Predictors of Taxonomic Inflation and its Role in Primate Conservation

Maria J.A. Creighton[a], Alice Q. Luo[a], Simon M. Reader[a] & Arne Ø. Mooers[b]

[a]Department of Biology, McGill University, Montreal, Quebec, Canada

[b]Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, Canada

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

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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 have unfavourable 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. We also do not find evidence of research effort in fields where work has been suggested to motivate splitting being associated with increases in species numbers among genera. To test the suggestion that splitting groups is likely to increase their perceived risk of extinction, we test whether genera that have undergone more splitting have also observed a greater increase in their proportion of threatened species since the introduction of the PSC. We find no cohesive signal of inflation leading to higher threat probabilities across primate genera. Overall, this analysis sends a positive message that threat statuses of primate species are not being overwhelmingly affected by splitting in line with what has recently been reported for birds. 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, 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. 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 clades (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 that occurred following the rapid adoption of the polytypic species concept beginning in the 1890's. 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 defines species as 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 often due to limited records of potential mating interactions or of hybrid forms (Tattersall, 2007). In these cases, genetic evidence is required to show that gene pools are linked, e.g., 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 species concept (PSC) (Cracraft, 1983; Isaac, et al., 2004) has been widely popularized in vertebrate taxonomy due to its diagnosable advantages over the BSC. Under the 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 PSC's emphasis on diagnosable evidence gives it an advantage over other species concepts because it allows users to establish a scientific proposition that is testable. As a result, shortly after being proposed influential taxonomists quickly advocated for use of the PSC over the BSC (see, e.g., Donoghue, 1985) and thus, the PSC began being used almost immediately after its inception.

Although the PSC offers diagnostic advantages over the BSC, it has also been subject to criticism, notably, for its tendency to split 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 the 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) lists over 500 distinct primate species (Estrada, et al., 2017). Some families (e.g., Cheirogaleidae and Indriidae) have more than tripled in species numbers since the introduction of the PSC (see Figure 1). While some new 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 (Tattersall, 2007). This trend of the PSC increasing species numbers by raising taxonomic statuses has been referred to as 'taxonomic inflation' (Isaac, et al., 2004; Rylands & Mittermeier, 2014). Taxonomic inflation has been criticized for being non-random, and biased toward certain taxonomic groups (Isaac, et al., 2004).

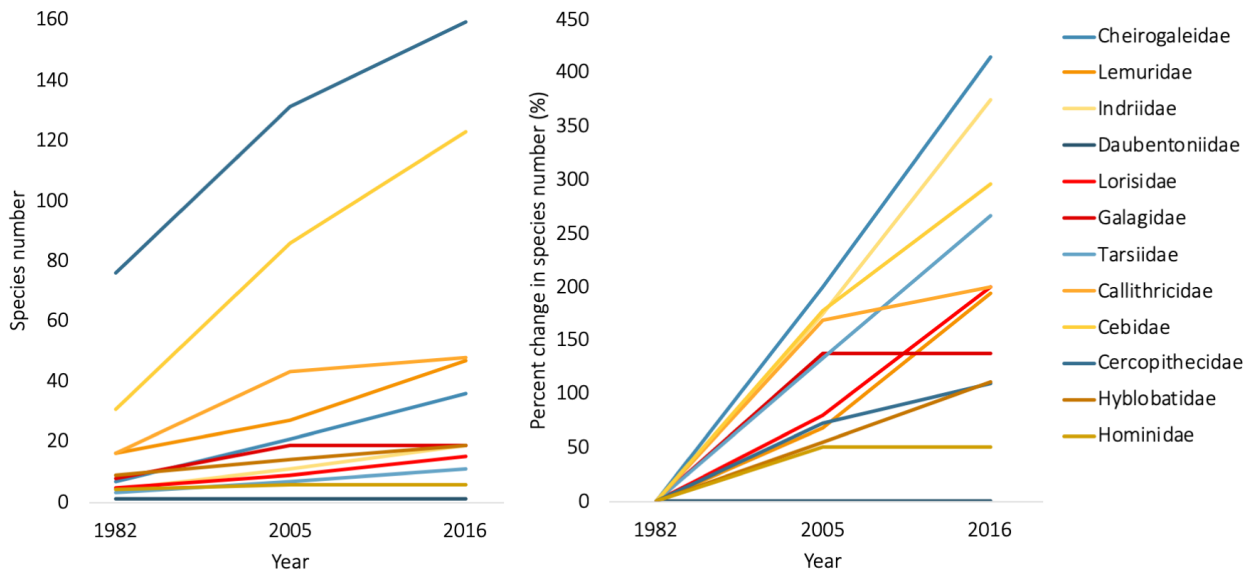


Figure 1: Species numbers and percentage change in species numbers for historic primate families recorded at three time points by Honacki et al. (1982), Wilson & Reeder (2005) and the IUCN species list from 2016 (documented in Estrada, et al., 2017).

Disproportional splitting among taxonomic groups could have several causes. 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 such that phylogenetic species are tracking 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, variation in inflation would simply reflect underlying biological reality. However, it is also possible that splitting is driven by other factors that may indeed be prone to bias. Critics have argued that much inflation is artificial,

reflecting major shortcomings of applying the PSC and a reliance on insufficient data (Zachos, et al., 2013; Zachos & Lovari, 2013). Zachos et al. (2013) provides evidence suggesting unwarranted splitting in select cases, advocating that the PSC has been taken to a "molecular extreme". In one cited example (Zachos, et al., 2013), Sumatran tigers (previously *Panthera tigris sumatrae*, raised to *Panthera sumatrae*) were split by Cracraft et al. (1998) and then subsequently split into an even greater number of species by Mazák & Groves (2006), based on diagnosable mitochondrial and craniometrics differences, respectively. By this logic, groups may continue to be split as an increasing amount of molecular work leads to the continual identification of increasingly exclusive diagnostic features such that we are likely to find more PSC species the more we look for them.

It is also possible that conservation interest in particular groups could motivate splitting. Limited funding for conservation research is increasingly focused on 'biodiversity hotspots' and it has been suggested that researchers could have a vested interest in declaring taxa in these regions as endemic species (Karl & Bowen, 1999; Isaac, et al., 2004). There is evidence from some charismatic groups that taxa receive 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). 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.

Along with being potentially biased toward certain taxonomic groups and related to the point made above, splitting under the PSC has been suggested to result in individually more imperilled populations which could negatively impact conservation agendas (Agapow, et al., 2004; Isaac, et

al., 2004; Morrison, et al., 2009; Zachos, 2015; Robuchon, et al., 2019). One criterion used by the IUCN to classify species as imperiled is population size: species may be designated "Vulnerable" if there are fewer than 1000 mature individuals found in the wild and “Endangered” if there are fewer than 250 (Agapow, et al., 2004; Frankham, et al., 2012). Thus, splitting one species into several new species may result in one or more receiving a (more) imperilled status (Agapow, et al., 2004; Isaac, et al., 2007). This could lead to seemingly rare but poorly-defined species being prioritized over well-defined and perhaps biologically more distinctive species (Pillon & Chase, 2007). Recent evidence suggests species splitting is not a driver of threat status for birds (Simkins, et al., 2020), however, it is unknown whether these findings are generalizable across other taxonomic groups (Garnett & Thomson, 2020).

Here, we set out to better understand the causes and consequences of taxonomic inflation in primates. We test (i) whether taxonomic inflation is associated with the amount of research being done in fields suggested to motivate splitting, or with a lineage's underlying diversification rate, and (ii) whether rates of inflation dictate which groups are considered to be most imperilled. Because many newly described primate lineages have previously been described as subspecies or subpopulations of multiple closely related BSC species, we ask these questions at the genus level.

To explore our first question regarding predictors of inflation, we consider whether biological factors or measures of human-induced bias explain increases in species numbers. 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 be associated with more splitting. We examine research effort in two fields: molecular genetics (since molecular work could cause

148 species to be split continuously as finer molecular distinctions are made) and conservation (since
149 splitting has been suggested to be motivated by conservation interests). To explore possible
150 biological explanations for inflation trends, we test to see if inflation is explained by diversification
151 rate, using a diversification measure designed to be uncoupled from changes in species naming
152 conventions (see Methods). Lineages with high recent diversification rates are expected to contain
153 more incipient or cryptic species than lineages diversifying at a lower rate, such that diversification
154 rate might be expected to correlate positively with inflation.
155
156 To explore our second question linking inflation and risk, we test whether inflation is associated
157 with a change in the number of threatened species listed in genera through time. Ideally we would
158 look at changes in a weighted measure of threat score that differentiates between threat categories
159 of varying severity (e.g., using the Red List Index (RLI); Butchart, et al., 2007; Bubb, et al., 2009);
160 however, criteria for inclusion in Red List threat categories have changed considerably over time,
161 meaning weights assigned to categories for RLI calculations do not match up with categories used
162 when the PSC was first introduced (e.g., see statuses in IUCN Conservation Monitoring Centre,
163 1986). Because of these changes in Red List criteria, we instead ask whether clades with species
164 that have been split more frequently have observed a greater increase in their proportion of
165 threatened species (defined below) through time in comparison to those which have been split less
166 frequently. We predict that if splitting is driving an increase in threatened species, we should
167 observe a positive association between inflation and change in the proportion of threatened species
168 listed in primate genera.
169
170 **METHODS:**

Data

To measure the number of primate species that were described 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). We then recorded if each species in this taxonomy was historically considered to be threatened by referencing the most complete IUCN Red List published around the same time (IUCN Conservation Monitoring Centre, 1986). 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), whether or not they were considered threatened (VU=Vulnerable, EN=Endangered, or CR=Critically Endangered), and biogeographic region. For each 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), i.e., 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 12 families and 50 genera found in Honacki et al. (1982). Family name "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). *Rungwecebus kipunji* was removed from the IUCN species list from 2016 as it represents a newly discovered genus that does not collapse into any of the genera provided by Honacki et al. (1982).

194 Research effort in the fields of molecular genetics and conservation were estimated for each genus
195 through a literature review of publications in the Web of Science Core Collection published
196 between 1983 (the year the PSC was first proposed) and 2016. To obtain papers in the field of
197 conservation we searched the genus name AND "conservation" (hereafter 'conservation research
198 effort'). To obtain papers in the field of molecular genetics we searched for genus name AND the
199 following terms: "mitochondrial DNA" OR "barcoding" OR "bar-coding" OR "cytochrome b" OR
200 "phylogeography" OR "microsatellites" OR "micro-satellites" OR "population genetics" OR
201 (species AND genetics) OR (taxonomy AND genetics) OR "SNP" (hereafter 'molecular genetics
202 research effort'). All hits from these searches were reviewed and irrelevant papers were eliminated
203 (see supplementary materials; Tables S1 and S2). In this study we used the genera listed in Honacki
204 et al. (1982) (n=50), many of which have since been further separated into multiple genera. Thus,
205 when appropriate we included new genus names in addition to those listed by Honacki et al. (1982)
206 in the literature search (see Table S3). Additional details on how searches were conducted are
207 provided in the supplementary materials.
208
209 Diversification rate was estimated with the method-of-moments approach described in Magallon
210 & Sanderson (2001) (i.e., ln(taxa richness)/stem age). Diversification rate estimates generated
211 using this method often rely on species numbers as their estimate of taxa richness, meaning that
212 diversification rate estimates are inherently biased by the inflation phenomenon we are studying
213 (i.e., highly inflated genera will receive disproportionally high diversification rates). Therefore,
214 richness scores for our diversification rate calculations were determined as the counts of the well-
215 resolved "lineages" described in Creighton et al. (2021). These lineages were determined by
216 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). 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 the analyses where diversification rate was a variable of interest: *Presbytis*, *Lemur*, *Galago*, *Cebuella*, *Cercocebus*, *Cercopithecus*, *Papio*, and *Pygathrix*. We discuss the limitations of having to remove these genera from these analyses in the discussion.

Analysis

To test our questions about the predictors of species-splitting and its consequences for conservation, we fit a series of linear effects and mixed effects models. We note that the response variables used in these analyses (i.e., measures of inflation and extinction risk) are likely to be phylogenetically clustered, and phylogenetic models could be used to account for this influence of phylogeny; however, many genera listed by Honacki et al. (1982) are non-monophyletic, making it unclear how to designate them a single branch in modern phylogenies (see discussion above on diversification rate). Importantly, after accounting for regional differences, family contributed little to no variance in any of our models, indicating that phylogenetic relationships at that level

were not confounding our results. We provide further discussion on model choice in the supplementary materials.

Data were analysed using R version 4.0.5 (R Core Team, 2021).

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 generalized 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). 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 natural logarithm of the number of species listed for each genus in Honacki et al. (1982) was included as 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). Mainland Africa and Asia (hereafter mainland Africa +

262 Asia) were grouped together and served as the baseline region in our models based on previous
263 studies that have shown that the taxonomy of primates from these regions has been relatively stable
264 compared to Madagascar and the Neotropics (e.g., Isaac & Purvis, 2004; Isaac, et al., 2004;
265 Tattersall, 2007). We also chose to group Asia and Africa together because one genus (*Macaca*)
266 is found in both regions. Genus ID was included as a random effect in these models to correct for
267 overdispersion. Family (nested within region) was originally included as a random effect but
268 contributed very little to model fit and created issues with convergence due to overfitting, and thus
269 was dropped from the final models. We tested potential interaction terms with all variables and
270 region to test for regional effects, but none were significant and so these terms were also dropped
271 from the final models. Before running models with other predictors included, we also ran a model
272 including only the linear and quadratic terms for the number of species listed for each genus in
273 Honacki et al. (1982) as predictors to assess their association with inflation in the simplest model.
274 We ran all models a second time after removing the 40 *de novo* species from our response (Tables
275 S4, S5 and S6). We checked model assumptions and fit by plotting residuals versus the fitted
276 values and versus each covariate in the model. Residual plots and analyses with the Diagnostics
277 for Hierarchical Regression Models (DHARMa) R package (Hartig, 2017) indicated acceptable
278 model fits.
279
280 *Inflation and Threat Score*
281 To test whether taxonomic inflation over time is associated with a change in the proportion of
282 threatened species within genera, we conducted a two-step (hierarchical) analysis on species'
283 threat probability between 1982 to 2016. We first fit a generalized linear mixed effects model with
284 a binomial distribution for the number of threatened and non-threatened species within a genus

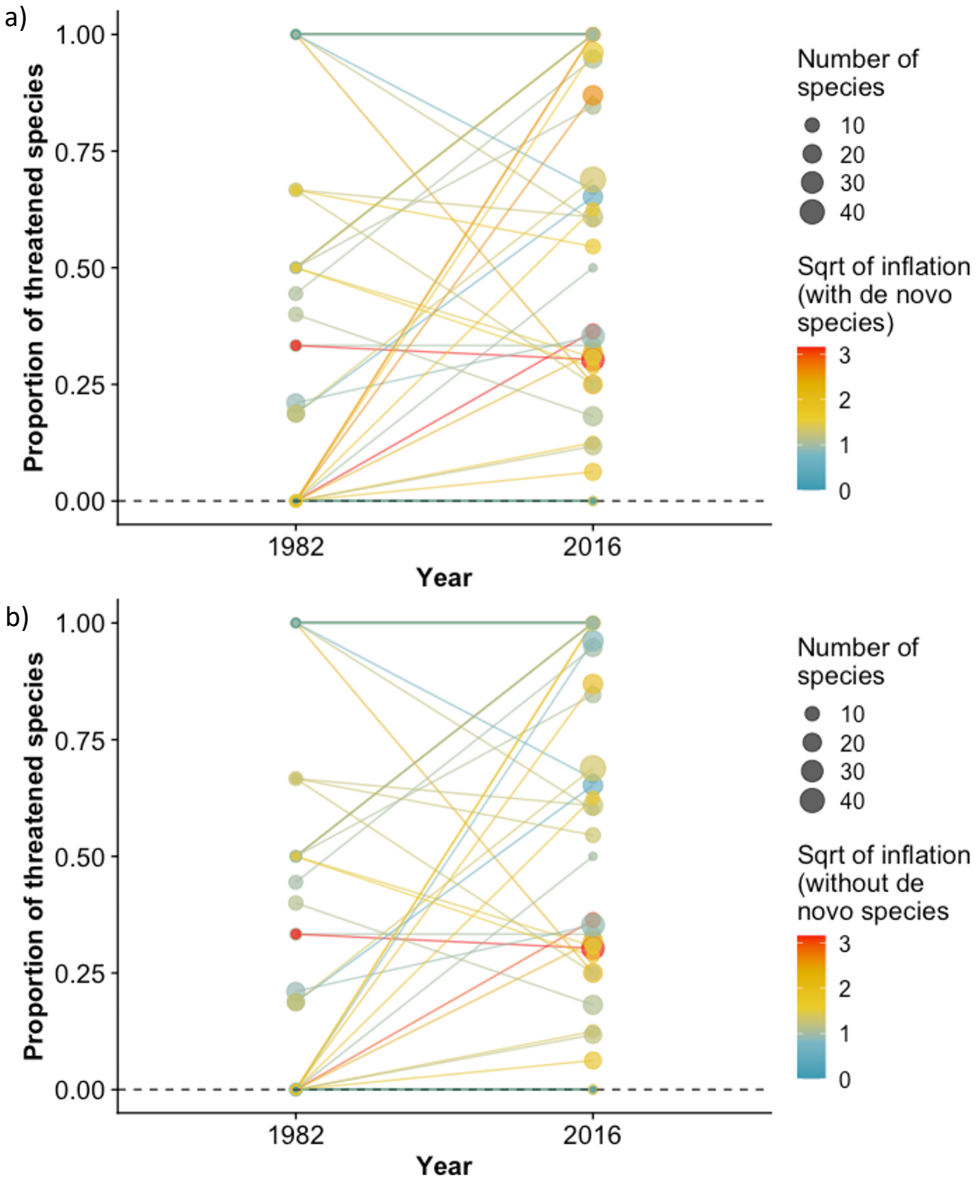
using the lme4 package in R (Bates, et al., 2014). In this first model, the response estimated the proportional counts of species at risk within genera (equivalent to the per-species probability of threat) in the periods of 1982 and 2016. Predictors for this model included fixed effects for the time period (the baseline of 1982 and the change to 2016), the region that encompasses each genus' natural distribution (Madagascar, Neotropics, mainland Africa + Asia), and an interaction between region and time period to account for geographic differences in threat probabilities through time. Genus identity was included as a random intercept, to account for repeated measures in 1982 and 2016, and as a random slope with time period to account for differences in changes to threat probabilities among genera. As discussed above, we included the taxonomic rank of family (nested within region) as a random effect but found that the variance in threat probabilities among families was minimal and that including this term also generated model convergent issues; given this, we subsequently omitted family from our models. Residual plots and analyses with the DHARMa R package (Hartig, 2017) indicated acceptable model fits for the final model. From this first model describing genus level changes in threat probabilities, we then used the REextract function implemented in the merTools package in R (Knowles & Frederick, 2020) to extract the genus level random slopes for time period and their associated standard errors, giving us an estimate of the varying effect of change in threat probability among genera (while conditioning on regional trends) between 1982 and 2016. We then fit a linear model where varying effect of change in threat probability from 1982 to 2016 was the response, and the proportional change in species within each genus (i.e., the number of new species in the IUCN species list from 2016 / original number of species in Honacki et al. (1982) – our measure of "inflation") – was the predictor. We weighted each estimate of genus level change in threat probability by its standard error (w = 1/SE) to propagate the error of model estimated random effects. We ran this model a second time after

308 removing *de novo* species descriptions from our response (Table S7). Raw data used for these tests
309 are visualized in Figure 2.
310
311 Plots of the raw data indicated that patterns in inflation, the proportion of species at risk in primate
312 genera today, and the changes the proportion of threatened species in primate genera between 1982
313 and 2016 show regional differences (Figures S1 and S2). We ran a subsequent set of models to test
314 for regional variation in the effect of taxonomic inflation. In this analysis, we removed region from
315 the first generalized linear mixed effects model and subsequently included region interacting with
316 taxonomic inflation as a predictor of the varying effect of change in genus threat probability in the
317 second-order model. However, interaction effects were not significant in this model and thus we
318 only considered the results of the first set of models reported above.
319
320 **RESULTS:**
321 *Predictors of Inflation*
322 None of our measures – conservation research effort (β = -0.220; p = 0.180; Table S4), molecular
323 genetics research effort (β= -0.188; p= 0.212; Table S5) nor diversification rate (β= 0.132; p=
324 0.477; Table S6) – were significantly associated with taxonomic inflation of primate genera.
325 Removing *de novo* species did not impact this pattern of results (Tables S4, S5 and S6). Notably,
326 in addition to sharing a significant linear relationship with inflation as expected (Tables S4, S5 and
327 S6), the quadratic term added for the original number of species in 1982 was significant in the
328 model with diversification rate, indicating a downwardly concave association with inflation (β= -
329 1.890; p= 0.042; Table S6); this term approached statistical significance in models that included
330 conservation or molecular genetics research effort as predictors (β= -1.529; p= 0.072; Table S4

and β= -1.626; p= 0.057; Table S5), indicating that the positive increase in splitting by initial genus size decelerates as genera become very large, even after accounting for other factors. We note that this quadratic term was also significant without other predictors (i.e., research effort or diversification rate) present in the model, both with *de novo* species included in the response (β= -2.268; p= 0.011) and without *de novo* species included in the response (β= -2.086; p= 0.013).

Inflation and Threat Score

Looking at the raw data on inflation and proportion of species at risk for all genera, there was no clear indication that highly inflated genera have observed a disproportional increase in perceived extinction risk (Figure 2).



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343 Figure 2: Scatterplots with trendlines showing the change in the proportion of species identified

344 as being threatened in primate genera in 1982 and 2016 painted by inflation a) including *de novo*

345 species, and b) excluding *de novo* species. Total number of species in each genus is indicated by

346 point size.

347

348 Results from our GLMM confirmed that inflation did not predict a change in threat score through
349 time (β= 0.002; p= 0.975; Table S7; Figure 3). Removing *de novo* species did not impact this
350 pattern of results (Table S7; Figure S3).
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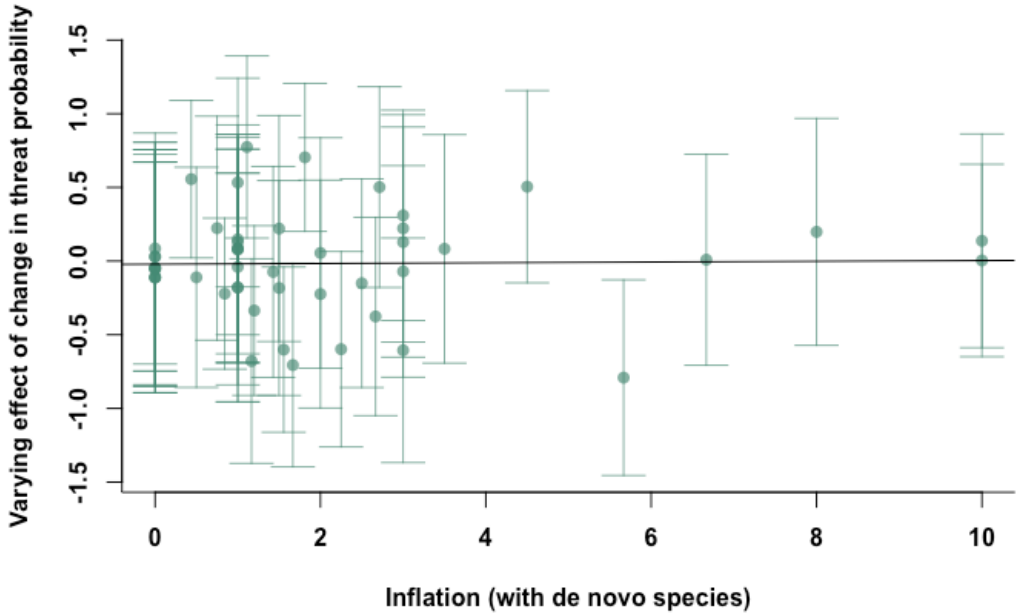

352
353 Figure 3: Inflation versus varying effect of change in threat probability (i.e., our measure of genus
354 level change in threat probability) (β= 0.001; p= 0.975; Table S7). Vertical bars indicate standard
355 errors on varying effect of change in threat probability values.
356

357 **DISCUSSION:**

358 Our results support neither a strong biological nor a strong interest-driven mechanism for variation
359 in new species designations across primate genera. If the naming of new PSC species captures
360 incipient speciation, we predicted that diversification rate might predict inflation. However, we
361 found no evidence for this as diversification rate was not a significant predictor of inflation in our
362 models. We also tested the prediction that splitting is motivated by conservation interest (Karl &

363 Bowen, 1999; Isaac, et al., 2004) or by increasing molecular research within certain taxa, with for
364 example, more new species designations arising as more population genetics work is done (Zachos,
365 et al., 2013; Zachos & Lovari, 2013). However, we found no evidence that research effort in either
366 of these areas was associated with inflation across genera. We did find that the positive increase
367 in splitting by initial genus size decelerates as genera approach the largest sizes. This could indicate
368 that inflation is being driven by something not captured by our models. Therefore, future studies
369 could aim to elucidate the origins of this decelerating association.
370
371 While inspection of the raw data suggested that genus level measures of inflation, threat
372 probability, and change in threat probability all varied by region, we found that there was no
373 cohesive signal of inflation leading to higher threat probability across these genera and regions.
374 Therefore, while there are idiosyncratic regional differences in both primate inflation and threat
375 probability there is no evidence for causal link between the two. While in some cases splitting may
376 lead populations to be considered more imperilled, overall, this analysis sends a positive message
377 that primates species threat statuses are not being overwhelmingly affected by splitting in line with
378 what has been reported for birds (Simkins, et al., 2020).
379
380 It should be considered that our analyses do have some limitations. First, quantifying research
381 effort of any kind is difficult due to the abundance of work published in different media. As such,
382 our estimates of research effort in conservation and molecular genetics may overlook some types
383 of research. More work should be done to determine if additional estimates of research bias can
384 explain increases in species numbers. For instance, cumulative funding estimates from various
385 sources (e.g., the IUCN, non-governmental organizations and regional governments) per taxon

386 could be used as an additional or alternative measure of conservation interest. Second, it was
387 necessary to remove eight non-monophyletic genera (some that have undergone substantial
388 splitting) from those analyses that included diversification rate, leading to a considerable reduction
389 in statistical power for those analyses. Third, due to changes in Red List criteria, species status,
390 and lack of information about which species had been assessed in the 1980s, we were not able to
391 consider differences in threat status severity (e.g., Vulnerable versus Endangered) when
392 considering associations between inflation and changes in threat score through time. This leaves
393 room for the possibility that change in risk could be under- or over-estimated for certain genera.
394 Future studies could look at the association between inflation and changes in weighted measures
395 of threat score (e.g., RLI) over time using a more recent starting point (i.e., after 1982) where Red
396 List criteria become stable and there is available information on which non-threatened species have
397 been evaluated.
398
399 Overall, we do not find support for biological processes (i.e., diversification rate) or human
400 imposed bias (i.e., measures of research effort) driving inflation across primate genera. We also
401 find no cohesive signal of inflation leading to higher threat probabilities across primate genera.
402 Generally speaking, relying on species as the central unit of conservation and primary object of
403 biological study behooves taxonomy to remain stable, while changing ideas about the concept of
404 species makes taxonomy inherently unstable (Mayr, 1996). We suggest that areas of research
405 requiring consistent estimates of diversity (i.e., conservation) may benefit from either (i) adopting
406 stable species criteria, i.e., that do not rely on increasingly fewer diagnostic distinctions; or, for
407 applied conservation specifically (ii) shifting more resources toward regional management efforts
408 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 (Redding & Mooers, 2010). 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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