and many individuals. If true, this would result in widespread genera with high rates of inflation having few imperilled species and thus explain the negative trend observed in the Neotropics (Figure 3.2). Meanwhile, in regions where splitting has occurred in geographically less widespread genera (e.g. Asia and Africa), splitting may result in increasingly imperilled statuses for already small populations. This is, of course, speculative, and future work should aim to tease apart the relationship between region, inflation and geographic range size. Overall, our results do not provide evidence for inflation driving threat priority among genera from Madagascar and the Neotropics, however, inflation may have some effect in Asia and Africa.

Our analyses do have some limitations. First, quantifying research effort of any kind is difficult due to the abundance of work published in different mediums. As such, our estimate of research effort in conservation and molecular genetics is indeed merely an estimate. More work should be done to determine if additional estimates of research bias can explain increases in species numbers. For instance, cumulative funding estimates from various sources (e.g. the IUCN, non-governmental organizations and regional governments) per taxa could be used as an additional or alternative measure of conservation interest. Second, it was necessary to remove eight non-monophyletic genera from our analyses that included diversification rate, leading to a reduction in statistical power for those analyses. Third, due to changes in Red List criteria and improved assessment efforts, we were not able to look at changes in threat score over time, and instead had to rely on present day threat status data. This means that while our study design allowed us to determine which groups are receiving conservation attention relative to inflation, we cannot make any inferences regarding the effect of inflation on threat scores through time. Future studies could attempt to map changes in listing criteria (e.g. number of individuals in the wild, geographic range size) for taxa that were well studied and reliably evaluated prior to the 1980s and document how measures for each of these criteria change as a result of splitting across species. Doing so could inform how inflation affects threat status and conservation activity on smaller scales (i.e. among closely-related species). Future studies could also look at the association of inflation and threat status over time using a more recent starting point (i.e. after 1982) to ensure all threat scores are assigned using comparable criteria.

Overall, we do not find support for biological processes (i.e. diversification rate) or human imposed bias (i.e. measures of research effort) driving inflation across primates. However, we do find an association between threat score and inflation that differs among regions that is consistent with the notion that inflation has stronger effects on threat score for genera encompassing smaller geographic ranges. Generally speaking, relying on species as the central unit of conservation and primary object of study behooves taxonomy to remain stable, while changing ideas about the concept of species makes taxonomy inherently unstable. We suggest that areas of research requiring consistent estimates of diversity (i.e. conservation) may benefit from either (i) adopting species criteria which eliminate the PSC criteria that may be particularly subject to human-induced bias (e.g. molecular distinctions based on few diagnostic sites in the mitochondrial cytochrome b gene; Zachos, et al., 2013) or, for applied conservation specifically; (ii) shifting more resources toward regional management efforts that are less likely to be influenced by changing species designations. It is well-known that closely related species are more similar to one another than they are to more distantly related taxa. Thus, treating all species independently and of equal weights in conservation listing may not lead to desired outcomes. As of 2016, approximately 60 percent of all primate species were threatened with extinction according to the IUCN Red List of Threatened Species (Estrada, et al., 2017), making it imperative that conservation efforts are spent wisely to ensure optimal conservation of primate biodiversity writ large.

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Data and code accompanying the manuscript will be made available on publication through Dryad or a similar repository.

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“Predictors of Taxonomic Inflation and its Role in Primate Conservation” – Supplementary Material

SUPPLEMENTARY METHODS:

Research Effort

Estimates of research effort for each genus listed by Honacki et al. (1982) in the fields of conservation and molecular genetics were determined through an extensive literature review of papers in the Web of Science Core Collection (Tables S3.1, S3.2 and S3.3). The search included studies published between 1983 – the year the ‘phylogenetic species concept’ (PSC) was first proposed, and 2016 – the year the IUCN species list and associated data documented in Estrada et al. (2017) were collected. In this study we used the 50 genera listed in Honacki et al. (1982), many of which have since been further separated into multiple genera. Thus, when appropriate we included new genera names in the literature search in addition to those listed by Honacki et al. (1982) to ensure our search returned all relevant papers (Table S3.3). Four genera included names that were associated with unrelated topics or doubled as a common name for species in other genera (e.g. genus *Lemur*). For these genera, all possible species names were added to the search to prevent irrelevant hits (Table S3.3).

To obtain papers in the field of conservation we searched the genus name/names AND “conservation”. To obtain papers in the field of molecular genetics we searched the genus name/names AND the following terms: "mitochondrial DNA" OR "barcoding" OR "bar-coding" OR "cytochrome b" OR "phylogeography" OR "microsatellites" OR "micro-satellites" OR "population genetics" OR (species AND genetics) OR (taxonomy AND genetics) OR "SNP". All hits from these initial searches were reviewed on a case by case basis and NOT terms were created to eliminate unrelated hits (see Tables S3.1 and S3.2). We did this rather than manually removing records from the research effort so that searches could be replicated. We reran searches on a subset of genera to confirm that this procedure did not eliminate relevant papers. Searches for some genera returned hits that were not relevant to the genus of interest, but were relevant to others in which case NOT terms specific to each genus were included in the search (see Table S3.3). When it came to molecular genetics, we were interested in the contribution of new molecular work that could lead to splitting, therefore, results in this search were filtered by articles and letters to exclude material like reviews that would not make such contributions. Once the final search terms were established, the searches were repeated with the full list of NOT terms and the number of results returned for each genus using these terms was recorded, providing us with a comprehensive estimate of research effort on each topic per genus. These searches can be replicated in the Web of Science databases using the terms included in Tables S3.1, S3.2 and S3.3.

Table S3.1: Terms used for literature review to obtain an estimated research effort in the field of conservation per genera in Honacki et al. (1982) between 1983 and 2016. Terms in inverted commas are those entered into the search engine. “Genus A”, Genus B” etc. represent the alternative genus names presented in Table S3.3. Asterisk in search term denotes a wildcard character representing any group of characters, including no character.

Topic	**Search**
Conservation	**Database: Web of Science Core Collection** **Year Range: 1983-2016** _"GenusA" OR "GenusB"_ **[Search field: TOPIC]** **AND** "Conservation" **[Search field: TOPIC]** **NOT** "Pathalog*" OR "Seminal" OR "Semen" OR "Protein" OR "Numerical Competence" OR "*sterone" OR "Memory" OR "Chromosome" OR "DNA" OR "Molecul*" OR "Euterpe edulis" OR "Mico-particles" OR "Gut passage time" OR "MHC" OR "PAXBP1" OR "Cathemerality" OR "Arabic" OR "Vomeronasal Receptor" OR "CT Repeats" OR "Butterfly" OR "microRNA" OR "Mirrors" OR "Kinematics" OR "geogenetic" OR "archaeology" OR "monuments" OR "quantum" OR "political crisis" OR "neutral theory" OR "baobabs" OR "tor macrolepis" OR eichhornia crassipes" or "ethnobotany" OR "movement corridors" OR "null errors" OR "skeletal indices" OR "resource defense" OR "energetic demand" OR "chromosomes" OR "floristic composition" OR "sickness behavior" OR "appearance-reality" OR "object permanence" OR "number processing" OR "quantity judgement" OR "quantity discrimination" OR "visual illusions" OR "oil extraction" OR "object manipulation" OR "piagetian" OR "personality" OR "forest regeneration" OR "Bergmann's Rule" OR "female dominance" OR "publication" OR "rhinoceros" OR "photopigments" OR "opsin" OR "FSH" OR "IFITM10" OR "IFITM5" OR "energy expenditure" OR "myopia" OR "fovea" OR "museum" OR "cacao cultivation" OR "cabruca plantation" OR cabrucas" OR "discrimination learning" OR "architecture" OR "tocoplasma goondii" OR "dung beetle" OR "meat science" OR "year span" OR "los toxtlas" OR "lipid droplets" OR "nephropathy" OR "battelle" OR "luncheon address" OR "fruit-eating fish" OR "parrots" OR "nest fate" OR "bird community" OR "retinal development" OR "edinger-westphal nucleus" OR "fur mites" OR "alliances" OR "energy metabolism" OR "nucleotide sequence" OR "transcriptional effector" OR "lymphotropic" OR "RNA secondary" OR "ischemic stroke" OR "lifetime achievement award" OR "number representation" OR "metabolic activity" OR "natureculture" OR "fruit fly" OR "pluripotent stem cells" OR "locus ERVWE1" OR "duffy blood group system" OR "p58" OR "coraco-clavicular joint" OR "kaya" OR "Shannon-Weiner index" OR "kisspeptin" OR "linkage map" OR "killer whales" OR "female athlete" OR "acetyl salicylic acid" OR "periaqueductal gray" OR "DQA1" OR "dentate granule cells" OR "descartes" OR "haplotype network analysis" OR "OCOM-6" OR "Participatory risk mapping" OR "Fribourg-Blanc genome" OR "browser" OR "atherosclerosis" OR "rapid lateral flow" OR "VBEKAP" OR "super-eruption" OR "fossil mammals" OR "evolution of dance" OR "biate tribe" OR "antiphonal songs" OR "energy conservation" OR "strongyle egg excretion" OR "divergence date" OR "phylogenic niche conservation" OR "spatial autocorrelation" OR "conservation of heat" OR "local terrestrial tradition" OR "first fossil record" OR "nonhuman primate amygdala" OR "skin cell proliferative potential" OR "nuclear hormone receptors" OR "prehistoric populations" OR "last glacial maximum" OR "prehistoric demographic event" OR "sugar-rich fruit pulp" OR "quantity conservation" **[Search field: TOPIC]** **AND** _*Insert 'Species Names (if applicable)' – see Table S3.3*_ **[Search field: TOPIC]** **NOT** _*Insert 'Genus-specific NOT Terms (if applicable)' – see Table S3.3*_ **[Search field: TOPIC]**

Table S3.2: Terms used for literature review to obtain an estimated research effort in the field of molecular genetics per genera in Honacki et al. (1982) between 1983 and 2016. Terms in inverted commas are those entered into the search engine. “Genus A”, Genus B” etc. represent the alternative genus names presented in Table S3.3. Asterisk in search term denotes a wildcard character representing any group of characters, including no character.

Topic	Search
Molecular genetics	**Database: Web of Science Core Collection** **Year Range: 1983-2016** "_GenusA_" OR "_GenusB_" **[Search field: TOPIC]** **AND** "Mitochondrial DNA" OR "Barcoding" OR "Bar-coding" OR "cytochrome b" OR "Phylogeography" OR "Microsatellites" OR "Micro-satellites" OR "Population Genetics" OR (Species AND Genetics) OR (Taxonomy AND Genetics) OR "SNP" **[Search field: TOPIC]** **NOT** "Disease" OR "Virus" OR "Parasite" OR "Single Origin" OR "Color Vision" OR "Colour Vision" OR "Cyprinine fishes" OR "Schizothorax" OR "Ground boa*" OR "Tenrecidae" OR "Climate-Change" OR "Galaxy Tools" OR "Primatology in China" OR "Hand morphology" OR "Human Genome" OR "Bifidobacteri*" OR "Plasmodium" OR "Spondias" OR "Vestigial structures" OR "Social behavior, reproductive strategies" OR "Tuberculosis" OR "Social dynamics of male" OR "Skull shape" OR "Diet diversity" OR "Functional cues" OR "Video stimuli" OR "Human specific" OR "Carrion fly" OR "Arctocephalus" OR "Bushmeat" OR "Elephants" OR "Human-Population Genetics" OR "Antimicrobial" OR "Vertebral formulae" OR "HIV-1*" OR "Genotoxicity" OR "Habitat fragmentation" OR "Primer design" OR "Plant DNA" OR "Parasitic lice" OR "Primates of Gashaka" OR "Marmot" OR "Captive breeding" OR "Captive-bred" OR "Behavioral genetics" OR "Toxicolo*" OR "Pharmacolo*" OR "Blood type" OR "Tissue expression" OR "Behavioral plasticity" OR "Medicine" OR "Immuno*" OR "Infection" OR "Reproductive efficiency" OR "Pinworm" OR "Diffusion tensor" OR "Female homosexual behavior" OR "Cryodamage" OR "Adult mortality" OR "iSCNT" OR "Resources for genetic management" OR "Hearing loss" OR "Macular degeneration" OR "Biomedical Information Research Network" OR "Korean cattle" OR "Sinus volume" OR " Alcoholism" OR "Dominance rank" OR "Therapeutic cloning" OR "Literature survey" OR "Grasshopper*" OR "Leptin" OR "Macaca-rabbit" OR "Nitrate tolerance" OR "Human evolution" OR "South American rodents" OR "hepatic CYP2C" OR "Baroreceptor-related neurons" OR "Nasalis posterior" OR "Salamander" OR "Gasterophilus nasalis" OR "Grooming bouts" OR "Rainfall" OR "Craniofacial" OR "Diabetes" OR "Sexual size dimorphism" OR "Mesopithecus" OR "Hybrid origin of the kipunji" OR "Schistosoma mansoni" OR "Limb bones" OR "Acinonyx jubatus" OR "Early life mortality" OR "Human pigmentation" OR "Modern Humans" OR "Balsaminaceae" OR "Meat consumption" OR "Tracking of a gorilla death" OR "Antrocaryon klaineanum" OR "ATP synthetase in orangutan" OR "Human mitochondrial DNA" OR "Maximal lifespan" OR "Mummified baboon" OR "Kin bonds" OR "Kinship" OR "Bipolar disorder" OR "Cultural differences" OR "Sex-specific dispersal" OR "Nest-building" OR "Vocalizations" OR "Neuroticism" OR "Stone handling" OR "Bowhead whale" OR "Canis rufus" OR "Caledonian crows" OR "Paternity" OR "Black rhinoceros" OR "Eptesicus fuscus" OR "4q syndrome" OR "Monozygotic twin" OR "Autism spectrum" OR "Skeletal analysis" OR "Furcifer lateralis" OR "Long-fingered bats" OR "Jomon period" OR "Cranial nerve perforations" **[Search field: TOPIC]** **NOT** "Toxicolo*" OR "Pharmacolo*" OR "Immuno*" OR "Medicine" **[Search field: PUBLICATION NAME]** **AND** *_Insert 'Species Names (if applicable)' – see Table S3.3_* **[Search field: TOPIC]** **NOT** *_Insert 'Genus-specific NOT Terms (if applicable)' – see Table S3.3_* **[Search field: TOPIC]** **Refined by: Article or Letter**

<u>Table S3.3:</u> Genera names included in each literature review for research effort with species names and additional NOT terms included in each search where applicable. Genus names were matched to Honacki et al. (1982) from the IUCN species list documented in Estrada et al. (2017). Additional alternative genus names were obtained from the IUCN Red List of Threatened Species (2019). Asterisk in search term denotes a wildcard character representing any group of characters, including no character.

Genus Name/Names	**<u>AND</u> Species Names** *(if applicable)*	**Molecular genetics genus-specific <u>NOT</u> Terms** *(if applicable)*	**Conservation genus-specific <u>NOT</u> Terms** *(if applicable)*
"Allocebus"			
"Cheirogaleus"			
"Microcebus" OR "Mirza"		"Saguinus mystax" OR "Sportive lemurs (Lepilemur, Primates)" OR "Bornean orang-utans (Pongo pygmaeus)" OR "Black-and-white ruffed lemur"	
"Phaner"			
"Hapalemur" OR "Prolemur"			
"Lemur" OR "Eulemur"	"albifrons" OR "cinereiceps" OR "collaris" OR "coronatus" OR "fulvus" OR "macaco" OR "flavifrons" OR "mongoz" OR "rubriventer" OR "rufus" OR "sanfordi" OR "sanfordi" OR "albocollaris" OR "mayottensis" OR "petterus" OR "catta" OR "rufifrons"	"Microcebus" OR "Mouse lemur"	"divergence from other mouse lemur clades" OR "preferred habitat type of Prolemur simus" OR "the Critically Endangered greater bamboo lemur Prolemur simus" OR "(Tarsius spectrum) in Tangkoko Nature Reserve" OR "presence of Prolemur simus at 18 sites" OR " critically endangered greater bamboo lemur Prolemur simus" OR "(Allocebus trichotis) to determine habitat needs" OR "the third species, Microcebus mittermeieri" OR "the third species, Microcebus mittermeieri" OR "205 Microcebus ravelobensis" OR "focal individuals of the weasel sportive lemur" OR "low reproduction rate for Lepilemur edwardsi" OR "Avahi occidentalis extends north and east of the Betsiboka River" OR "genetic structure of the solitary grey mouse lemur" OR "physiological parameters in healthy wild Varecia populations" OR "uneven distribution pattern of the golden-brown mouse lemur" OR "subspecies of the single species Varecia variegata" OR "First discovery of the hairy-eared dwarf lemur (Allocebus trichotis)" OR " almost extinct lemur species, Allocebus trichotis" OR "large breeding center for ruffed lemurs (Varecia variegata)" OR "Rediscovery of Allocebus-Trichotis Gunther"

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"Varecia"		"Mouse lemur"	"Cheirogaleus" OR "Lemur" OR "Canarium" OR "chimpanzee"
"Lepilemur"			
"Indri"			
"Avahi or Lichanotus"			
"Propithecus"		"Lemur catta"	"Ateles" OR "Chiropotes"
"Daubentonia"			
"Arctocebus"			
"Loris"	"tardigradus" OR "lydekkerianus"		"Mirza" OR "Nycticebus"
"Nycticebus"			
"Perodicticus"			
"Galago" OR "Galagoides" OR "Paragalago" OR "Sciuricheirus" OR "Euoticus"	"elegantulus" OR "pallidus" OR "demidoff" OR "thomasi" OR "orinus" OR "rondoensis" OR "granti" OR "cocos" OR "zanzibaricus" OR "senegalensis" OR "gallarum" OR "moholi" OR "matschiei" OR "alleni" OR "alleni cameronensis" OR "gabonensis" OR "makandensis" OR "demidovii" OR "inustus" OR "tonsor" OR "apicalis" OR "talboti" OR "pallida" OR "demidovii" OR "udzungwensis" OR "zanzibaricus" OR "nyasae" OR "bradfieldi" OR "cameronensis"		
"Otolemur"			

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"Tarsius" OR "Carlito" OR "Cephalopachus"		
"Callimico"	"Owl monkey*"	
"Cebuella"		"Alouatta"
"Callithrix" OR "Mico" OR "Calibella"	"Owl monkey*"	"Saguinus" OR "Lemur" OR "litter size of wild cotton-top tamarins" OR "reproductive potential of wild- and captive-born golden-headed lion tamarins" OR "two tamarin species (Saguinus fuscicollis and S. oedipus)"
"Leontopithecus"		"Saguinus" OR "threats to populations of Alouatta guariba clamitans "
"Saguinus" OR "Leontocebus"	"Leontopithecus caissara" OR "Rondon's Marmoset" OR "Cebus apella paraguayanus" OR "skull of Catarrhini" OR "masticatory apparatus of Galagos" OR "cranial diversification of neotropical monkeys"	"cuxius formed associations" OR "breast height, 42.2 +/- 21.9 cm" OR "(Callicebus cupreus) to adapt to forest edges" OR "Callimico goeldii is a rare primate" OR "dung in latrines" OR "matrix diagonalization" OR "Sleeping Sites of Rhinopithecus brelichi" OR "Leontopithecus rosalia Linnaeus, 1766" OR "night monkeys Aotus vociferans" OR "Habitat use by Chiropotes satanas utahicki " OR "20 Alouatta species and subspecies"
"Alouatta"	"Owl monkey*" OR "Hooded capuchin" OR "Squirrel monkey"	"Rhinopithecus" OR "Lemur" OR "Harpia" OR "Coleoptera" OR "Eulemur" OR "Scarabaeidae" OR "Chiropotes" OR "Hylobates" OR "population of white-bellied spider monkeys (Ateles belzebuth)" OR "1 adult and subadult brown spider monkeys " OR "ability of spider (Ateles geoffroyi)" OR "Ateles marginatus, is endemic to Brazilian Amazon" OR "A. geoffroyi live in highly fragmented landscapes"
"Aotus"	"Woolly monkey" OR "Saguinus" OR "MHC Polymorphisms"	
"Ateles"		"Rhinopithecus" OR "Papio" OR "Cebidae" OR "Inga" OR "(Alouatta palliates, Alouatta pigra and" OR "Demographic features of Alouatta pigra populations" OR "20 Alouatta species and subspecies"

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"Brachyteles"	"Howler monkey*"	"Chiropotes" OR "Tapir" OR "brown howler monkey (Alouatta clamitans)" OR "brown-howler-monkey Alouatta guariba clamitans " OR "20 Alouatta species and subspecies"
"Cacajao"		"Pitheciid"
"Callicebus" OR "Cheracebus" OR "Plecturocebus"		"Pitheciid"
"Cebus" OR "Sapajus"	"Saguinus mystax" OR "Howler monkey*"	"Papio" OR "calithrix" OR "Presbytis" OR "Harpia" OR "Dasypus" OR "Leopardus" OR "Macaca" OR "9 healthy captive ring-tailed lemurs" OR "cuxius (genus Chiropotes) form" OR "northern bearded sakis (Chiropotes sagulatus) in Guyana" OR "recently-discovered titi, Callicebus coimbrai" OR "last in-depth review of Saimiri biology" OR "L. rosalia is a legitimate seed disperser" OR "endemic Chiropotes satanas utahicki" OR "20 Alouatta species and subspecies" OR "Central American squirrel monkeys, Saimiri oerstedi"
"Chiropotes"		"Pitheciid" OR "Pitheciinae"
"Lagothrix" OR "Oreonax"		"Nomascus" OR "Burseraceae" OR "Varecia" OR "Brachyteles" OR "Chiropotes"
"Pithecia"		"20 Alouatta species and subspecies"
"Saimiri"	"Colobine monkeys" OR "Saguinus" OR "Owl monkey*" OR "Howler monkey*"	"rhesus monkeys (Macaca mulatta) succeeded" OR " 20 Alouatta species and subspecies"
"Allenopithecus"		
"Cercocebus" OR "Lophocebus"	"Rungwecebus"	"drill population ecology"
"Cercopithecus" OR "Allochrocebus" OR "Chlorocebus" OR "Miopithecus"		"Alouattta" OR "Macaca" OR "Canis" OR "Erythrocebus" OR "endemic Udzungwa red colobus (Procolobus gordonorum)" OR "drills on 25 occasions" OR "conflict in the guanaco (Lama guanicoe)" OR "15,000 Papio hamadryas hamadryas" OR "gorilla nest-site densities" OR "leopard was ascertained only "

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"Erythrocebus"		
"Colobus" OR "Procolobus" OR "Piliocolobus"		"Chiropotes" OR "Eulemur" OR "Callicebus" OR "Presbytis" OR "Simias" OR "Semnopithecus" OR "Rhinopithecus" OR "Trachypithecus" OR "Lepilemur" OR "village-dwelling populations (Lagwa and Akpugoeze)" OR "cercopithecid conservation" OR "Supplementation in Black howlers (Alouatta pigra)" OR " Boutourlini's blue monkeys (Cercopithecus mitis boutourlinii)" OR "Foraging Behavior of Red Howler Monkeys" OR "drills on 25 occasions" OR "Cercocebus sanjei in the Udzungwa Mountains"
"Macaca"	"Rhinopithecus roxella*" OR "Rhinopithecus bieti" OR "Infra-order catarrhini" OR "Southern African baboons" OR "Hylobates lar" OR "Wild orangutans" OR "captive group of chimpanzees (Pan troglodytes)" OR "Cercopithecus aethiops aethiops" OR "wild living community of Bonobos (Pan paniscus)" OR "Bolivian squirrel monkeys (Saimiri boliviensis)" OR "Captive lowland gorillas and orangutans" OR "Population genetics in Eulemur"	"Rhinopithecus" OR "Neofolis" OR "Callithrix" OR "Cercopithecine" OR "Propithecus" OR "Cebus" OR "Theropithecus" OR "indian giant squirrel" OR "terrestriality in orangutans (Pongo spp.)" OR " zoo-housed Javan gibbons (Hylobates moloch)" OR "abituated orangutans (Pongo pygmaeus morio)" OR "crop-raiding by orangutans (Pongo abelii)" OR "discrimination skills of chimpanzees " OR "Panthera pardus have a catholic diet " OR "BFMS also contain C. vellerosus"
"Nasalis" OR "Simias"		"Rhinopithecus" OR "Cercopithecidae"
"Papio" OR "Mandrillus"		"Cercopithecine" OR "Prosopis" OR "West African savanna chimpanzees (Pan troglodytes verus)" OR "parasites of savanna chimpanzees (Pan troglodytes schweinfurthii)" OR "(Pan troglodytes) misperceived food" OR "Endangered Lion-Tailed Macaques (Macaca silenus)" OR "Cercocebus sanjei in the Udzungwa Mountains" OR "infecting greater spot-nosed monkeys (Cercopithecus nictitans)" OR "Tibetan macaques (Macaca thibetana) at Mt. Emei"
"Presbytis" OR "Semnopithecus" OR "Trachypithecus"	"Sichuan snub-nosed monkeys"	"Andrias" OR "Pongo" OR "Saimiri" OR "Pardofelis" OR "indian giant squirrel" OR "Simias concolor (simakobu or pig-tailed langur)" OR "(Rhinopithecus bieti) 14" OR "Food habits of tigers Panthera tigris"

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"Pygathrix" OR "Rhinopithecus"			"Endangered Shortridge's capped langur Trachypithecus shortridgei" OR "(Presbytis rubicunda) in Sabangau" OR "Responses of Cao Vit Gibbon (Nomascus Nasutus)" OR "(Trachypithecus delacouri) in Van Long Nature Reserve"
"Theropithecus"		"Macaca arctoides"	
"Hylobates" OR "Hoolock" OR "Nomacus" OR "Nomascus" OR "Symphalangus" OR "Brunopithecus"		"Cercopithecidae" OR "New World Monkey"	"Neofelis" OR "Saimiri" OR "Garcinia" OR "Choerospondias" OR "(Trachypithecus crepusculus) in the Wuliang Mountains" OR "one wild troop of northern pigtailed macaques "
"Gorilla"		"Wild chimpanzees (Pan troglodytes)" OR "Unhabituated chimpanzees" OR "Leontopithecus caissara" OR "White-handed gibbon" OR "Common gibbon"	"Hylobates" OR "Alouatta" OR "Neofelis" OR "captive hamadryas baboons (Papio hamadryas hamadryas)" OR "Cercopithecus mitis kandt i, the golden monkey"
"Pan"	"paniscus" OR "troglodytes"	"natural populations of orang-utan (Pongo pygmaeus)" OR "Mitochondrial DNA diversity in gorillas" OR "Barbary macaques (Macaca sylvanus)"	"Leontopithecus" OR "Chlorocebus" OR "cercopithecids" OR "Japanese macaques (Macaca fuscata yakui) " OR "Vulnerable owl-faced monkey Cercopithecus hamlyni" OR "(Trachypithecus phayrei crepusculus) in Phu Khieo" OR " capuchin monkeys' quantification"
"Pongo"		"Brown Spider Monkey" OR "Gorilla systematics" OR "Tooth morphology" OR "White-handed gibbon"	"Cebus" OR "Tapiridae" OR "Trypanosoma " OR "Nigerian/Cameroon chimpanzee (Pan troglodytes ellioti)" OR "chimpanzees' food preferences" OR "(Pan troglodytes) misperceived food" OR "Chimpanzees made judgments" OR "chimpanzees (Pan troglodytes) discriminate"

SUPPLEMENTARY RESULTS:

Predictors of Inflation (removing de novo species descriptions from inflation estimates)

Table S3.4: Results of a general linear effects model testing the effect of conservation research effort on inflation. Model set-up: the number of species added to primate genera since 1982 excluding those determined to have *de novo* species descriptions (dependent variable) vs. original number of species in each genus in 1982 (included as a linear (^{1}) and quadratic (^{2}) term), conservation research effort and region using Asia/Africa as the baseline (all independent variables), with observation ID included as a random effect. +P≤0.1; * P<0.05; ** P<0.01.

Effect	**Estimate**	**SE**	**z**	**p**
(Intercept)	0.873	0.214	4.084	<0.001**
Conservation research effort	-0.157	0.156	-1.011	0.312
Region Madagascar	0.237	0.337	0.702	0.483
Region Neotropics	0.597	0.288	2.071	0.038*
log(# of species in 1982)^1	7.178	1.017	7.060	<0.001**
log(# of species in 1982)^2	-1.413	0.821	-1.722	0.085+

Continuous variables scaled to have a mean of zero and standard deviation of one

Table S3.5: Results of a general linear effects model testing the effect of genetics research effort on inflation. Model set up: the number of species added to primate genera since 1982 excluding those determined to have *de novo* species descriptions (dependent variable) vs. original number of species in each genus in 1982 (included as a linear (^{1}) and quadratic (^{2}) term), molecular genetics research effort and region using Asia/Africa as the baseline (all independent variables) where observation ID included as a random effect. +P≤0.1; * P<0.05; ** P<0.01.

Effect	**Estimate**	**SE**	**z**	**p**
(Intercept)	0.867	0.213	4.074	<0.001**
sqrt(Molecular genetics research effort)	-0.173	0.145	-1.194	0.232
Region Madagascar	0.281	0.330	0.851	0.395
Region Neotropics	0.585	0.289	2.025	0.043*
log(# of species in 1982)^1	7.239	1.011	7.160	<0.001**
log(# of species in 1982)^2	-1.449	0.818	-1.772	0.076+

Continuous variables scaled to have a mean of zero and standard deviation of one

Table S3.6: Results of a general linear effects model testing the effect of diversification rate on inflation. Model set up: the number of species added to primate genera since 1982 excluding those determined to have *de novo* species descriptions (dependent variable) vs. original number of species in each genus in 1982 (included as a linear (^{1}) and quadratic (^{2}) term), diversification rate and region using Asia/Africa as the baseline (all independent variables) where observation ID included as a random effect. +P≤0.1; * P<0.05; ** P<0.01.

Effect	**Estimate**	**SE**	**z**	**p**
(Intercept)	0.603	0.274	2.204	0.028*
Diversification rate	0.099	0.174	0.567	0.570
Region Madagascar	0.406	0.391	1.040	0.298
Region Neotropics	0.708	0.352	2.011	0.044*
log(# of species in 1982)^1	4.877	1.126	4.330	<0.001**
log(# of species in 1982)^2	-1.830	0.887	-2.064	0.039*

Continuous variables scaled to have a mean of zero and standard deviation of one

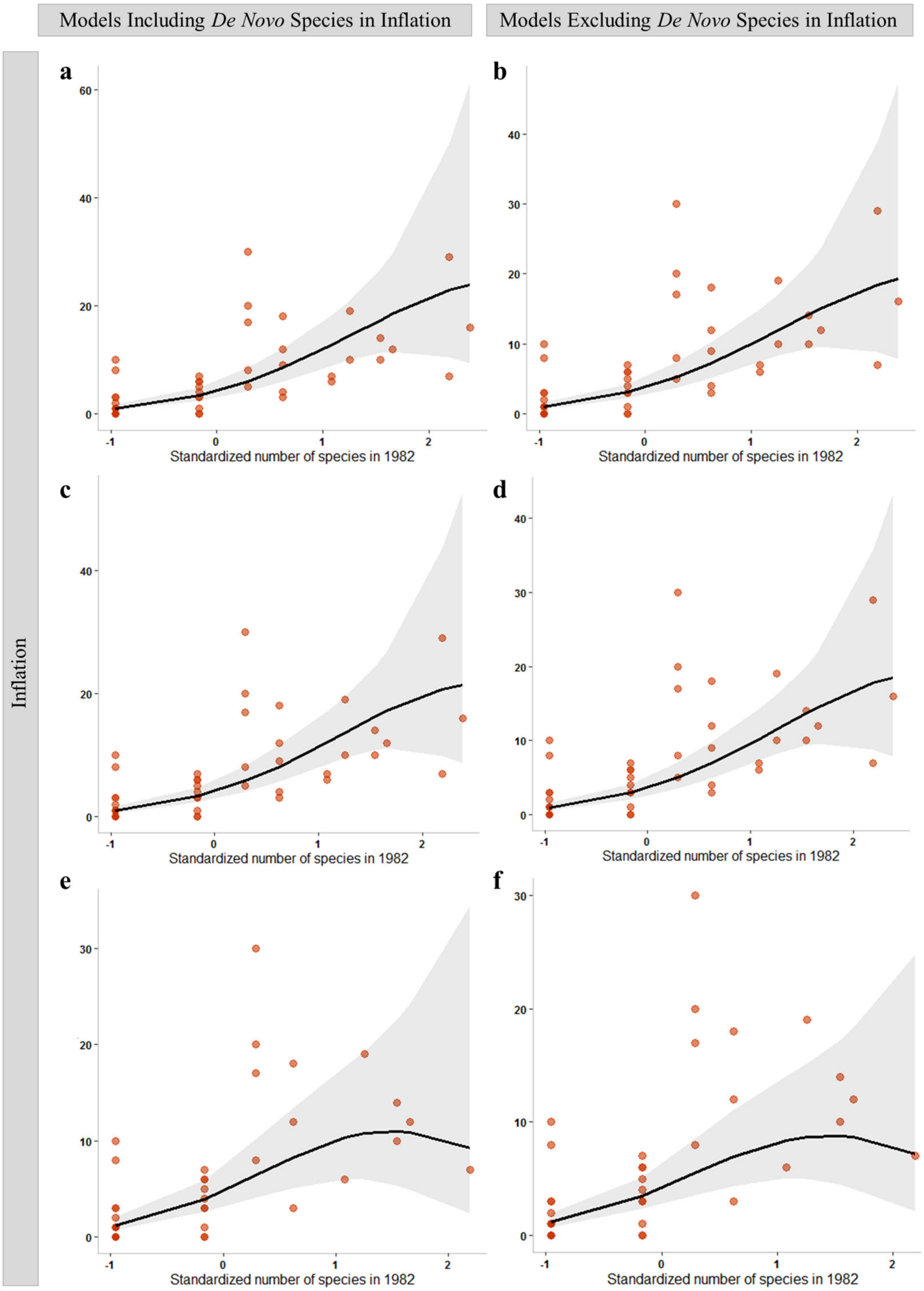

Figure S3.1: The modelled relationship between inflation (the number of species added to a genus since 1982) and the standardized (ln x/(1sd)) number of species originally listed in each primate genus in 1982 from general linear effects models testing the effect of (a-b) conservation research effort, (c-d) genetics research effort, and (e-f) diversification rate on inflation. Grey shading indicates standard error. See main text for further details on how models were fit.

Inflation and Threat Score (removing de novo species descriptions from inflation estimates)

Table S3.7: Results of general linear effects model comparing genus threat score (dependent) to inflation (the proportional increase in species between 1982 and 2016 excluding those determined to have *de novo* species descriptions), region using Asia/Africa as the baseline and inflation × region interaction term (independent) where family (nested within region) is a random effect. +P≤0.1; * P<0.05; ** P<0.01.

Effect	**Estimate**	**SE**	**z**	**p**
(Intercept)	-0.829	0.355	-2.339	0.019*
Inflation	0.266	0.114	2.327	0.020*
Region: Madagascar	1.058	0.613	1.726	0.084+
Region: Neotropics	-0.090	0.639	-0.140	0.889
Inflation1: Region Madagascar	-0.222	0.176	-1.260	0.208
Inflation1: Region Neotropics	-0.342	0.118	-2.910	0.004**

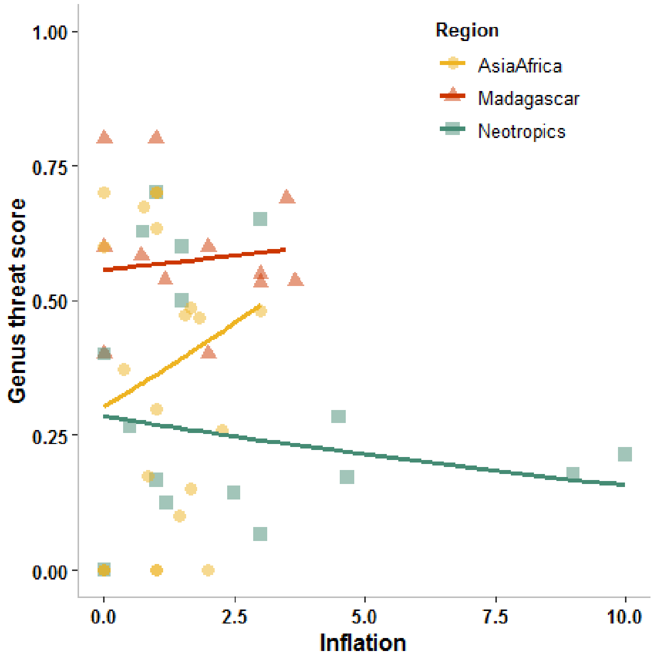

Figure S3.2: The interaction between inflation excluding *de novo* species descriptions and region on threat score for genera of primates. Threat score approaching 1 denotes high risk of extinction and threat score approaching 0 denotes low risk. Points represent raw values with trend-lines estimated from a general linear effects model. Points are transparent with darker values corresponding to overlapping points.

SUPPLEMENTARY REFERENCES:

Estrada, A., Garber, P. A., Rylands, A. B., Roos, C., Fernandez-Duque, E., Di Fiore, A., ... & Rovero, F. (2017). Impending extinction crisis of the world's primates: Why primates matter. Science Advances, 3: e1600946.

Honacki, J. H., Kinman, K. E., & Koeppl, J. W. (1982). Mammal species of the world; a taxonomic and geographic reference. Allen Press, Inc. and Association of Systematic Collections, Lawrence.

The IUCN Red List of Threatened Species. (2019). Retrieved from https://www.iucnredlist.org/ [accessed 2 April 2019].

CHAPTER 4: GENERAL DISCUSSION

In my thesis I have explored the determinants of species diversity across primate clades, emphasizing the role of both evolutionary processes and naming conventions in driving variation. I have additionally discussed the possible consequences of these two related but also potentially confounding determinants of species diversity for fields of biology which rely on species as primary objects of study. Here, I will briefly review the major findings of my research, provide some cautionary notes on the use of species as it pertains to the relevant areas of study, highlight the implications of my work and recommend some directions for future research not discussed in earlier chapters.

MAJOR FINDINGS:

In Chapter 2 I focused on the evolutionary consequences of behavioural flexibility, specifically examining whether behavioural flexibility promotes primate diversification while also attempting to control for systematic biases which may influence diversification rate estimates. In Chapter 3 I investigated determinants of taxonomic inflation following applications of the 'phylogenetic species concept' (PSC) in primate taxonomy, and went on to explore the potential consequences for applied conservation. I found that behavioural measures of behavioural flexibility (i.e. innovation and social learning) were positively associated with some but not all diversification measures. The strongest associations between these behavioural measures and diversification rate were found deeper in the primate tree which may support a role for behavioural flexibility enhancing lineage persistence, as opposed to driving speciation events. Turning to inflation, I found that neither biological processes (i.e. diversification rate) nor interest-driven mechanisms (i.e. measures of research effort) predicted inflation among primate genera. However, a decelerating association shared by the number of species originally listed in primate genera in 1982 and inflation could point to influences on inflation not captured in these tests. When assessing how inflation interacted with threat scores (i.e. extinction risk), I found that associations between inflation and threat score varied by region, sharing a positive association in Asia and mainland Africa, no detectable association in Madagascar, and a negative association in the Neotropics. These regional differences may indicate that other factors (e.g. the total geographic range size of genera) impact how inflation affects threat score. Together, these chapters provide useful insights into the factors influencing described species diversity across primate taxa, and meaningful considerations for the use of 'species' across biological disciplines.

ON THE USE OF SPECIES:

Species are often assumed to reflect biological diversity (Clarke, 1975; Wilson, 1988). Acting as the lowest level of biological unity (Linnaeus, 1753; Svenson, 1953), species have become primary objects of study across many fields of biology (Zink & McKitrick, 1995; De Queiroz, 2005). However, for primates, the number of species added to genera under the PSC is not proportional to the number of species originally listed in each genera under the BSC. This indicates that not only ultimate (total species richness), but also relative species richness changes across taxa based on which species concept is employed i.e. a primate genus that is speciose relative to other genera under the BSC may not be speciose relative to other genera under the PSC and vice versa. Notably, both ultimate and relative changes in species richness across taxa can pose problems for fields relying on species as reliable units of comparison.

Species as an Evolutionary Metric

In Chapter 2 I discussed the potential biases associated with changing species definitions when it comes to estimating diversification rate – especially with regards to recent applications of the PSC. In particular, different species definitions result in different estimates of species diversification (Zink & McKitrick, 1995), potentially influencing the results of comparative macroevolutionary studies such as Chapter 2. For instance, genus *Leontopithecus* (Lesson, 1840) contains one biological species (*L. rosalia*) with four subspecies according to Honacki et al. (1982)'s application of the 'biological species concept' (BSC; see Chapter 3). Therefore, following methods in Magallon & Sanderson (2001) the subspecific diversification rate of this species would be estimated as ln(4)/ 15.03 taxa per million years (my), where 15.03 my is the stem age of *L. rosalia* (Arnold, et al., 2010). However, following the emergence of mitochondrial and phylogenetic evidence provided in Perez-Sweeney et al. (2008), all *L. rosalia* subspecies have since been elevated to the full species status in modern species lists (e.g. see IUCN/SSC Primate Specialist Group, 2018). Thus, when referencing modern species lists, *L. rosalia* contains no subspecific diversity and genus *Leontopithecus* quadruples in species diversity compared to Honacki et al. (1982). This illustrates that overall estimates of diversification rate change based on taxonomic reassessment. Moreover, this creates the potential for taxonomic reassessments to influence how diversification rates of lineages compare to one another, thus influencing observed macroevolutionary trends.

In Chapter 2 I attempted to minimize biases associated with the PSC when estimating shallow divergences by creating a time cut-off in the primate tree which acted as a secondary criteria in defining our "species", which I termed "lineages". This reduced biases caused by subspecies being elevated to the full species rank more persistently in some taxonomic groups than others. However, the taxa used to estimate richness scores (i.e. species and subspecies) were still determined via systematic processes, so while our method avoided biases in subspecies elevations across taxonomic groups, we could not be certain that some groups did not have biases associated with the processes determining how many taxa (species and subspecies) they contained overall (e.g. if some primate clades observe disproportional additions of new species that are never formally recognized as subspecies). Approaches relying directly on phylogenies to infer evolutionary rates (e.g. QuaSSE estimates from FitzJohn, 2012) are also influenced by taxonomic reclassifications since phylogenies and taxonomies inform one another (Hillis, 1998; Wheeler, 2000; Hinchliff, et al., 2015).

In this sense, macroevolutionary studies serve as a great example of why it is important for biologists to have a comprehensive understanding of all the processes involved in determining described species diversity. Understanding how systematic discrepancies influence our respective areas of work can help us to account for them when possible – and when not possible – allow us to speculate as to how they may influence observed results. In our case, we observed positive associations among proxies of behavioural flexibility and diversification rate of well-established lineages, but not among proxies of behavioural flexibility and diversification rate estimates considering recently evolved taxa. We suggested that this pattern could be a result of behavioural flexibility buffering against ephemeral extinction events and that this would be consistent with previous studies (e.g. Shultz, et al., 2005; Rossmanith, et al., 2006; Sol, et al., 2007, Ducatez, et al., 2020). However, we also acknowledged that this could alternatively be an effect of biases in the total numbers of described taxa (species and subspecies) across clades obscuring underlying biological patterns if, for some reason, less flexible clades are more likely to have a larger number of taxa described overall. Therefore, we went on to suggest how future studies could determine if this is a likely explanation for our results. In this case, considering the caveats of relying on taxonomic stability and consistency helped to improve our study design, making us less likely to experience Type I or Type II errors, while also helping us to develop suggested avenues for future research.

Species-Level Observations in Comparative Biology

In addition to influencing evolutionary metrics, changes in species designations can complicate the process of generating species-level data. Many large species-level datasets (e.g. Jones, et al., 2009; Storchová & Hořák, 2018) rely on taxonomy when creating quantitative estimates of species traits (e.g. life history, ecological and geographical traits). Creating species-levels estimates from existing literature is particularly challenging because one must account for changes in taxonomic classifications through time. In Chapter 2 our analysis relied on summarized behavioural and morphological data. Troubles can arise when summarizing species traits from different sources due to changing nomenclature. For instance, measures of brain volume or body mass originally recorded under one species name might come from a specimen which represents a completely different species under a revised or more speciose taxonomy. Similar problems apply to compiling behavioural data that has been recorded over many years, leading researchers to favour lumping over splitting of taxa (Reader, et al., 2011). This is particularly relevant when it comes to applications of the PSC since species in older datasets have often been subsequently split into multiple species in newer taxonomies. Details on specimens are not always well documented, making it difficult to account for these changes in nomenclature. In Chapter 2 we estimated trait values for well-established lineages, referencing very liberal taxa names therein to assign and summarize data. This allowed us to avoid discrepancies in nomenclature since our lineages were very conservative, thus, data were placed in the correct lineage regardless of discrepancies in nomenclature among comprised taxa. However, taxonomic instability – particularly those caused by applications of the PSC for primates – can pose problems when compiling data for less inclusive taxonomic units and may compromise analyses at shallower taxonomic depths.

Species as a Unit for Conservation

Species lists are often used to determine which taxa should receive conservation attention (Mace, 2004), and drastic changes in species designations as a result of e.g. changing species concepts, have been suggested to influence which groups are prioritized. In particular, some have speculated that inflation in species numbers following applications of the PSC may put a strain on primate conservation by increasing numbers of threatened species (Agapow, et al., 2004; Isaac, et al., 2007) and causing poorly-defined taxa to be prioritized over well-defined and biologically unique ones (Pillon & Chase, 2007). Results presented in Chapter 3 show that extinction risk and inflation in species numbers under the PSC are only positively associated across genera from Asia and Africa, sharing no association in Madagascar and sharing a negative association in the Neotropics. This, of course, does not rule out any influence from the PSC in increasing threat scores for Malagasy or Neotropical taxa, but simply indicates that splitting is not resulting in a general pattern of inflated groups being prioritized over lesser inflated groups in these regions. In some cases, inflation could very well still be leading to more imperilled species statuses among taxa in Madagascar and the Neotropics. For instance, many newly described Malagasy mouse lemur (*Microcebus*) populations elevated to the full species status by Louis et al. (2006; 2008) based on molecular data (*M. mittermeieri*, *M. jollyae*, *M. simmonsi*, *M. mamiratra*) are now classified as endangered or critically endangered by the IUCN. The species these populations were previously assigned to: *M. rufus*, is considered to be vulnerable according to its latest assessment. In the assessment details, the description of new species by Louis et al. (2006; 2008) is quoted as a contributing factor causing the now reduced geographic range size of *M. rufus* (Wright, et al., 2020). Thus, in this case it seems there is some suggestive evidence in support of the PSC influencing listing of at risk species, even in Madagascar where it does not result in an overall trend of inflated groups being prioritized.

While many have been critical of the PSC, it does have some advantages over the BSC when it comes to listing and management of at risk species. The use of less inclusive conservation units can help ensure less diversity is lost to extinction. When populations are lumped together and managed as such, some biodiversity may be overlooked and subsequently lost. In a world where conservation funding and resources were unlimited, listing and management of species described under the PSC would be ideal as it would help to preserve the greatest amount of biological diversity. The problem, of course, is that in reality conservation funding and resources are quite limited, and those involved in conservation listing and management often have to make decisions about which units should receive priority. Therefore, we must consider whether it is better to (i) list conservative conservation units that may overlook some biological diversity but often result in the most imperilled and evolutionarily distinct units receiving highest priority and ample resources, or (ii) list less inclusive conservation units, risking the division of resources but ultimately preventing biological diversity presented by closely related yet phylogenetically distinct populations from being neglected. In this sense neither species concept results in infallible units for conservation purposes. When using less inclusive units (i.e. those described under the PSC), incorporating evolutionary measures in conservation is one method of ensuring biologically unique species are still prioritized. The Evolutionarily Distinct and Globally Endangered (EDGE) conservation program combines information on a species' conservation status and their genetic distinctiveness in order to determine which species should be prioritized (Redding & Mooers, 2006; Isaac, et al., 2007). Among primates specifically, it has been demonstrated that species with high EDGE scores capture a large range of biological diversity (Redding, et al., 2010). Using EDGE scores and related metrics (e.g. I-HEDGE; Jensen, et al., 2016) in applied conservation can help to ensure that evolutionarily distinct populations are still prioritized when relying on species lists determined using the PSC, while still allowing less evolutionarily distinct populations to be listed and managed independently.

Other Considerations

While I have discussed the particular ways that aspects of comparative biology and conservation may be directly impacted by recent taxonomic changes, these are not the only fields relying on species as primary objects of study. As discussed in the general introduction, many other areas of biology are reliant on species lists. For instance, Zink & McKitrick (1995) show how changing species concepts can influence studies of historical biogeography if conservative species lists conceal important information required to create biogeographic reconstructions if, for instance, investigators that are not familiar with a taxon overlook events that separate gene pools among populations because they are described under one biological species. Carrasco et al. (2016) discuss the potential implications of taxonomic instability for toxinology and public health research when it comes to treating snake bites. Changing nomenclature and taxonomic inaccuracy is suggested to interfere with the reliable identification of venom samples while also adversely affecting the interpretation of related studies (e.g. studies of venom composition) and repeatability of experiments (e.g. experiments isolating toxins that may be of value to the pharmaceutical industry) (Carrasco, et al., 2016). Thus, the specific ways in which changing species designations influence studies relying on species as a central unit of comparison should continue to be explored across other sub-disciplines biology not discussed here.

IMPLICATIONS:

Understanding the processes involved in determining described species diversity improves our understanding of biological diversity and allows us to better evaluate the use of species across various areas of biology. Evidence presented in Chapter 2 indicates that behavioural flexibility is associated with rates of evolution across primates. If patterns observed in our results are indeed a function of behavioural flexibility buffering against ephemeral extinction events as we suggest, this could be informative in helping biologists anticipate how different organisms may respond to external change (e.g. habitat modification). This would, in turn, allow biologists to better anticipate which organisms might be particularly vulnerable to extinction in a changing world, especially when it comes to anticipating extinction events among recently diverged species or subspecies (i.e. ephemeral lineages). In Chapter 3 we discussed the potential implications of taxonomic inflation for applied conservation. While results indicated that inflation has not led to the prioritization of highly inflated groups – at least within Madagascar and the Neotropics where a great deal of inflation has occurred – we discussed how increasing designations of new species units should still be a consideration for conservation efforts. As described in Chapter 2, it is likely that many species units used by the IUCN represent recent diversification events considering that the PSC has facilitated the splitting of very closely related populations. Thus, while some may view an increase in the overall number of at risk species a burden for conservation (e.g. Zachos, et al., 2013; Zachos & Lovari, 2013), in this sense listing and management of less inclusive species units (i.e. those described under the PSC) can actually assist us in projecting the ephemeral extinction events discussed above, since these populations are already being assessed, monitored and managed as independent units. This is one potential benefit of using less conservative species concepts for conservation listing.

In addition to having implications for conservation, my thesis additionally draws attention to the possible problems associated with creating quantitative estimates of recent evolutionary events (i.e. species diversification) while failing to account for influence from biases in systematic processes. This is an important consideration for other studies of macroevolutionary trends among taxonomic groups that have undergone or are continuing to undergo substantial taxonomic revision. Finding ways to account for such biases can allow evolutionary biology to make advancements while also allowing taxonomy to progress. Finally, in addition to the implications of results presented in Chapters 2 and 3 (discussed in their respective chapters), my thesis generally provides important insights into the processes involved in determining described primate species diversity and thus has implications for our understanding of biological diversity observed across the Tree of Life.

DIRECTIONS FOR FUTURE RESEARCH:

Here, I will suggest some additional areas of research to those discussed in Chapters 2 and 3 that could provide useful insights into the causal factors determining species diversity more broadly. In Chapter 2, we provided evidence for behavioural flexibility promoting primate evolution after attempting to control for systematic biases which may influence diversification estimates. I suggest that future studies relying on evolutionary rate estimates could test macroevolutionary hypotheses using rate estimates generated from different taxonomic or phylogenetic sources. One could test the same hypothesis using these different estimates of evolutionary rate keeping all other data sources constant to see how results vary based on the taxonomy or phylogeny used. This would help determine how influential choices of taxonomic or phylogenetic references are in driving observed macroevolutionary trends.

In Chapter 3, we explored some potential predictors of species inflation and did not find significant effects from biological processes (i.e. diversification rate) or interest-driven mechanisms (i.e. measures of research effort) in driving inflation. While we focused on primates, inflation and general taxonomic instability are widespread across many taxa. Many vertebrates including birds (Barrowclough, et al., 2016), reptiles (Uetz, 2000; Torstrom, et al., 2014) and amphibians (Hanken, 1999) have experienced drastic changes in described species diversity following an increased use of molecular data and the applications of phylogenetic systematics. Thus, a large scale study across a variety of vertebrates may be useful in revealing what makes taxa particularly susceptible to splitting (e.g. research interest, region, cryptic diversity). Addressing this is complicated as many factors likely contribute to which groups undergo splitting, however, identifying some common characteristics among highly split groups would be useful for determining how taxonomic change is likely to bias other areas of study. For instance, using our Chapter 2 tests as an example, if it were determined that highly charismatic groups are more likely to be split, and these groups are also likely to be large brained and successful innovators (i.e. behaviourally flexible), failing to account for biases in species inflation when estimating diversification rates may have led us to falsely infer an association between behavioural flexibility and diversification rate.

Lastly, I focused specifically on applications of species concepts and subsequent re-evaluations of lesser taxa because I was interested in estimating diversification rates of shallow lineages (i.e. species and subspecies) and because conservation listing and management occurs at the species level (Chapters 2 and 3, respectively). However, classifications of higher taxa (e.g. genera and families) have also been impacted by taxonomic change. These changes are not dictated by changing species concepts but could be impactful to some of the areas of study discussed above. Thus, more work could be done to elucidate how changes in nomenclature at higher taxonomic levels influence these areas of biological research.

GENERAL CONCLUSIONS AND SUMMARY:

In summary, the aim of my thesis was to delve into the complex determinants of species richness and diversity across primate clades. When testing evolutionary drivers of diversity, I found some evidence that behavioural flexibility promotes the rate at which primates evolve – ultimately having some influence on extant species diversity across clades. However, this finding was dependent on the measure of flexibility and diversification rate employed. Further research will be required to confirm whether this influence stems from behavioural flexibility (i) promoting speciation – if taxonomic biases are obscuring biological patterns among recent splitting events, or (ii) buffering against extinction of recently evolved lineages. When exploring potential explanations for differences in taxonomic inflation across primate clades, I did not find significant influence from biological processes (i.e. diversification rate) or interest-driven mechanisms (i.e. measures of research effort). The appearance of a quadratic relationship shared by the number of species originally listed in primate genera in 1982 and inflation may, however, suggest that inflation is influenced by underlying process not captured by these models. Along with exploring determinants of primate diversity, I additionally addressed the role of taxonomic instability in influencing areas of biology which remain reliant on species as primary objects of study. In particular, I focused on the problems changing species designations pose for comparative studies of macroevolution, which I addressed when attempting to estimate primate diversification rate. I also examined how recent taxonomic re-classifications have influenced conservation. In doing so I found that the association between rates of taxonomic inflation and threat score vary by region, with highly inflated genera being considered most at risk in some regions, but least at risk in others. In short, both evolutionary and systematic processes have played a role in driving described primate species diversity and inconsistencies in the latter can result in implications for many areas of research. Future studies will be essential in further explaining the determinants of primate species diversity and their relative contributions. Species are used as the fundamental unit of comparison across many areas of biology (De Queiroz, 2005). Thus, continuing to tackle questions regarding the processes governing species diversity across taxa and the biological significance of species realities is essential to shaping our understanding of biological diversity.

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