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A Macroevolutionary View on Extinction in Aves, Chiroptera, and Odonata

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A Macroevolutionary View on Extinction Risk in *Aves*, *Chiroptera*, and *Odonata*

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ABSTRACT

A central goal of conservation biology is to identify and understand the factors that lead to extinction. The Earth is currently undergoing a 6th mass extinction event, in large part because of human activity. In the last century, rates of extinction have increased anywhere from 8-100 times the background rate of 2 extinctions per 10,000 species every 100 years. However, there remains a debate over whether certain species are predisposed to a higher extinction risk. In particular, it is not known if the macroevolutionary history of a lineage is a major contributor to the probability of extinction, nor is it clear whether the current rise in extinction rates is due strictly to anthropogenic activity. Using life history trait information and the International Union for Conservation of Nature (IUCN) Red List rankings for bats, birds, and odonates in combination with a novel diversification method, MiSSE (Missing State Speciation and Extinction), we test if there is an evolutionary signal of extinction susceptibility independent of the influence that traits can have on rates of diversification. Phylogenetic and non-phylogenetic regressions were run to determine if any specific traits correlated with extinction risk ranking. We find that there is no correlation between diversification rates and IUCN extinction risk. However, larger clutch sizes and range sizes correlated with lower extinction risk and that longer generation lengths for birds did correlate with higher levels of extinction risk. We found no correlation of extinction risk and life history traits in bats and odonates. Our modeling suggests that other factors, such as human-mediated activities, better explain the increased extinction rates.

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INTRODUCTION

Biological diversity, in a macroevolutionary view, is maintained through two key

processes: speciation, the rate at which species are gained, and extinction, the rate at which

species are lost. For most of Earth's history, average speciation and extinction rates have been

approximately equal (Marshall 2017). However, there are times when the magnitude of

extinction greatly exceeds speciation. These so-called mass extinctions have occurred at least

five times in Earth's history, and there is increasing evidence that we are experiencing a sixth

event (Dirzo and Raven 2003; Wake and Vredenburg; 2008; Barnosky et al., 2011; Ceballos

2015). Recent fossil evidence has shown that the current background extinction rate is twice as

high as previous estimates, going to 2 extinctions per 10,000 species every 100 years for

vertebrates (Barnosky et al. 2011; Ceballos et al. 2015). Background extinctions refer to the

normal rate at which species go extinct through natural processes, free from anthropogenic

influences (Wiens & Slaton 2012). While the background rate has doubled, the current extinction

rate has increased anywhere from 8- to 100-fold over the last century. Modern, or current

extinction rates, are measured in terms of the number of species that have been recognized as

having gone extinct, extinct in the wild, or possibly extinct since 1500 AD (Ceballos et al. 2015).

This precise timing of 1500 AD coincides with what many believe to be the time that *Homo*

sapiens began to have a major impact on the planet (Ceballos et al. 2010; Drizo and Raven 2010;

Mace et al. 2012;Ceballos et al. 2015) In other words, under typical conditions, the number of

species that have gone extinct in the last century would have taken between 800 and 10,000

years to occur (Ceballos et al. 2015). This sudden and drastic increase in extinction rates over the

past 100 years is likely driven by a myriad of anthropogenic factors. Previous studies have found

that habitat fragmentation (Wake and Vredenburg 2008), introduction of non-native species

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(Hoffman et al. 2010), over-harvesting (Rosser and Mainka 2002), spread of pathogens (Wake and Vredenburg 2008; Vredenburg et al. 2010), and climate change (Stork 2010) have contributed to higher extinction risk. In addition to anthropogenic factors causing increased extinctions, it has been shown in a variety of taxa that life history traits such as large body mass, small range size, increased habitat specialization, and longer generation time correlate with increased extinction risk, therefore making species that exhibit these traits more vulnerable to extinction (Purvis et al. 2000; Cardillo et al. 2005; Cooper et al. 2008; Böhm et al. 2016).

Although previous studies have identified several biological correlates of extinction risk more recent studies have attempted to link diversification rates to increased extinction risk (Purvis et al. 2000; Cardillo et al. 2005; Verde Arregoitia et al. 2013; Greenberg & Mooers 2017), it is unknown whether these at-risk species were already on a macroevolutionary trajectory towards extinction. Diversification rate studies to date have provided mixed results with more rapidly diversifying clades, such as the angiosperms of the South African Cape (Davies et al. 2011) and in Amphibia genera, (Greenberg & Mooers 2017) showing higher rates of extinction, while no such signal has been detected in terrestrial mammals (Verde Arregoitia et al. 2013), birds (Jetz et al. 2014), or squamate reptiles (Tonini et al. 2016). A commonly used approach to estimate diversification rates is the methods-of-moments and has been used to investigate diversification rate relationship with extinction risk in terrestrial mammals and amphibians (Magallon & Sanderson 2001; Verde Arregoitia et al. 2013; Greenberg & Mooers 2017). However, this method ignores phylogenetic structure and defines lineages on a per-genera basis. For a more accurate relationship between diversification rates and extinction we view that it is necessary to use species-level diversification rates and a species-level phylogeny.

Species-level diversification methods can be thought of as lying on a continuum: on one end lie methods for attributing diversification rates to specific focal traits (i.e., SSE, or state speciation and extinction models; Maddison et al. 2007; Beaulieu and O'Meara, 2016), and on the other end lie models that fit diversification rates to trees but ignore character information entirely (LASER, Rabosky 2006; MEDUSA; Alfaro et al. 2009; TreePar, Stadler 2011; BAMM, Rabosky 2014; among others). However, all these models can be considered different forms of so-called "hidden state" models (Beaulieu and O'Meara, 2016; Caetano et al. 2018). In other words, all of these approaches assume that most, if not all, traits have at least some influence on diversification, however trivial, and that even when not explicitly identifying a character focus, we are doing so implicitly (see Caetano et al. 2018). Here, we devise and utilize a new implementation of a "trait-free" SSE model that tracks "shifts" in diversification as lineages follow the evolution of any number of unobserved, hidden states. As we are not able to account for all of the traits that may impact diversification and recognize that diversification rates may vary independent of our character of interest, we must also take into account the complicated correlations between known and unknown traits and that they may vary among clades. We view that it is best to remove any biases that known characters can have on estimating diversification rates and avoid the risk of exaggerating the potential impact that a trait can have on diversification rates (Caetano et al. 2018). Rather than focusing on speciation and extinction, or even net diversification rate (speciation rate - extinction rate), our modelling approach focuses on changes in turnover rate (speciation rate + extinction rate) to measure the frequency of events that happen over evolutionary time. Tracking changes in turnover through time gives us insights into the unique evolutionary dynamics of target clades and allows us to investigate whether these groups show a predisposition to extinction.

In order to study the relationship between diversification rates and extinction risk on a large scale, we conducted independent analyses on several monophyletic clades. Using the chiropteran phylogeny from Welch and Beaulieu (2018), the odonate supertree (Waller & Svensson 2017), and the avian genetic supertree created by Jetz et al. (2012) we address the potential evolutionary predisposition to extinction risk in bats, birds, and odonates. We use a novel state speciation and extinction model (MiSSE) to estimate the diversification rates. This approach decouples trait change from shifts in diversification, giving novel insights into the macroevolutionary signal of extinction risk. Our study also examines the influence of several life history traits on diversification and extinction risk. Our results suggest that there is no link between diversification rates and extinction risk. We find that the species we have listed as "not at-risk" and "at-risk" are not evolutionarily prone to extinction when compared to their species specific turnover rates, and that the cause(s) for this increase in background extinction rates are likely human-mediated.

MATERIALS AND METHODS

Phylogenetic tree construction

We relied on published phylogenies for all analyses. For *Chiroptera*, we used a 910-tip phylogeny of Welch and Beaulieu (2018) representing 64% of the 1,421 recognized species of the clade (Simmons & Cirranello 2020). For birds, we used the GenBank phylogeny from Jetz et al. (2012), which contains 6,670 species, or roughly 62% of the 10,770 extant species (Gill et al. 2020). Finally, we relied on the 809-tip phylogeny from the supertree available on the odonate phenotypic database (OPDB) (Waller & Svensson 2017), which comprises roughly 13% of the 6,400 known extant species of odonates.

Trait data collection

Following Welch & Beaulieu (2018) we used Wilson & Reeder's mammal species of the world v2005 (MSW05) (Benson et al. 2014) and the Red List v3.1 (IUCN 2018) to obtain a list of bat species and to ensure that there were no duplicate species in our analysis. We collected traits known to be common correlates of extinction risk from PanTHERIA (Jones et al. 2009), the supplementary data set from Jones et al. (2003), the Red List v3.1 (IUCN 2018), and Welch & Beaulieu (2018). All continuous variables were $\log_{10}$-transformed prior to analysis. Avian traits (body size, clutch size, extent of occurrence (a surrogate for range size), and generation length) were collected from the IUCN's Partner Birdlife International and the amniote life-history database (Myhrvold et al. 2015). Odonate traits (aquatic habitat, climate, and hindwing length, which is a surrogate for overall size and correlates with range size) were obtained through the OPDB and the IUCN.

For bats, we built a data frame containing 344 species which had full data for all traits under analysis: turnover, net diversity, speciation, extinction, extinction fraction, IUCN Red List ranking, body mass, dietary breadth, trophic level, range size, and superorder designation. For birds, our dataset contained 3,797 species with complete trait information for turnover, net diversity, speciation, extinction, extinction fraction, IUCN Red List ranking, body mass, clutch size, generation length, and extent of occurrence (a surrogate for range size). For odonates, we built a data frame containing 155 species that had full trait data for turnover, net diversity, speciation, extinction, extinction fraction, IUCN Red List ranking, aquatic habitat, climate, and hindwing length.

Estimating species-specific diversification rates

We used MiSSE (Missing State Speciation and Extinction; Beaulieu et al. 2020) to identify changes in diversification in each of our empirical trees. MiSSE is an extension of the Hidden State Speciation and Extinction model (HiSSE; Beaulieu & O'Meara 2016). Both the HiSSE and MiSSE models include hidden states, unobserved characters for species whose influence on diversification rate shifts can nonetheless be accounted for (e.g., a biologist may not consider geological factors, like soil acidity, that significantly control extinction rates in plants under consideration). Where MiSSE differs from HiSSE is that MiSSE (and associated MiSSE functions) operate as a completely trait-free model in which one only needs a tree to run it. The exclusion of traits allows MiSSE to track shifts in diversification by solely unknown factors, instead of drawing rates of diversification from certain traits. Specifically, we used the function *MiSSEGreedy* to assign anywhere from 1 to 26 different turnover and extinction fraction categories in a stepwise approach. First, *MiSSEGreedy* begins its search with equal rates for turnover and extinction fraction, and then the complexity of the model is gradually increased

until it reaches 26 rate categories for both parameters. Next, *MiSSEGreedy* runs through 26 models again, but this iteration has only one extinction fraction while it runs through 26 more categories of turnover, giving the user 52 possible models to average across. It should be stated that even though there is a possibility of 52 total models, the user can set a halting criterion so that once the models no longer improve the fit based on AICc (Hurvich & Tsai 1989), the search is stopped. Our halting criterion was set so that it stopped after three consecutive runs of not improving AICc by more than 10. The ancestral states were then reconstructed for each accepted model. Finally, we used model-averaging to estimate turnover, net diversity rates, speciation rates, extinction rates, and extinction fraction for all species at the tips of their respective phylogeny. These results provided our final measure of diversification rates for each clade.

Predicting extinction risk

In order to determine the macroevolutionary signal of extinction, we first examined diversification rate variation dependent on extinction risk across the chiropteran, avian, and odonate phylogenies. We conducted a phylogenetic ANOVA to test whether differences among species-specific turnover rate estimates can be predicted based on each species' Red List ranking. We treated the Red List category as binary to avoid creating an unequal ranking across the Red List categories that can come with treating this data as continuous (Jones et al. 2003; Boyles & Storm 2007). Specifically, we ask whether species we have designated as "at-risk" (species ranked as endangered, critically endangered, extinct in the wild, and extinct by the International Union for Conservation of Nature Red List) show different turnover rates compared to those we have designated "not at-risk" (species ranked as least concern, not threatened, and vulnerable). The phylogenetic ANOVA was conducted using the R package *phytools* (Revell 2012).

Finally, we used phylogenetic logistic regression and non-phylogenetic logistic regression to determine correlates of extinction risk. We treated our threat categories as binary to avoid creating an unequal ranking across the Red List categories that can come with treating categorical data as continuous (Jones et al. 2003; Boyles & Storm 2007). Non-phylogenetic regression models were included to account for the differences when models do not consider independent contrasts when analyzing related species. With our dependent variable being binary we used phylogenetic logistic regression (Ives & Garland 2009) to determine correlates of extinction risk. These regression models were run using the *phylolm* package (Ho & Ané 2014). Specifically, we used the function *phyloglm* to account for independent contrasts and the function g*lm* for our non-phylogenetic regression. Our base regression model used our binary extinction risk as our dependent variable, while using each individual trait, turnover, and an interaction between trait and turnover per clade as predictors (Red List ranking ~ trait + turnover + trait*turnover). We built our multivariate extinction risk models by selecting traits that were either identified as significant correlates of extinction risk for other groups of taxa or traits that were suspected to be significant for understudied clades.

RESULTS

Across all three clades, extinction risk was a not significant predictor of species-specific turnover rates (*Chiroptera*: $F_{678} = 0.014$, $P = 0.84$ *Aves*: ($F_{5,196} = 1.73$, $P = 0.22$; *Odonata*: $F_{530} = 0.67$, $P = 0.60$; Figures 1A-1F). This suggests that within these clades conservation status cannot be explained by turnover. Interestingly, in our phylogenetic regressions *Chiroptera* did not show a significant relationship between any of our predictor variables and our binary extinction risk (Table 1A.). We did find a negative correlation between the single predictor trait of range size and a positive correlation for dietary breadth with extinction risk for bats in our non-phylogenetic regression (Table 1B.).

In *Aves*, we found significant negative correlations between the predictors of clutch size and estimated area of occupancy (EOO), while generation length was positively correlated with extinction risk in our phylogenetic regression models (Table 1A.). That is to say that as birds' clutch size and range size increase their extinction risk decreases, and as their generation length increases their extinction risk increases. Significant relationships were also found between turnover and extinction risk in our body mass and generation length models, along with the interaction between turnover and generation length regression models (Table 1A.) Our non-phylogenetic logistic regressions reported that all the single traits (body mass, clutch size, EOO, and generation length) have generated a significant relationship with extinction risk. Turnover was found to be a significant predictor in our EOO and generation length models as well as the interactions between the traits clutch size, EOO, generation length, and turnover. (Table 1B.). For *Odonata*, we found no significant correlations between any of our traits and extinction risk in our phylogenetic and non-phylogenetic regression models.

DISCUSSION

As evidence for a sixth mass extinction has grown, it has become clear that we must prioritize conservation efforts more so than ever before. Previous research methods have focused on various life history traits as indicators of extinction risk (Purvis et al. 2000; Cardillo et al. 2005; Cooper et al. 2008; Böhm et al. 2016). Many conservation researchers are now taking macroevolutionary history into account when studying extinction risk (Davies et al. 2011; Verde Arregoitia et al. 2013; Jetz et al. 2014; Tonini et al. 2016; Greenberg & Moores 2017). We have demonstrated with a novel model that there is no detectable macroevolutionary signal between turnover rates and extinction risk in three distantly related lineages, *Aves*, *Chiroptera*, and *Odonata*. In other words, our analyses suggest that the increased background rates of extinction are likely better explained by more recent human mediated activities than a natural predisposition to go extinct, in these three taxonomic groups.

The majority of previous studies have no correlation between diversification rates and extinction risk (Jetz et al. 2014; Tonini et al. 2016; Verde Arregoitia 2017). However, a correlation has been found in more rapidly diversifying groups of angiosperms in the Cape of South Africa (Davies et al. 2011) and amphibians (Greenberg & Mooers 2017). One possible explanation for the differing results between the previous studies lies in the methods used to generate diversification rates. Issues can stem from Methods-of-Moments (Magallon & Sanderson 2001; Verde Arregoitia et al. 2013; Greenberg & Mooers 2017) in that their diversification rates stop at the genus level. Other studies have been focused on specific species in an isolated geographic area (Davies et al. 2011) or have allowed traits to influence their diversification rates (Jetz et al. 2014, Tonini et al. 2016). By allowing diversification rates to be estimated solely by the information present in a phylogenetic tree, we have shed a direct light on

the macroevolutionary signal of extinction risk. Another potential issue with the previous studies is that they have focused on a single taxonomic group per study. To resolve this, we analyzed three distantly related clades in *Aves*, *Chiroptera*, and *Odonata.*

Our analysis showed no correlation between diversification rates and extinction, meaning there is not a macroevolutionary indicator for these clades to be prone to extinction. This supports the hypothesis that the increase in current extinction rates is human driven (Ceballos et al. 2015). We did find significant relationships between extinction risk and the traits: clutch size, EOO, generation length, turnover (in our body mass and generation length regressions) and turnover's interaction with body mass for birds. Range size (EOO for our birds) has been shown to be a common correlate for extinction risk in a variety of taxa mammals (Purvis et al. 2000; Cardillo et al. 2005), frogs (Cooper et al. 2008), and squamate reptiles (Böhm et al. 2016) where species that have smaller range sizes were shown to be more vulnerable than those with larger ranges. Our phylogenetic regression models have shown that larger range sizes correlate with lower risks of extinction for birds. Generation time and low reproductive rates (clutch size) have also been found to be a correlate of extinction risk in other taxonomic groups (Purvis et al. 2000; Cardillo et al. 2005; Cooper et al. 2008). Our models indicate that increased clutch sizes can lower extinction risk and are in agreeance with other taxonomic groups, in that species of birds with larger clutch sizes were shown to be less vulnerable to extinction. Species who reproduce at a slower rate and with fewer offspring are often thought to be more vulnerable to extinction due to their inability to rapidly compensate to increased mortality rates (MacArthur & Wilson 1967). Finally, in bats and odonates, there was no significant relationship between any of our traits and extinction risk. This finding is contradictory with previous studies, which found that a

specialized diet can increase extinction risk in bats (Boyles & Storm 2007) and squamate reptiles (Böhm et al. 2016).

One possible reason for the disparity of significant predictors between bats, birds, and odonates could be due to data availability. We were able to collect trait information for 3,797 bird species while we only able to collect trait data for 344 bat species and 155 odonate species, highlighting the need to place higher priorities on studying and collecting trait information in under studied groups of organisms.

With the continuous growth and expansion of the human race across the planet, there will be an uptick in activities that can increase extinction rates (i.e., habitat fragmentation from land development, pollution, introduction of non-native species, etc.). As more evidence of the negative impacts of human-mediated activities on the natural world accumulate, it is our responsibility to understand our influence and alter our behaviors. We have shown that recent increases in modern extinction rates are not due to a macroevolutionary predisposition. Likely, the increase in modern extinction rates is a direct consequence of human-mediated extreme environmental degradation (Ceballos et al. 215). Our results underscore the fact that, now more than ever, we must research and work toward possible solutions to recover our planet's ecosystems and species to preserve them for future generations.

CONCLUSIONS

The Earth has experienced five mass extinction events to date, and many scientists agree that we are likely in the midst of a sixth due to a drastic increase in the background extinction rate. Numerous studies have pointed out that certain human activities such as, habitat degradation, pollution, and introduction of non-native species are likely responsible for the increased extinction rate. In addition to anthropogenic activities, certain animal life history traits like body mass, range size, and habitat specialization have been shown to be correlated with elevated extinction risks. Recent computational advances and increased availability of data have allowed researchers to start investigating possibility of evolutionary links to extinction risk. These past studies have found mixed results of a macroevolutionary signal of extinction risk.

However, earlier studies have been coarsely grained in their estimation of evolutionary rates, restricted to certain species in a specific area, allowed their estimations to be influenced by focal traits, and were focused on one taxonomic group per study. Our novel model *MiSSE*, and accompanying function *MiSSEGreedy*, has addressed these previous issues. We present a completely "trait-free" diversification rate estimation method that is species specific. We implemented this novel model on three distinct clades of animals, bats, birds, and odonates. Our results showed no evolutionary signal for being extinction prone in any of our three clades. We also found that the life history traits of larger clutch size and EOO in birds to be predictors of decreased extinction risk, while longer generation times lead to increased extinction risk. We did not find any correlates of extinction risk from biological traits in bats or odonates.

These results indicate that the possible cause for the modern-day increase in extinction rates is not due to an evolutionary predisposition but is instead more likely due to human mediated activities on the environment.

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TABLES AND FIGURES

Table 1. Results of eleven multivariate phylogenetic logistic regressions that were run using the function *phyloglm* in the R package *phylolm* to identify correlates of extinction risk. Slope values in bold are significant at p < 0.05. A) phylogenetic regression values. B) non-phylogenetic values.

| A Phylogenetic				
Chiroptera	**Body Mass**	**Range**	**Trophic**	**Diet**
Trait	1.171	-0.863	0.135	1.026
Turnover	-8.771	31.238	5.825	10.525
Trait **x Turnover**	1.370	-8.015	-11.439	-6.356
Aves	**Body Mass**	**Clutch Size**	**EOO**	**Gen.**
Trait	0.105	**-2.390**	**-0.995**	**4.869**
Turnover	**-0.483**	-0.749	0.022	**2.150**
Trait **x Turnover**	**5.004**	1.870	0.061	-2.154
Odonata	**Aq. Habitat**	**Climate**	**Hind Wing**	
Trait	0.270	0.485	2.540	
Turnover	-5.722	2.109	114.184	
Trait x Turnover	4.298	-0.885	-95.925	
B Non-phylogenetic				
Chiroptera	**Body Mass**	**Range**	**Trophic**	**Diet**
Trait	**0.098**	**-0.106**	0.008	**0.093**
Turnover	-0.346	1.242	0.492	0.859
Trait **x Turnover**	-0.004	-0.212	-0.518	-0.698
Aves	**Body Mass**	**Clutch Size**	**EOO**	**Gen. Length**
Trait	**0.055**	**-0.094**	**-0.057**	**0.267**
Turnover	0.023	**-0.037**	**0.082**	**0.101**
Trait **x Turnover**	-0.012	**0.079**	**-0.012**	**-0.121**
Odonata	**Aq. Habitat**	**Climate**	**Hind Wing**	
Trait	-0.003	0.010	-0.052	
Turnover	-0.124	0.007	0.093	
Trait x Turnover	0.063	-0.007	-0.086	
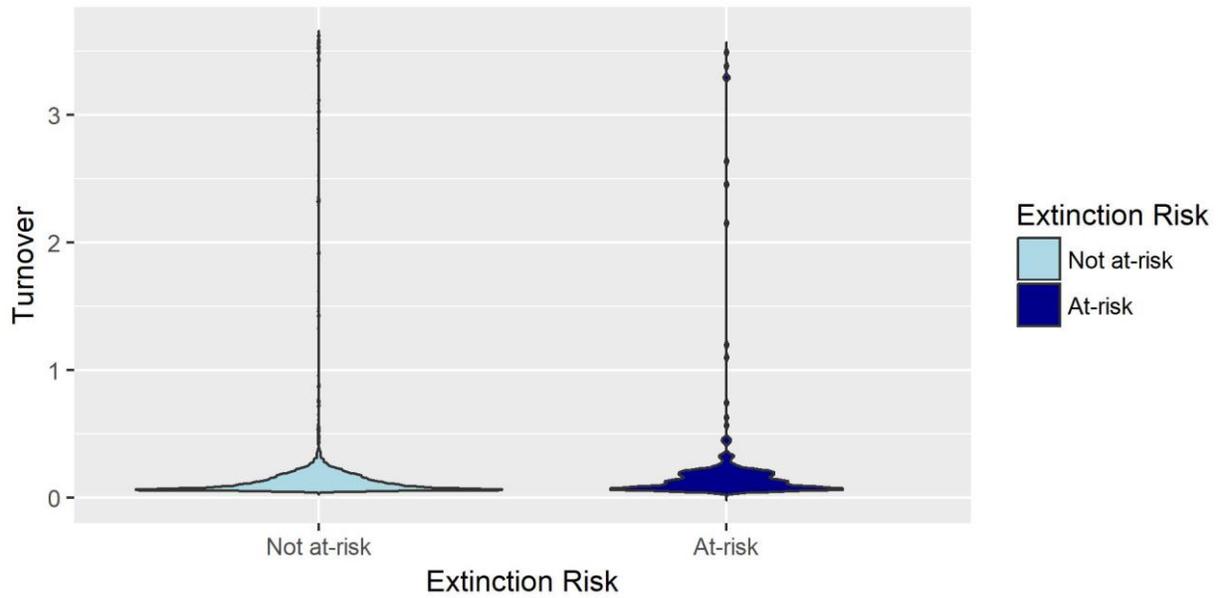
Figure 1A. Plot of phylANOVA results showing *Aves*' macroevolutionary signal of extinction risk. Lighter blue designates those species considered "Not at-risk" and darker blue represents species categorized as "At-risk". Turnover is measured in speciation + extinction per million years.
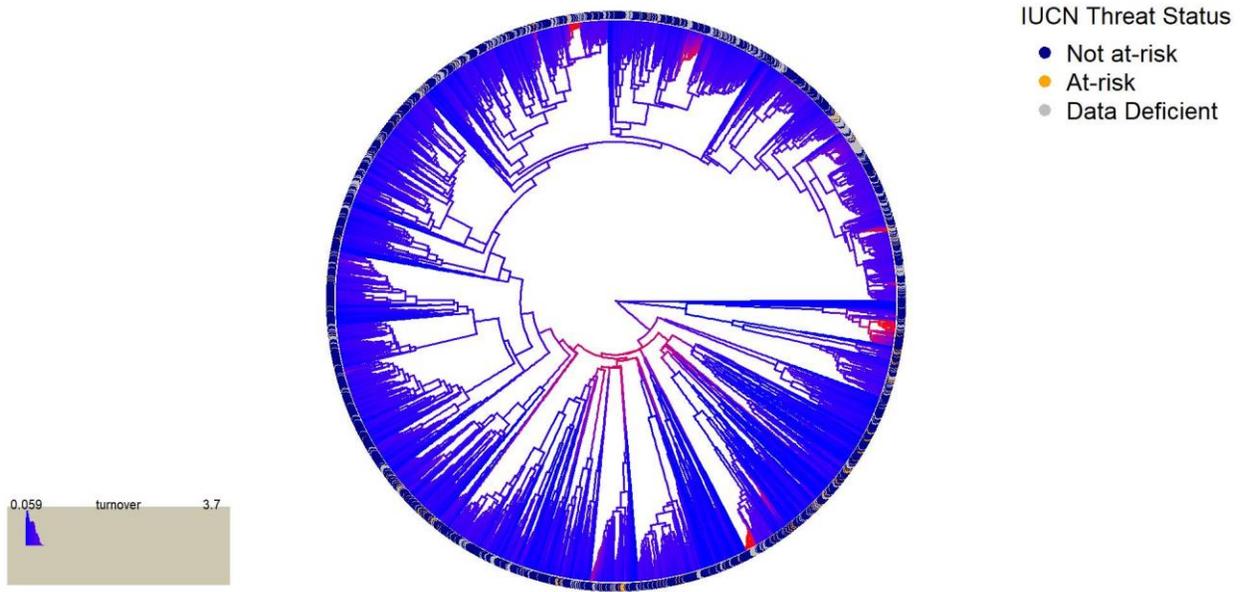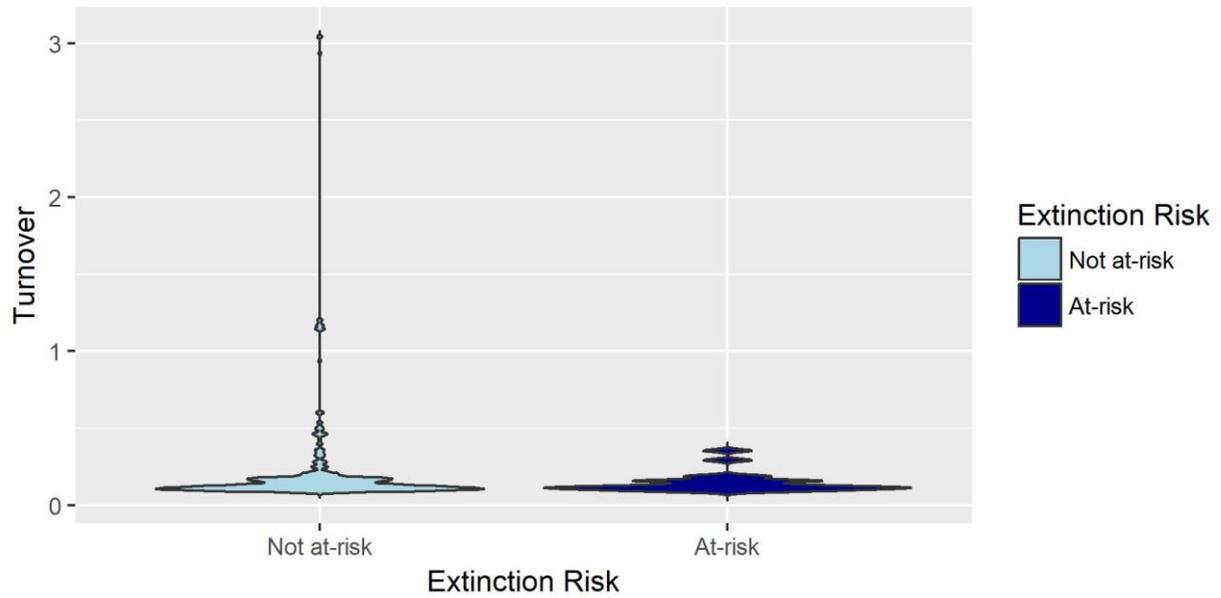
Figure 1B. MiSSEGreedy diversification results plotted, showing *Aves'* turnover phylogeny with extinction risk plotted at the tips. Blue coloration in the phylogeny represents lower levels of turnover, while red represents higher levels of turnover (speciation + extinction per million years). Dots at the tips colored dark blue show species designated as "Not at-risk", yellow-orange dots show the "At-risk" species, and grey dots show any species that the IUCN did not have extinction risk data for.

Figure 1C. Plot of phylANOVA results showing *Odonata*'s macroevolutionary signal of extinction risk. Lighter blue designates those species considered "Not at-risk" and darker blue represents species categorized as "At-risk". Turnover is measured in speciation + extinction per million years.
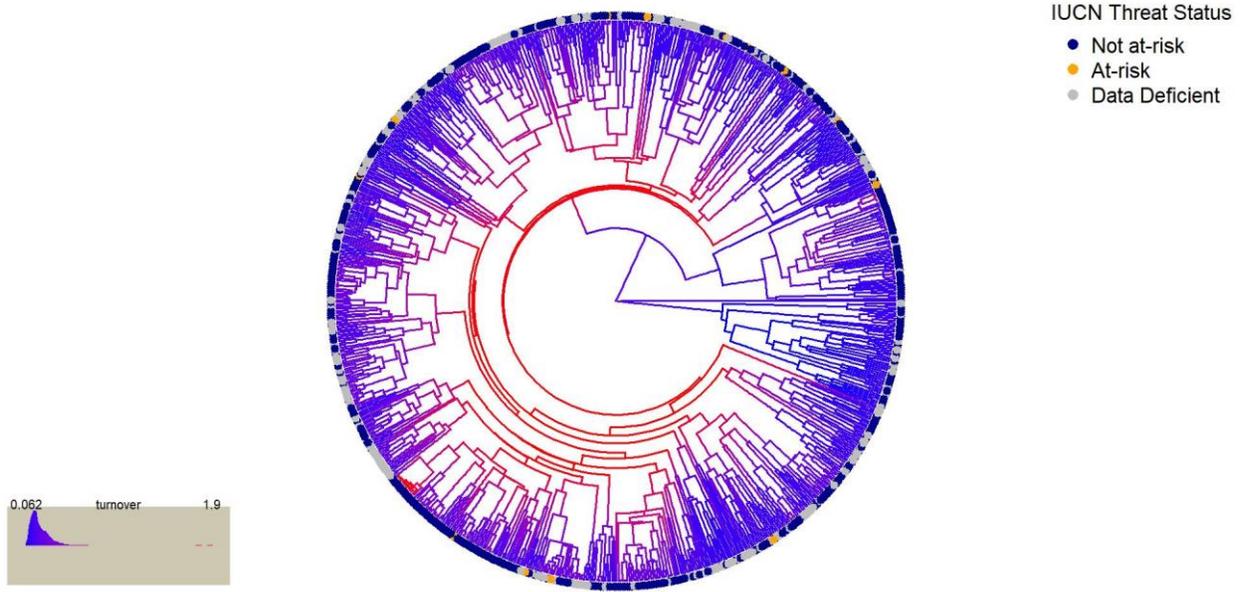
Figure 1D. MiSSEGreedy diversification results plotted, showing *Odonata*'s turnover phylogeny with extinction risk plotted at the tips. Blue coloration in the phylogeny represents lower levels of turnover, while red represents higher levels of turnover (speciation + extinction per million years). Dots at the tips colored dark blue show species designated as "Not at-risk", yellow-orange dots show the "At-risk" species, and grey dots show any species that the IUCN did not have extinction risk data for.
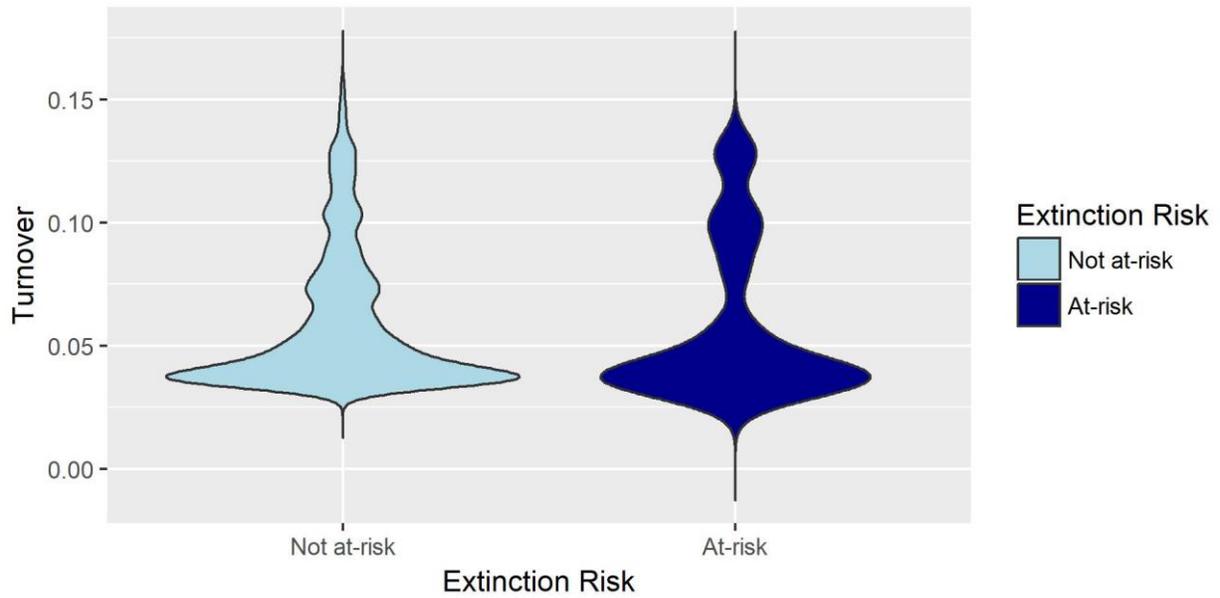
Figure 1E. Plot of phylANOVA results showing *Chiroptera*'s macroevolutionary signal of extinction risk. Lighter blue designates those species considered "Not at-risk" and darker blue represents species categorized as "At-risk". Turnover is measured in speciation + extinction per million years.
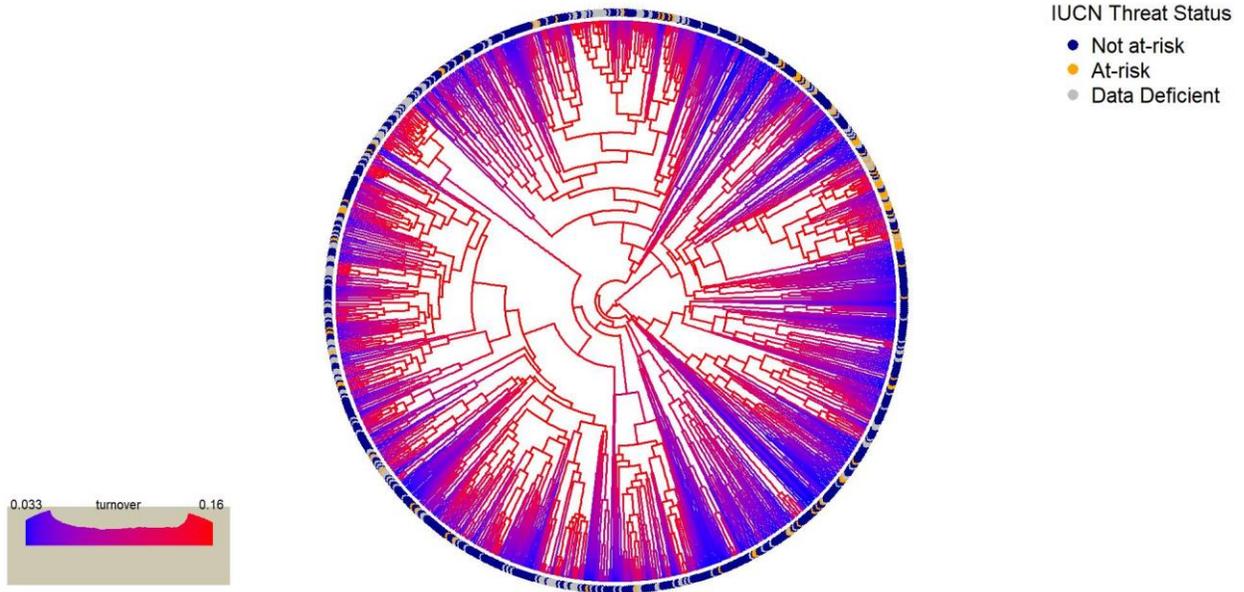
Figure 1F. MiSSEGreedy diversification results plotted, showing *Chiroptera*'s turnover phylogeny with extinction risk plotted at the tips. Blue coloration in the phylogeny represents lower levels of turnover, while red represents higher levels of turnover (speciation + extinction per million years). Dots at the tips colored dark blue show species designated as "Not at-risk", yellow-orange dots show the "At-risk" species, and grey dots show any species that the IUCN did not have extinction risk data for.