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Rapid radiations underlie most of the known diversity of life

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Rapid radiations, including adaptive radiations, are of considerable interest to evolutionary biologists, in large part because they are thought to underlie much of the species diversity of life. Yet, this fundamental idea has only been tested at a limited scale, within frogs. Here, we test this idea across living organisms and within many of the largest clades (e.g. animals, plants). Specifically, we quantify how much of Earth's species richness is contained within rapid radiations (clades with high net diversification rates). We find that among the major clades of living organisms and among land plant phyla and animal phyla, >80% of known species richness is contained within the few clades in the upper 90th percentile for diversification rates in each group. Thus, these exceptionally rapid radiations contain most of Earth's extant species diversity. Patterns were broadly similar using smaller clades (orders, families) and in insects and vertebrates, with the majority of species generally contained within clades in the upper 75th percentile. Results were also similar using large-scale clades defined by their ages instead of taxonomic ranks. Overall, these results show for the first time that most of the known species richness of life is explained by rapid radiations. Moreover, phenotypic evidence from previous studies suggests that some of the most species-rich rapid radiations across life, animals, and plants may also qualify as adaptive radiations.

KEYWORDS

adaptive radiation, biodiversity, diversification, macroevolution, species richness

1 Introduction

Adaptive radiation has become a central topic in modern evolutionary biology. Adaptive radiations are generally thought to involve rapid diversification of species (i.e. high rates of speciation minus extinction) accompanied by the evolution of ecologically relevant phenotypes (Schluter, 2000; Gillespie et al., 2020; Moen et al., 2021). One reason that adaptive radiations are of such great interest is that they are thought to underlie much of the species diversity and phenotypic diversity of life (Simpson, 1953; Schluter, 2000; Glor, 2010; Givnish, 2015). After all, if the idea of adaptive radiation applied to only a few exceptional clades with limited species diversity (e.g. African rift-lake cichlids, Caribbean anoles, Galápagos finches, sticklebacks), then it is unclear why adaptive radiation should be a broadly important topic in the field. However, with the exception of a recent study in

frogs (Morinaga et al., 2023), no studies have explicitly quantified how much of Earth's overall species richness is contained in clades resembling adaptive radiations.

The study in frogs (Morinaga et al., 2023) developed a framework for addressing how much species diversity and phenotypic diversity is explained by clades with different dynamics of diversification and phenotypic evolution (following Moen et al., 2021). Thus, they classified clades as resembling adaptive radiations (those with rapid phenotypic change and rapid species diversification), non-adaptive radiations (those with rapid species diversification but unexceptional rates of phenotypic change), adaptive non-radiations (with rapid phenotypic change but unexceptional diversification rates), and non-adaptive, non-radiations (with relatively slow rates of phenotypic change and species diversification). They found that in frogs ~75% of both species richness and phenotypic diversity was contained in clades resembling adaptive radiations, with above-average rates of diversification and phenotypic change. Here and throughout, we refer to diversification rates as the rate of speciation minus the rate of extinction, or the rate of species accumulation over time. For brevity, we use "diversification rate" instead of "net diversification rate".

Here, we apply this general framework (Moen et al., 2021; Morinaga et al., 2023) to ask: how much of life's current species diversity evolved from relatively rapid radiations? It would be very difficult to estimate comparable species-level rates of phenotypic change for hundreds of species in every major clade across life. Therefore, without phenotypic data and rates, one cannot distinguish adaptive radiations from non-adaptive radiations, adaptive non-radiations, and non-adaptive non-radiations. Nevertheless, we can quantify how much of life's species richness is contained within relatively rapid radiations (i.e. clades with high diversification rates) as opposed to non-radiations (i.e. clades with lower diversification rates).

Some previous analyses have found that variation in species richness of named clades of comparable rank (e.g. families, phyla) is strongly related to the diversification rates of these clades (Scholl and Wiens, 2016). However, this relationship alone says nothing about what proportion of species belong to rapidly diversifying clades as opposed to clades with more moderate diversification rates. For example, in both of the hypothetical examples in Figure 1, diversification rates and species richness are very strongly related (Example A: r^2 = 0.98, P=0.002; Example B: r^2 = 0.93, P=0.008; details in Figure 1, Supplementary Table S1). But in Example A, the most rapidly diversifying clade contains only 30% of the group's species richness, whereas in Example B, the most rapidly diversifying clade contains 80%. Overall, the contribution of rapid radiations to life's species diversity remains unknown, and is not addressed by the relationship between diversification rates and species richness.

Two factors now facilitate addressing this question. First, several recent studies have analyzed patterns of diversification rates and richness across all of life, and among major clades of land plants, animals, insects, and vertebrates (see Methods for details). Thus, many of the building blocks needed to address this question are now available. Second, recent studies have also shown that the clade-based estimator of diversification rates used in these studies (Magallón and Sanderson, 2001) yields estimates that are

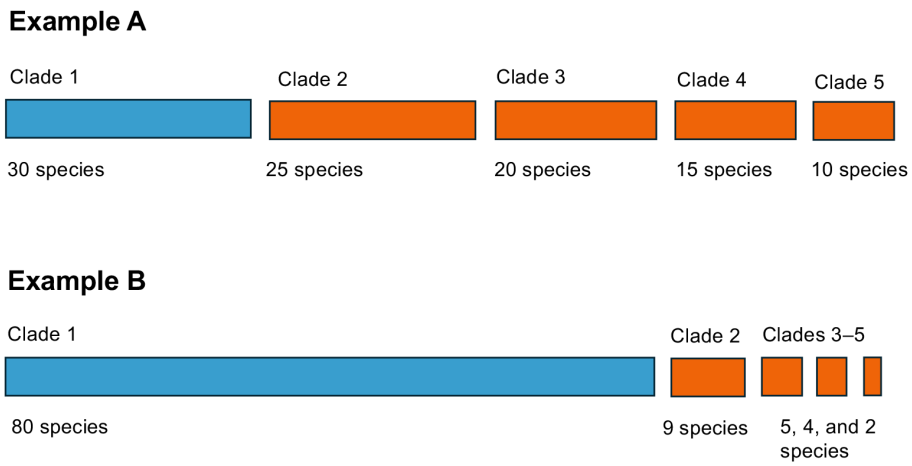

FIGURE 1
Two hypothetical examples, illustrating how the proportion of species in a group that are contained in the most rapidly diversifying clade(s) can vary. In Example A, the most rapidly diversifying clade (Clade 1) includes only 30% of the group's overall richness. In Example B, the most rapidly diversifying clade (Clade 1) contains 80%. Our hypothesis is that, within a given taxonomic group, the majority of species will belong to the most rapidly diversifying clade (Clade 1), as in Example B This hypothesis follows from the idea that rapid radiations (such as adaptive radiations) contain most of the diversity of life. The alternative hypothesis is that species richness will be more evenly distributed among clades (Example A), such that only a minority of species are in the most rapidly diversifying clade (Clade 1). Importantly, the proportion of species in a clade that are contained within the most rapidly diversifying clade can be independent of the relationship between diversification rates and species richness among clades. Thus both of these examples show a strong relationship between species richness and diversification rates among clades (Example A: r^2 = 0.98, P=0.002; Example B: r^2 = 0.93, P=0.008), regardless of whether the most rapidly diversifying clade contains a minority (Example A) or majority (Example B) of the group's overall species richness. For these examples, we assumed that all clades were 50 million years old and estimated diversification rates using the stem-group MS estimator with ε=0.5 (values in Supplementary Table S1).

strongly related to true diversification rates in simulations (r^2~0.7), including simulations in which speciation and extinction rates vary within clades over time and among subclades (Meyer and Wiens, 2018; Meyer et al., 2018). Empirical analyses of randomly selected clades across life (Yu and Wiens, 2024; see also Supplementary Dataset S1, Supplementary Table S2) show that these clade-based estimates (Magallón and Sanderson, 2001) generally are strongly related (r^2~0.8) to estimates from a new Bayesian species-based method (ClaDS; Maliet et al., 2019; Maliet and Morlon, 2022). These two lines of evidence suggest that these clade-based estimates are accurate and a reasonable proxy for estimates from this Bayesian species-level method. These clade-based estimators can estimate diversification rates given only the age and species richness of each clade (Magallón and Sanderson, 2001). Therefore, a well-sampled, fully-resolved, time-calibrated, species-level phylogeny is not necessary to estimate diversification rates within each clade using this clade-based approach, unlike ClaDS and many other estimators based on species-level branch lengths. By using this clade-based estimator, we can conduct analyses across all of life and within many major groups that lack a comprehensive species-level phylogeny (i.e. most of them).

In this study we quantify how much of life's species richness is contained within relatively rapid radiations. We do this across living organisms and within some of the most species-rich groups, including land plants, animals, insects, and vertebrates. For each of these five groups, we compile data on diversification rates and species richness for named clades. We then determine what proportion of the richness of each group is contained within clades with above-average diversification rates (following Morinaga et al., 2023), and those with diversification rates in the upper 75th, 90th, and 95th percentiles. These new analyses allow us to address the long-standing question of whether most of the diversity of life is contained within rapid radiations.

2 Materials and methods

2.1 Data sources

We first assembled data on species richness and diversification rates of named, ranked clades (e.g. kingdoms, phyla, classes, orders, families) from studies across all of life (Scholl and Wiens, 2016; Chen and Wiens, 2021), and among clades of land plants (Hernández-Hernández and Wiens, 2020), animals (Wiens, 2015a, Jezkova and Wiens, 2017), insects (Wiens et al., 2015), and vertebrates (Wiens, 2015b). These sources contained information on the richness, stem-group age, and estimated diversification rate for each named, ranked clade. We initially used this information directly for our calculations. We then explored the sensitivity of the results to new analyses based on alternative estimates of species richness, clade age, and the corresponding diversification rates (Supplementary Appendix S1). All species numbers refer to extant, described species. The taxonomy used here (e.g. ranking of groups as phyla vs. classes) followed the taxonomy used in those papers. We performed separate analyses comparing clades of the same rank (e.g. kingdoms), across life and within selected major groups (animals, plants, insects, vertebrates). Some clades were nested inside others (families within kingdoms) but nested clades were not included in the same analysis (Table 1).

For some groups, two or more trees were used to estimate diversification rates in the original studies (see details below): different trees can lead to different clade ages and different rate estimates. We performed separate analyses on each tree, to address the sensitivity of the results to these differences in clade ages.

Across life, we used the 17 higher-level clades (Supplementary Dataset S2) analyzed by Chen and Wiens (2021). The tree used in that study was from Parfrey et al. (2011). These clades encompass the groups usually ranked as kingdoms (bacteria, archaeans, fungi, animals, plants) and various clades interspersed among them that are usually referred to as protists and algae. These 17 clades collectively encompassed 2.068 million extant, described species (i.e. most of the 2.18 million species currently known; Bánki et al., 2024). We corrected errors in a few divergence dates reported in the supplementary materials in that study, such that the dates fully matched the methods given in that study. Note: all supplementary tables and appendices are available in the Supplementary Material, and all datasets (Supplementary Datasets S1–S27) are available on FigShare: https://figshare.com/s/09c264942aab86d1cc05.

These 17 clades do not include the "Asgard archaea", the recently discovered clades that are more closely related to eukaryotes than to other archaeans (Williams et al., 2013; Zaremba-Niedzwiedzka et al., 2017). We do not know of time-calibrated phylogenies that include them. However, those taxa encompass very few species (all described archaeans together include ~400 species; Bánki et al., 2024), and so their exclusion here should have minimal impact. Specifically, by excluding small clades with (presumably) low rates, it makes it less likely that most species will be in the few large clades with higher rates. The latter pattern is the pattern that we typically observed (see Results).

We also used the 2,545 families across life (Supplementary Dataset S3) analyzed by Scholl and Wiens (2016). These clades collectively encompass only 1.409 million species, because generally only clades included in time-calibrated phylogenies could be used to estimate diversification rates. These families encompassed most species of animals and plants, and many families of archaeans, bacteria, protists, and fungi. We did not analyze classes or orders across life because their coverage is relatively incomplete in that dataset. However, we analyzed orders of land plants and insects along with classes and orders of vertebrates. Our coverage was more complete in these groups.

For analyses across land plants, we initially used the data from Hernández-Hernández and Wiens (2020). These included all phyla (Supplementary Dataset S4), orders (Supplementary Dataset S5), and families (Supplementary Dataset S6), spanning 306,976 species. The ages were based on two time-calibrated trees, from Fiz-Palacios et al. (2011), which included all land plant families. These two trees account for the considerable uncertainty regarding the crown-group age of angiosperms, and span much of the range among most recent estimates (Sauquet et al., 2022). Specifically, in these two trees, the crown-group age of angiosperms ranges from 130–267

TABLE 1 Percentage of species diversity contained within clades with high diversification rates.

Group	Rank	Tree	Total clades	Total species	Clades above average	Percentage of species in high-diversification clades			
						Above average	75th	90th	95th
Life	Kingdoms	NA	17	2,068,138	6	99.0	91	90.5	16.7
Life	Families	NA	2,545	1,409,134	941	77.4	58.5	32.4	19.2
Plants	Phyla	FPU	10	306,976	5	98.0	94.8	90.6	90.6
Plants	Phyla	FPC	10	306,976	5	98.0	90.8	90.6	90.6
Plants	Orders	FPC	140	306,976	62	96.2	84.5	46.0	26.0
Plants	Orders	FPU	140	306,976	55	92.0	69.4	49.4	26.0
Plants	Orders	FPCM	140	306,976	61	96.6	84.5	59.2	39.2
Plants	Families	FPC	678	306,976	262	94.0	82.6	43.7	32.8
Plants	Families	FPU	678	306,976	257	91.9	74.5	54.6	30.8
Animals	Phyla	Tree 1	28	1,515,954	12	98.4	97.8	86.5	1.6
Animals	Phyla	Tree 2	28	1,515,954	13	99.2	97.3	86.5	1.6
Animals	Phyla	Tree 3	28	1,515,954	14	99.3	97.8	89.4	1.6
Animals	Families	NA	1,710	1,092,718	630	74.5	53.2	27.1	16.5
Vertebrates	Classes	Tree 1	12	66,113	6	97.9	38.6	15.6	15.6
Vertebrates	Classes	Tree 2	12	66,113	6	97.9	38.6	15.6	15.6
Vertebrates	Orders	NA	144	58,636	63	79.2	63.9	44.6	39.8
Vertebrates	Families	NA	778	51,763	299	81.1	61.4	26.4	10.4
Insects	Orders	NA	31	1,063,532	15	96.2	71.0	29.9	29.6
Insects	Families	NA	870	1,036,830	304	72.3	52.8	26.3	14.9

For each group, we give the rank of the clades used, the specific tree used, the total number of clades of that rank included, the total number of species contained among those clades, the number of those clades with above-average diversification rates (based on the stem-group estimator with ε=0.5), and then the percentage of all species contained among clades with above-average diversification rates and among clades with diversification rates in the upper 75th, 90th, and 95th percentiles. FPC = constrained tree (Fiz-Palacios et al., 2011). FPU = unconstrained tree (Fiz-Palacios et al., 2011). FPCM = constrained tree (Fiz-Palacios et al., 2011), modified to reflect the tree of Magallón et al. (2015). NA, not applicable (only a single tree was analyzed).

million years. One tree was called "Fiz-Palacios constrained" (FPC; constrained to the younger age) and the other "Fiz-Palacios unconstrained" (FPU). Because the trees had different ages for each clade, their diversification rates differed. For plant orders, we also used a third tree, which corresponded to the FPC tree but with the phylogeny in angiosperms following Magallón et al. (2015). We refer to this as the FPCM tree. We did not use the family-level version of that tree because it did not include all angiosperm families.

For analyses across animals, we used the three phylum-level trees used by Jezkova and Wiens (2017), originally from Wiens (2015a). These trees differ in the topological and age constraints used. These trees included 28 of the ~32 known animal phyla and collectively encompassed 1,515,954 animal species (Supplementary Datasets S7–S9). The four unsampled phyla contain relatively few species (~200 in total; Wiens, 2015a).

For animal families, we used the dataset of Scholl and Wiens (2016). This dataset included 1,710 families that encompass 1,092,718 species (Supplementary Dataset S10).

For insect orders, we used the dataset from Wiens et al. (2015). This dataset included 31 hexapod orders, encompassing 1,063,532 species (Supplementary Dataset S11). This included most known species (1.0 million; Bánki et al., 2024). Those authors used three trees, but here we used the tree from Misof et al. (2014), which was based on the most extensive molecular dataset (in terms of markers). We refer to hexapods here as insects, although hexapods also include three relatively small non-insect clades (Collembola, Protura, and Diplura).

For insect families, we used a portion of the family-level dataset from Scholl and Wiens (2016), which was originally from Rainford et al. (2014). We included data from 870 families (Supplementary Dataset S12), which encompassed 1,036,830 species (again, almost all known species).

For major vertebrate clades, we initially used the dataset of Wiens (2015b), which included 12 major clades (Supplementary Dataset S13). These are largely equivalent to classes (Bánki et al., 2024), but with Reptilia separated into Lepidosauria (lizards, snakes, tuatara), Testudines (turtles), Aves (birds), and Crocodylia (crocodilians). Wiens (2015b) included two trees, which differed only in the placement of the two clades of cyclostomes (hagfishes [Myxini], lampreys [Petromyzontiformes]). These 12 clades

together encompass 66,113 species. For vertebrate orders and families we used the dataset of Scholl and Wiens (2016). These taxa encompassed 58,636 species and 51,763 species, respectively.

The data described above were used for our baseline analyses. We also performed sensitivity analyses using alternative, updated estimates of clade ages, species numbers, and diversification rates (Supplementary Appendix S1). These results were generally very similar to the baseline results, strongly suggesting that the overall conclusions are robust to reasonable variation in these parameters.

2.2 Diversification rates

For diversification rates, we used the method-of-moments estimator (Magallón and Sanderson, 2001). We refer to this as the MS estimator hereafter. We focused on the MS estimator for stem-group ages:

$$r = 1/t_{*} \log[n(1-\varepsilon)+\varepsilon]$$

where r is the estimated net diversification rate, t is the clade's age, n is the clade's species richness, and ε is the assumed ratio of speciation to extinction rates (see below). For a given clade (e.g. phylum), the diversification rate is calculated based on its richness and age, not based on a summary of rate estimates for included taxa within that clade. Nevertheless, previous analyses (Scholl and Wiens, 2016) show that diversification rates of higher taxa (e.g. kingdoms) are strongly related to the mean rates of the clades within them (e.g. families).

We used the stem-group estimator because it allows clades to be included even when only one species from that clade is included in the tree, and is fully insensitive to incomplete phylogenetic sampling of species within clades (Meyer and Wiens, 2018) and largely insensitive to incomplete sampling among clades (Scholl and Wiens, 2016). By contrast, the crown-group estimator requires at least two species per clade, and is biased when taxon sampling does not encompass the crown-group age (i.e. the oldest split within the clade; Sanderson, 1996; Meyer and Wiens, 2018).

Yu and Wiens (2024) tested if rate estimates from the MS estimator are significantly related to those from ClaDS (a Bayesian estimator based on species-level phylogenies; Maliet et al., 2019; Maliet and Morlon, 2022). They found a strong relationship between these rate estimates across and among groups, using the crown-group MS estimator (animals: r^2 = 0.73; plants: r^2 = 0.94; fungi: r^2 = 0.93; bacteria: r^2 = 0.92; archaeans: r^2 = 0.67; across life: r^2 = 0.86). We found generally similar results using the stem-group estimator, except in bacteria and archaea (animals: r^2 = 0.67; plants: r^2 = 0.89; fungi: r^2 = 0.88; bacteria: r^2 = 0.04; archaeans: r^2 = 0.37; across life: r^2 = 0.82; Supplementary Table S2; Supplementary Dataset S1). Both ClaDS and the crown-group MS estimator focus on the age and relationships within the crown group, which might explain the weaker relationships between ClaDS and the stem-group estimator.

The MS estimator includes a correction (ε) for the inclusion of only living clades in rate estimation (Magallón and Sanderson, 2001). This correction is the assumed ratio between extinction and speciation rates across the tree (Magallón and Sanderson, 2001). For the stem-group estimator, simulations show that the value of ε used does not strongly affect the accuracy of the estimated rates (despite extensive variation in speciation and extinction rates among clades; Meyer and Wiens, 2018). Similarly, empirical studies show that ε generally has little impact on relationships between rates and richness and other conclusions (e.g. Wiens, 2015a; Scholl and Wiens, 2016; Chen and Wiens, 2021; Morinaga et al., 2023). Therefore, for simplicity, we primarily present results using an intermediate value (ε=0.5). However, we also performed analyses assuming a higher value (ε=0.9). The results were generally similar and often identical for the question asked here.

Some authors have criticized the MS estimator on the grounds that diversification rates estimated from fossils using this method do not necessarily predict later species richness in time series of fossils (Rabosky and Benson, 2021). Unsurprisingly, the MS estimator is unable to predict future mass extinctions and key innovations based on patterns of richness before these events occurred. However, the method is used to estimate diversification rates, not future richness. Therefore, their results do not address the usefulness of this method for estimating diversification rates. Moreover, those authors only subjected the MS estimator to this test. Thus, the MS estimator might actually be the best method according to this test, if other methods were included in the comparison. We note that the standard approach to evaluating diversification-rate estimators is instead using simulations in which the true diversification rates are known and one evaluates the correlation between the true and known rates. The MS estimator performs well by this standard criterion (i.e. with strong correlations between true and estimated rates; Meyer and Wiens, 2018; Meyer et al., 2018), and better than a widely used Bayesian species-level estimator (review in Wiens, 2024).

Those authors (Rabosky and Benson, 2021) also implied that the MS estimator performs poorly when the true diversification rates are not constant. Yet, simulations repeatedly show that this method yields similarly strong relationships between true and estimated rates, regardless of whether rates are constant within clades, variable among clades, or variable within clades (Kozak and Wiens, 2016; Meyer and Wiens, 2018; Meyer et al., 2018). These simulations included variable rates among subclades within a clade and rates that changed over time within a clade, including linear and exponential increases and decreases in extinction rates and speciation rates. Furthermore, the MS estimator does not estimate separate speciation and extinction rates, and therefore does not suffer from the problem of the potential non-identifiability of these rates (Louca and Pennell, 2020). Again, our conclusions are largely robust to different assumptions about the ratio of extinction to speciation rates (ε).

Another misconception is that strong relationships between diversification rates and richness are inevitable when using the MS estimator, because richness is used to calculate diversification rates. Simulations show that strong relationships between species richness and diversification from the MS estimator are not artifactual (Kozak and Wiens, 2016). Further, empirical analyses show that such strong relationships are not inevitable (Scholl and Wiens, 2016;

Yu and Wiens, 2024). For example, relationships between richness and diversification rates are generally weak when clades are chosen randomly instead of comparing clades of the same rank (Yu and Wiens, 2024). Simulations and empirical analyses also show that faster diversification rates in younger clades can decouple richness and diversification rates (Kozak and Wiens, 2016; Scholl and Wiens, 2016). Therefore, there is no circularity associated with examining the relationships between diversification rates and richness of clades, nor with examining the percentage of species that belong to clades with high diversification rates (a percentage which can vary extensively even when there is a strong diversification-richness relationship; Figure 1). Finally, under standard definitions of circularity, the method determines the results (which is not true here) and the results are then used to justify the method (also not true).

There has been debate about the extent to which diversification rates are dependent on the ages of clades (e.g. Henao-Diaz et al., 2019; Louca et al., 2022). However, the more important point is that the method used here gives strong relationships between true and estimated rates, even if there can be significant relationships between clade age and diversification rates (but not always; e.g. Yu and Wiens, 2024). Furthermore, if faster diversification rates were solely a function of clade age, then there is no reason to expect a few clades with exceptional diversification rates to contain most species richness. This latter pattern is the focus of our paper, not the relationship between diversification rates and richness. Named clades of the same rank do not have identical ages, but instead can have higher variance in clade ages than randomly selected clades, at least for the ranks examined here (families and above; Yu and Wiens, 2024).

2.3 Statistical analyses

For each group and each taxonomic rank (e.g. animal phyla; Table 1), we examined the distribution of diversification rates among clades and determined the mean and the upper 75th, 90th, and 95th percentiles. We then summed the number of species contained in the clades with above-average diversification rates, and calculated the percentage of the total number of species (all clades summed) that belonged to the above-average clades. We followed the same procedure for the upper 75th, 90th, and 95th percentiles.

Based on past statements about the importance of adaptive radiations for species diversity (see Introduction), we predicted that the majority of species in each group would belong to clades with above-average diversification rates (i.e. rapid radiations). For example, Morinaga et al. (2023) found that ~75% of frog species belonged to clades with above-average rates.

Note that this question is not based on a statistical comparison to a simulated null distribution. Instead, this question is about empirical patterns. Deviations in the observed richness of clades relative to simulated constant diversification rates or randomly varying diversification rates are not the question of interest here. Simulations show that variation in diversification rates can drive variation in richness among clades (Kozak and Wiens, 2016), but we do not know how much richness belongs to the most rapidly diversifying clades in empirical datasets. That is our question here.

Similarly, there is empirical evidence that diversification rates vary across living organisms and that this variation seems to underlie variation in species richness (e.g. Scholl and Wiens, 2016). Therefore, comparison to a null model of equal rates among clades (or over time) would be pointless: we already know that rates are not constant. But the fact that rates vary among clades does not tell us how species richness will be distributed among those clades (Figure 1).

2.4 Potential methodological issues

Here we describe several potential methodological issues, and the additional analyses performed to address them.

2.4.1 Use of named clades

The use of named clades can be controversial (Poe et al., 2021; Baker et al., 2021). For our study, it was essential to use named clades because phylogenies do not yet include all species in every group. Using named clades allowed us to assign species to clades without including every species in the tree. To address the sensitivity of the results to the particular set of clades used, we performed analyses for most groups using different taxonomic ranks (e.g. phyla vs. families). However, we do not expect the results to be identical when using higher taxonomic ranks (e.g. kingdoms, phyla) vs. lower-ranked clades (e.g. orders, families). Specifically, when using higher-ranked clades, richness may be aggregated into a smaller number of clades. When using lower-ranked clades, richness may be more evenly distributed among clades (because large clades will be divided into many subclades).

There are also different ways to divide species among major clades. We explored the impacts of making taxonomic groups based on the ages of clades at the largest taxonomic scales (kingdoms, plant phyla, animal phyla). Thus, the clades were aggregated based on their minimum ages rather than based on taxonomy alone. We describe the details of how this was done in Supplementary Appendix S2. Note that if we defined clades to have identical ages, then the diversification rates of clades would depend strongly on their species richness. We emphasize that these were merely alternative analyses designed to test the robustness of the results to alternative clade divisions.

We acknowledge that using named clades of the same rank (or unranked clades of similar age) influences the results relative to using randomly selected clades. Recent analyses (Yu and Wiens, 2024) demonstrated that when using randomly selected clades, the richness of clades tends to be more strongly related to their ages than to their diversification rates. Here, we focused on comparing clades of the same rank or similar age, such that there is the potential for richness to be divided more evenly among these clades (rather than biasing our results in favor of larger disparities). For example, when clades are selected randomly, most clades are very young and have very limited richness relative to older clades (Yu and Wiens, 2024).

2.4.2 Non-comparability of species

Another potential issue is the idea that species are not comparable across life. However, across most living organisms, species are typically united by gene flow with their conspecifics (Hernández-Hernández et al., 2021). Although bacteria might appear to be an exception, recombination occurs between closely related individuals in >90% of examined bacterial species (Diop et al., 2022). Given this, bacterial species may be generally comparable to species in other groups (Bobay and Ochman, 2017). There are also asexual eukaryote species, but these solely or predominantly asexual groups appear to have limited species diversity (Chen and Wiens, 2021). Nonetheless, to partially address this issue, we performed a set of analyses using only eukaryotic species.

We note that our study relies on previous taxonomy and species delimitation. We recognize that diverse lines of evidence can be used to recognize species, and that most presently described species have traditionally been recognized based on morphological evidence. We think that morphological data should provide a minimum estimate of species numbers, even if these morphology-based species contain many morphologically cryptic species. We addressed how large numbers of undescribed species would impact our conclusions with focused analyses (see next section). Importantly, the larger projections of undescribed species numbers explicitly incorporate morphologically cryptic species (Larsen et al., 2017).

2.4.3 Described vs. undescribed species

The most important issue for our conclusions may be that many species remain undescribed. These undescribed species could number in the millions, billions, or trillions (Mora et al., 2011; Locey and Lennon, 2016; Larsen et al., 2017; Li and Wiens, 2023; recent review in Wiens, 2023).

Chen and Wiens (2021) estimated richness and diversification rates among 17 kingdom-level clades using projections of undescribed richness (largely from Larsen et al., 2017). We also performed analyses using these projections, including both "low" projected richness (282 million species across life) and high projected richness (2.2 billion). The lower value might still be considered unrealistically high, but these analyses were intended to address the robustness of our conclusions to species numbers that are very different from current numbers of described species. The number of bacterial species is especially uncertain (Wiens, 2023), so we included analyses both across all kingdoms and among eukaryotes only.

2.4.4 Incomplete sampling of clades and species

Our sampling of higher-level clades is nearly complete (e.g. kingdoms, plant and animal phyla), such that the sampled clades incorporate most known species within each group. However, some analyses of lower-level clades did not include every named taxon (i.e. they were not present in the same time-calibrated tree as the others) and so did not include all species (e.g. families across life [~70% of species included], animals [~67%], and vertebrates [~78%]). The impact of this sampling on our analyses is difficult to address. However, our conclusions from families are similar across groups, regardless of whether those groups have relatively complete sampling of families (e.g. plants, insects) or less complete sampling (e.g. life, animals). Therefore, it seems unlikely that this factor explains our results.

2.4.5 Variation in rates within clades

We appreciate that some readers might be skeptical of our results because diversification rates vary within clades. Our measure of diversification for each clade reflects the overall rate within that clade, which (in effect) averages over time and among subclades within each clade. Diversification rate is a continuous variable, and we expect it to vary extensively among subclades and over time. Furthermore, some clades may have an overall fast rate primarily because of an exceptional subclade with a fast rate (e.g. angiosperms within plants). But this general pattern could apply to any clade at any level. We dealt with this issue primarily by exploring patterns at different taxonomic levels (e.g. among kingdoms, phyla, orders, and families). It would be problematic to selectively include and exclude subclades based on variation in their rates. Furthermore, we note again that diversification rates of higher taxa tend to be strongly related to the mean rates of the clades within them (Scholl and Wiens, 2016).

3 Results

Among known species, we found that clades with above-average diversification rates generally encompassed >70% of the species in each major clade (Table 1). Furthermore, when considering higher-level clades (kingdoms, phyla), those clades with exceptional diversification rates (upper 90th percentile, 10% of the clades) generally included >85% of the species in each group (Figures 2, 3; Table 1). However, the clades with the fastest diversification rates (upper 95th percentile) often contained only a minority of species. When clades were subdivided into lower ranking taxa (e.g. families), richness was more evenly distributed among clades (Table 1), but the majority of species in each group generally belonged to those clades in the upper 75th percentile for diversification rates (Figure 3, Table 1). We describe these results in detail for each taxonomic group below.

Across 17 kingdom-level clades spanning all of life (Figure 2; Table 1; Supplementary Dataset S2), we found that the six clades with above-average diversification rates encompassed 99% of known species, and the two clades in the upper 90th percentile (animals and land plants) included 90% of known species (Figure 3). However, the most rapidly diversifying of these clades (land plants) included only 17% of known species. Among these 17 clades, land plants are much younger than animals but have higher diversification rates and less richness. When these clades were subdivided into families (Supplementary Dataset S3), the majority of species (58%) were in clades in the upper 75th percentile for diversification rates, but with only a minority of species among those clades in the upper 90th and 95th percentiles (Table 1).

Among the 10 phyla of land plants (Figure 2; Table 1; Supplementary Dataset S4), 98% of species belonged to clades with

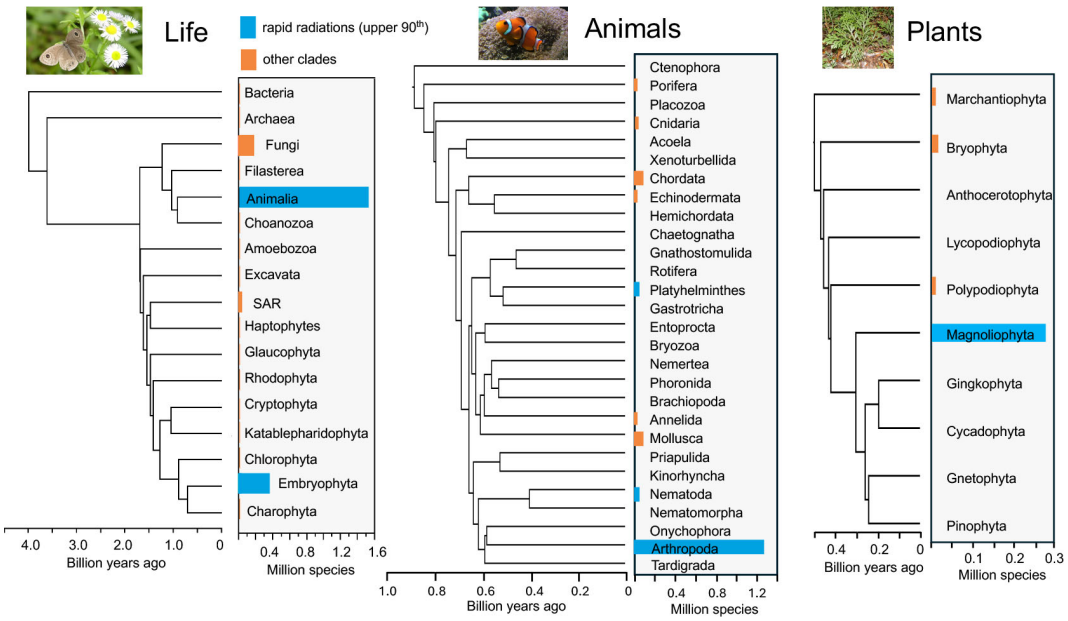

FIGURE 2
Phylogeny, divergence times, and species richness of major clades across life, animals, and plants. For each group, we show a time-calibrated phylogeny and the species richness of each higher taxon. The species richness of clades that are in the upper 90th percentile for diversification rates (rapid radiations) are indicated with blue, whereas richness for other clades are shown in orange. Many of the clades with lower diversification rates are barely visible or not visible because they have relatively low species richness (note that all rapid radiations are visible). However, not every group with relatively high richness has rapid diversification rates (e.g. fungi, chordates, mollusks, bryophytes). We did not use a log scale here, in order to better show the relative differences in richness among groups. The tree for kingdom-level clades across life is from Chen and Wiens (2021; modified from Parfrey et al., 2011), the tree for animal phyla is from Wiens (2015a; Tree 2), and the tree for land plant phyla is the constrained tree from Fiz-Palacios et al. (2011). The data on species richness, clade ages, and diversification rates used here are given in Supplementary Dataset S2 (life), Supplementary Dataset S4 (plants), and Supplementary Dataset S8 (animals, Tree 2). Images of plants and animals are from John J. Wiens.

above-average diversification rates, and 91% belonged to a single clade (angiosperms, Magnoliophyta) with the fastest diversification rate (95th percentile). Among 140 land plant orders (Figure 3; Table 1; Supplementary Dataset S5), 92–97% of species belonged to orders with above-average diversification rates (ranges refer to different trees), whereas 69–84% belonged to those in the upper 75th percentile and 46–59% in the upper 90th percentile. Among the 678 land plant families (Table 1; Supplementary Dataset S6), 92–94% of species were in families with above-average diversification rates, 74–83% were in those with high diversification rates (upper 75th percentile; Figure 2), and 44–55% were in those with exceptional diversification rates (upper 90th percentile).

Among 28 phyla of animals (Figure 2; Table 1; Supplementary Datasets S7–S9), 97–98% of species belonged to phyla with high diversification rates (75th percentile) and 86–89% were in phyla with exceptional diversification rates (90th percentile; Figure 3). These patterns are largely explained by the relatively rapid diversification and numerical dominance of arthropods (Figure 2). Among 1,710 animal families (Table 1; Supplementary Dataset S10), 75% of included species belonged to clades with above-average diversification rates and 53% belonged to those with high diversification rates (upper 75th percentile; Figure 3). Only a minority of species (16–27%) belonged to families with exceptional diversification rates (upper 90th–95th percentiles).

Among 31 insect (hexapod) orders (Table 1; Supplementary Dataset S11), 96% of species belonged to those with above-average diversification rates, and 71% belonged to those with high diversification rates (75th percentile; Figure 4). Only a minority of species belonged to orders with exceptional diversification rates (90th and 95th percentile). Among 870 insect families (Table 1; Supplementary Dataset S12), 72% of species belonged to families with above-average diversification rates, and 53% belonged to families with high diversification rates (75th percentile).

Among the 12 major clades of vertebrates (classes or equivalent; Table 1; Supplementary Dataset S13), 98% of species belonged to clades with above-average diversification rates (Figure 4), but only a minority of species (16–39%) belonged to clades with high and exceptional diversification rates (75th to 95th percentiles; Figure 4). This pattern occurred because almost half of vertebrate species belonged to the clade Actinopterygia (ray-finned fishes), which has diversification rates that are merely above-average and not high or exceptional (Supplementary Dataset S13). For 144 vertebrate orders (Supplementary Dataset S14), 79% of species were in orders with above-average rates, and 40–64% belonged to orders with high and exceptional rates (75th to 95th percentiles). Among 778 vertebrate families (Supplementary Dataset S15), 81% of species richness was in families with above-average rates, 53% was in families with high rates (75th percentile), and a minority of species belonged to families with exceptional rates (90th and 95th percentiles).

These baseline results utilized the MS estimator with ε=0.5. Results were similar using ε=0.9 (Supplementary Table S3). The most notable difference was among animal phyla: using ε=0.9, most

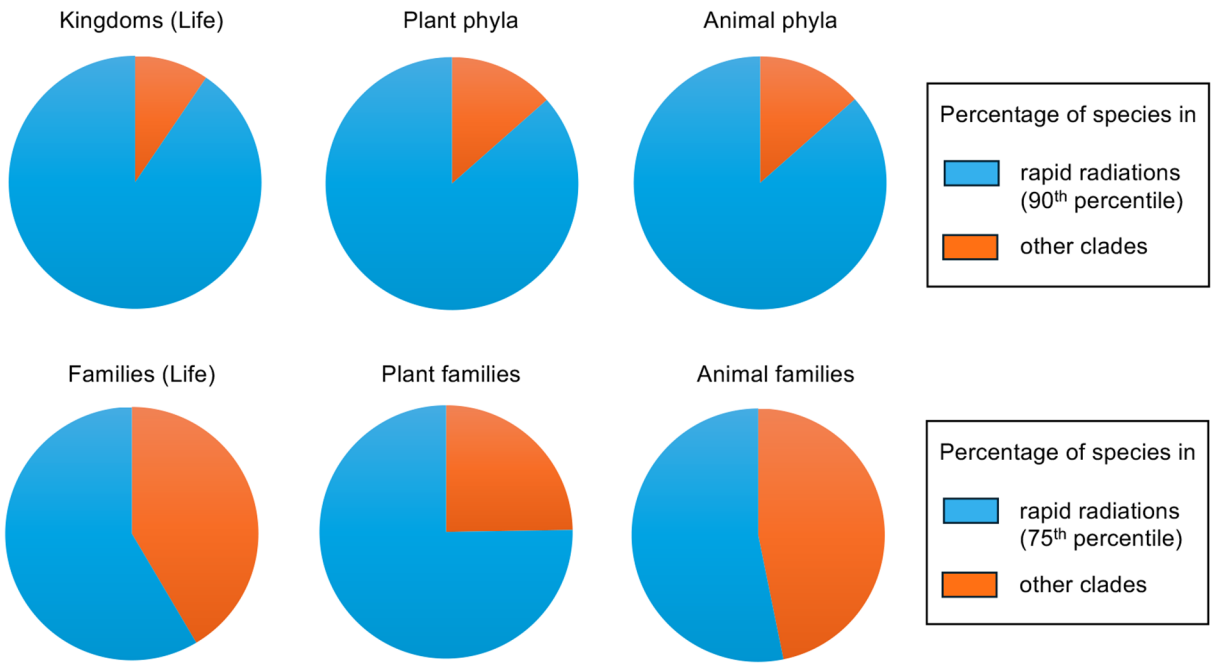

FIGURE 3
The percentage of species belonging to rapid radiations and to other clades, across life and across plants and animals. The top row shows that most known species richness belongs to clades that are in the upper 90th percentile for diversification rates. The bottom shows that species are more evenly distributed among families, but that the majority of species nevertheless belong to clades with relatively rapid diversification rates (upper 75th percentile). The results for plants are based on the FPU tree (unconstrained tree of Fiz-Palacios et al., 2011). Data for all trees, taxonomic ranks, and diversification cutoffs are given in Table 1.

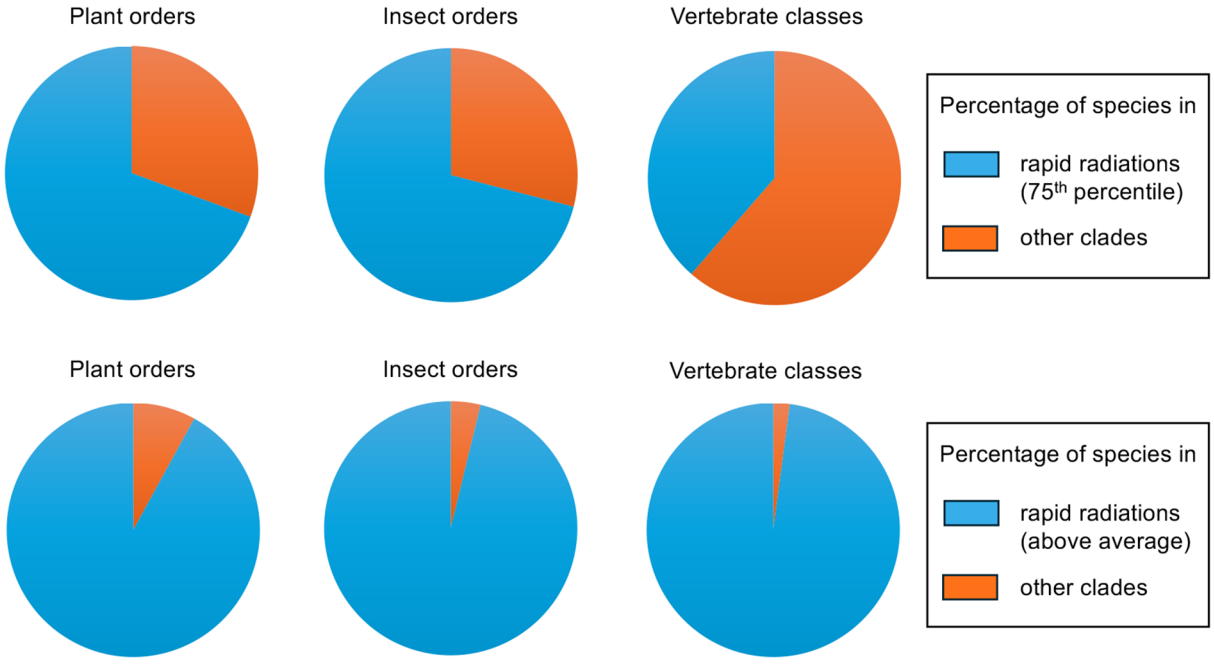

FIGURE 4
The percentage of species richness belonging to rapid radiations and other clades, among land plant orders, insect orders, and vertebrate classes. The top row shows that most known species richness belongs to clades that are in the upper 75th percentile for diversification rates for plant and insect orders, but not for vertebrate classes. The bottom row shows that most known species in these groups do belong to clades with above-average diversification rates. The results for plants are based on the FPU tree (unconstrained tree of Fiz-Palacios et al., 2011). Data for all trees, taxonomic ranks, and diversification cutoffs are given in Table 1.

species richness (83%) was in the clade with an exceptionally fast diversification rate (Arthropoda; upper 95th percentile), but using ε=0.5 the clade with the fastest rate (Nematoda) contained relatively little known richness (2%).

We then revisited the higher-level analyses with new estimates of diversification based on new estimates of species richness (Table 2; Supplementary Appendix S1; animal phyla: Supplementary Datasets S16–S18; insect orders: Supplementary Dataset S19), and new estimates of richness combined with new estimates of clade ages (vertebrate classes: Supplementary Dataset S20; land plant phyla: Supplementary Dataset S21). The results were very similar, in terms of how much richness was contained within rapidly diversifying clades. The only substantive difference was (again) that in some analyses of animal phyla with revised richness data, the clades with exceptional rates (95th percentile) included 78% of the species (for Trees 1 and 2), instead of 2%.

We also examined the impact of using projected species numbers across life (Table 3; Supplementary Dataset S22), instead of only described species. We found that only 22–23% of projected species belonged to clades with above-average diversification rates. This disparate pattern arose because in these projections ~77% of all species are bacteria, which have below-average diversification rates, given their ancient age relative to other clades.

Considering only eukaryotes (Table 3; Supplementary Dataset S22), then among the 15 kingdom-level clades, 99.9% of projected species belonged to those with above-average diversification rates and 68.1–99.9% belonged to those with high diversification rates (75th percentile; range represents low and high richness projections). Only a minority of projected species belonged to clades with exceptional diversification rates (90th and 95th percentiles).

Additionally we examined the impact of defining the largest-scale clades based on clade ages rather than taxonomic ranks alone (Table 4). Among kingdoms, we used 14 clades that were each at least 1 billion years old (range=1.08–4.20 billion years; Supplementary Dataset S23) and then 9 clades that were at least 1.5 billion years old (range=1.55–4.20 billion years; Supplementary Dataset S24). Using this approach, almost all species richness (98–99%) was in clades with above-average or high diversification rates (75th percentile). With these 14 clades, 74% of species richness was in clades with exceptional diversification rates (90–95th percentile), but only 18% was when using the 9 clades that were >1.5 billion years old (similar to the original results). Among land plant phyla (Table 4), we used 6 clades that were at least 400 million years (Myr) old (range=459–556 Myr or 431–511 Myr depending on the tree; Supplementary Dataset S25): the results were almost identical to those using 10 phyla (with 91% of richness contained among clades with exceptional diversification rates; 90th–95th percentile). Among animal phyla (Table 4; Supplementary Datasets S26–S27), we used seven clades that were at least 700 Myr old (Tree 1: range=757–1,031 Myr; Tree 2: 703–876). Results were similar to those based on 28 phyla, except that 94% of richness was contained in clades with exceptional diversification rates (90th–95th percentile). In summary, using clades defined based on clade ages gave similar results to the original analyses based on named clades, but with the most rapidly diversifying clades often encompassing more richness.

4 Discussion

Rapid radiations are thought to contain most of life's species diversity, but this idea has not been tested explicitly. Here, we find that most known species belong to a small fraction of higher-level clades with relatively rapid diversification rates. We show this pattern across the major clades of life and among the major clades of plants and animals (Figures 2, 3; Table 1).

These results are not apparent from previous studies nor do they appear to be methodological artifacts. Given previous analyses showing a relationship between diversification rates and species richness across life (Scholl and Wiens, 2016), one might argue that it is inevitable that those clades with more species would have higher diversification rates. But the patterns described here depend on how

TABLE 2 Percentage of species diversity contained within clades with high diversification rates, using alternative estimates of species numbers and clade ages.

Group	Rank	Tree	Total clades	Total species	Clades above average	Percentage of species in high-diversification clades			
						Above average	75th	90th	95th
Land plants	Phyla	new	10	299,162	6	99.4	92.3	88.4	88.4
Animals	Phyla	Tree 1	28	1,523,141	12	97.8	96.1	87.8	77.8
Animals	Phyla	Tree 2	28	1,523,141	13	99.1	95.2	80.6	77.8
Animals	Phyla	Tree 3	28	1,523,141	14	99.2	95.9	87.8	1.2
Vertebrates	Classes	new	12	71,408	6	98.0	39.7	14.9	14.9
Insects	Orders	NA	31	989,369	16	95.5	71.9	34.4	34.1

See Supplementary Appendix S1 for details about alternative estimates. For each group, we give the rank of the clades used, the specific tree used, the total number of clades of that rank included, the total number of species contained among those clades, the number of those clades with above-average diversification rates (based on the stem-group estimator with ε=0.5), and then the percentage of all species contained among clades with above-average diversification rates and among clades with diversification rates in the upper 75th, 90th, and 95th percentiles. NA, not applicable (only a single tree was analyzed). new=a new tree was analyzed, different from those used in the baseline analyses.

TABLE 3 Percentage of species diversity contained within clades with high diversification rates, using projected species numbers instead of numbers of described species.

Group	Rank	Total clades	Total species	Clades above average	Percentage of species in high-diversification clades			
					Above average	75th	90th	95th
Life (low)	Kingdom	17	281,967,821	6	22.7	15.4	7.4	7.2
Eukaryotes (low)	Kingdom	15	63,967,444	6	99.9	68.1	32.4	31.9
Life (high)	Kingdom	17	2,238,367,821	6	22.0	22.0	7.3	7.3
Eukaryotes (high)	Kingdom	15	492,367,444	6	99.9	99.9	33.2	33.1

We used two projections for overall species richness, one that is relatively low and one that is relatively high. For each group, we give the rank of the clades used, the total number of clades of that rank included, the total number of species contained among those clades, the number of those clades with above-average diversification rates (based on the stem-group estimator with ε=0.5), and then the percentage of all species contained among clades with above-average diversification rates and among clades with diversification rates in the upper 75th, 90th, and 95th percentiles.

species are divided among clades with different diversification rates, not the relationship between diversification rates and species richness among clades (see example in Figure 1). We show that at the highest taxonomic levels (kingdoms, phyla), these rapidly diversifying clades (upper 90th percentile) contain >85% of all species (Table 1). This pattern is also not obvious because the clades with the very fastest diversification rates (95th percentile) need not contain the majority of species (Table 1). For example, among kingdom-level clades, plants have faster diversification rates than animals, but plants contain only a small minority of known species. These patterns of disparity in richness among clades are also reduced using lower taxonomic ranks (e.g. families). When using lower taxonomic ranks, the large, rapidly diversifying clades are subdivided into smaller clades that must each contain a smaller proportion of the group's overall species richness. Nevertheless, even when using these lower taxonomic ranks, a minority of rapidly diversifying clades (upper 75th percentile) typically contains the majority of a group's species richness (Table 1; Figure 2). These overall patterns were generally robust to alternative estimates of clade ages, richness, and diversification rates (Tables 2, 3; Supplementary Table S3), and the results for families were similar regardless of whether sampling of families in the group is largely complete or spanned ~67–78% of the group's species (Table 1). We obtained similar results using ages to define clades, rather than using named ranked taxa (Table 4). Thus, our results are not simply contingent on how humans divide the Tree of Life into named clades (see also Table 1, showing results from alternative divisions of species into clades). Furthermore, the estimator of diversification rates used here gives estimates that are strongly related to the true rates (in simulations) and to a Bayesian species-based estimator (ClaDS) in empirical analyses. Thus, there is no basis for claiming that this method is problematic. Our goal was not to test the overall relationship between diversification rates and richness, but even if it were, such relationships are neither inevitable nor artifactual (Kozak and Wiens, 2016) nor are they circular (see Methods). Indeed, other empirical studies have suggested that diversification rates often do not underlie richness patterns (McPeek and Brown, 2007; Rabosky et al., 2012; Hedges et al., 2015; Yu and Wiens, 2024), further showing that our results are not obvious. On the other hand, our goal was to empirically test a long-standing idea in the macroevolutionary literature, and so our results (which support that idea) are not shocking from that perspective.

The most important sensitivity of the results related to the inclusion of projected, undescribed bacterial species (Table 3). At

TABLE 4 Percentage of species diversity contained within clades with high diversification rates, using age-based clade definitions.

Group	Rank	Tree	Total clades	Total species	Clades above average	Percentage of species in high-diversification clades			
						Above average	75th	90th	95th
Life	1.0 Bya	NA	14	2,068,138	5	99.4	99.0	73.8	73.8
Life	1.5 Bya	NA	9	2,068,138	3	99.3	98.0	17.6	17.6
Plants	400 Mya	FPU	6	306,976	3	98.0	90.9	90.9	90.9
Plants	400 Mya	FPC	6	306,976	3	98.0	90.9	90.9	90.9
Animals	700 Mya	Tree 1	7	1,515,954	3	99.4	98.5	93.5	93.5
Animals	700 Mya	Tree 2	7	1,515,954	4	99.9	98.5	93.5	93.5

For each group, we give the age of the clades used (Bya=billion years ago; Mya=million years ago), the specific tree used, the total number of clades of that rank included, the total number of species contained among those clades, the number of those clades with above-average diversification rates (based on the stem-group estimator with ε=0.5), and then the percentage of all species contained among clades with above-average diversification rates and among clades with diversification rates in the upper 75th, 90th, and 95th percentiles.

present, there are only ~10,000 described species of bacteria (Bánki et al., 2024). Among recent estimates of actual bacterial richness, even lower estimates are in the millions (Louca et al., 2019) and upper estimates are in the billions or trillions (Locey and Lennon, 2016). Because bacteria are very old relative to other major clades, they would still have relatively low overall diversification rates even if they contained billions or trillions of species (see calculations in Scholl and Wiens, 2016). Thus, if actual bacterial richness really is much higher than described richness for other groups, then a clade with low diversification rates would contain the majority of species across life (unlike our other results). Therefore, we caution that our results apply primarily to known species diversity. Nevertheless, if we restrict ourselves to eukaryotes, then the majority of species belong to clades in the upper 75th percentile for diversification rates, even if there are tens of millions of undescribed eukaryotic species. We also acknowledge that these projections of undescribed richness could be incorrect, which is why we treat our analyses of known diversity as the baseline.

Our focus here has been on how much species richness is contained within rapid radiations, but how many of these rapid radiations might be adaptive radiations? There is considerable debate about the definition of adaptive radiation (e.g. Glor, 2010; Givnish, 2015; Hernández-Hernández, 2019; Gillespie et al., 2020; Moen et al., 2021). Some standard definitions require relatively rapid speciation within a clade, along with evidence for correlations between phenotypic traits and environments among species and the functional utility of the traits (Schluter, 2000; Gillespie et al., 2020). Many groups analyzed here may meet this broad criterion. Previous analyses have identified specific phenotypic traits and/or key innovations that seem to drive rapid diversification in these groups. Across life, a key trait that seems to explain rapid diversification rates is multicellularity (Chen and Wiens, 2021), which may have paved the way for much of the phenotypic variability (e.g. different cells and tissue types) in plants, animals, and fungi (Carroll, 2001). Within land plants, insect pollination seems to be a key trait that helps explain the rapid diversification of angiosperms relative to other land plant clades (Hernández-Hernández and Wiens, 2020), as suggested by many previous authors (e.g. Raven, 1977; Stebbins, 1981; Niklas, 2016). Insect pollination may drive considerable phenotypic diversification in flowers (Grant, 1949; Harder and Barrett, 2006) and much plant speciation (Grant, 1949; Sargent, 2004; Kay et al., 2006; van der Niet et al., 2014). In animals and vertebrates, terrestriality seems to be an important driver of diversification among major clades (Wiens, 2015a; 2015b; Jezkova and Wiens, 2017), and the invasion of land may represent a key innovation that allowed access to many open ecological niches (May, 1994; Benton, 2001; Vermeij and Grosberg, 2010). Analyses of diversification rates among insect orders suggest that herbivory may represent a key innovation in some insect clades (Wiens et al., 2015), a longstanding idea in evolutionary ecology (Ehrlich and Raven, 1964; Mitter et al., 1988; Farrell, 1998; Mayhew, 2007; Futuyma and Agrawal, 2009). Host shifts may be a particularly important driver of herbivory-related diversification in insects (e.g. Hardy and Otto, 2014; Forbes et al., 2017). In summary, previous studies identified key traits associated with many of these rapid radiations, and so these particular large clades might represent adaptive radiations (relative to comparable clades in these same groups that did not rapidly diversify). Conversely, the absence of these key traits may help why the majority of clades did not rapidly diversify in each of these groups.

On the other hand, these rapidly diversifying clades may not fit every definition of adaptive radiation. Some definitions require exceptional rates of diversification and phenotypic evolution relative to other clades (e.g. Poe et al., 2018; Moen et al., 2021), but this may be too restrictive. Thus, Morinaga et al. (2023) calculated the relative richness of clades that were "adaptive-radiation-like", having only above-average rates of diversification and phenotypic evolution. In our study, most species belonged to clades with above-average diversification rates, but not necessarily those in the upper 95th percentile (Table 1). Furthermore, to better test for adaptive radiation, future analyses might also incorporate rates of phenotypic evolution. However, it may be challenging to estimate phenotypic rates from species-level phylogenies from many species across life.

Our results cover all of life and several major groups (plants, animals, insects, vertebrates), but the pattern documented here may also occur within smaller groups. For example, many vertebrate groups are numerically dominated by a single relatively recent clade, such as teleosts within actinopterygian fishes, frogs within amphibians, placentals within mammals, neognaths within birds, and colubroids within snakes (trees from Irisarri et al., 2017; richness data from Bánki et al., 2024). Given that these clades are relatively recent and have high richness, they should have relatively high diversification rates. Similarly, within angiosperms, most species belong to the clade uniting the "core angiosperms" and not the species-poor clades at the base of the angiosperm tree (Magallón et al., 2015; Zuntini et al., 2024).

Similar patterns may also occur in groups that we did not examine in detail here. For example, among the 154,534 currently described species of extant fungi (Bánki et al., 2024), most species (98%) belong to the phyla Ascomycota (98,334 species) and Basidiomycota (52,979 species), and not the other 9 fungal phyla. Phylogenies of fungi show these two phyla as sister taxa that are relatively young among higher-level fungal clades (James et al., 2006; Li et al., 2021). Given their relatively young age and high species richness, these two phyla would almost certainly represent rapid radiations relative to other fungal phyla (higher rates were shown in Scholl and Wiens (2016) but relatively few fungal phyla were included). We acknowledge that we have not confirmed the patterns that we found here within every group across life and at every phylogenetic scale, but we have shown these patterns at the largest phylogenetic scales and within some of the largest groups (e.g. animals, plants). This was our initial question. If this pattern does not hold within most genera or families (for example), it would not overturn our conclusions, which are specifically focused at larger scales.

We emphasize that our study is focused on patterns of extant species richness. We recognize that the relative richness of many

clades has changed dramatically over geological time. For example, angiosperms began as a single species, and initially diversified when many other plant clades were already extant and relatively diverse (Knoll, 1986; Niklas, 2016). Moreover, many groups with low diversity today had higher diversity in the past (e.g. coelacanths; Torino et al., 2021), and this might also help explain some of the disparities in richness observed among clades today (especially why some ancient groups are species poor). These observations do not make the patterns described here incorrect. Within a group, the fact that some clades have declined does not invalidate other clades as rapid radiations: diversification includes extinction, and "rapid" is relative and pertains to the timescale of any given comparison. Instead, we caution that these patterns may apply primarily to present day richness patterns. Although it would be interesting to study these patterns in the fossil record for some exemplar groups, it would be difficult to conduct similar analyses across life based on paleontological data.

Many authors have suggested that adaptive radiations are characterized by declining diversification rates over time. We find that much of life (at multiple scales) is numerically dominated by relatively young clades with rapid diversification rates (e.g. animals among kingdoms, arthropods and angiosperms among animal and plant phyla). We favor the idea that adaptive radiations have relatively rapid diversification rates relative to other clades, and not simply declining rates over time within clades. The pattern of declining rates could have many explanations that are unrelated to adaptive radiation (Moen and Morlon, 2014).

5 Conclusions

In summary, we show here that most of life's known, extant species richness belongs to relatively rapid radiations. Furthermore, many of these rapid radiations seem to be related to specific phenotypic traits, and thus may qualify as adaptive radiations (under some definitions). Overall, these results support the emphasis in evolutionary biology on finding the drivers of adaptive radiations and other rapid radiations. These results also suggest that much of life's species diversity might be the products of a nested series of rapid radiations, with each radiation potentially triggered by a different trait (e.g. first multicellularity, then terrestriality, and then herbivory [within insects]). We speculate that such a pattern might help explain the paradox of how rapid radiation is sustained over long timescales (Martin and Richards, 2019). An exciting area for future research will be to see how general these nested radiations are across scales, and to understand how and why certain traits seem to trigger them.

Data availability statement

The original contributions presented in the study are publicly available. This data can be found here: FigShare, https://doi.org/10.6084/m9.figshare.25954669.v1.

Author contributions

JW: Investigation, Formal Analysis, Writing – review & editing, Writing – original draft, Data curation, Methodology, Visualization, Conceptualization, Supervision. DM: Writing – review & editing, Conceptualization.

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The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2025.1596591/full#supplementary-material

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