Chapter 3
Science Without Species: Doing Science with Tree-Thinking

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Abstract The focus of this volume is speciesism. While the concepts of species and speciation remain the focus of a great deal of research, it is worth exploring how in recent decades evolutionary biology has, in several ways, moved away from species as the key unit of analysis of biological questions. I begin by outlining how phylogenetic comparative methods have become essential methodological tools in statistical analyses of relationships between traits. Species are not statistically independent observations, because the reality is that they are related, genetically and statistically, on a phylogenetic tree. Phylogeny also plays a key role in modern analyses of spatial patterns in biodiversity, and in fact relying on phylogenetic biodiversity measures can avoid a number of problems created by attempting to impose a uniform species rank across different continents and clades. Similarly, a major challenge in modern studies of diversification and extinction concerns the units of analysis and how they are defined and recognized. Both "genus" and "species" are human-defined ranks imposed on the phylogenetic tree. The phylogenetic tree is the more fundamental reality that is produced by the macroevolutionary process, and it could include every level of gradation of genetic and morphological divergence. Once ranks are imposed upon it, a variety of methodological problems are created as scientists attempt to make these ranks standardized and comparable across different datasets and timescales. I outline how phylogenetic thinking might help provide a solution. I conclude with other examples where cutting-edge science is done with phylogenies without much need of the "species" rank—for example, in the battle against Covid-19.

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3.1   From Comparative Methods to Phylogenetic Comparative Methods

Common research questions in ecology and evolution are about the relationship between different traits, observed across many extant taxa. Is brain size related to body size in vertebrates? Is height related to seed dispersal distance in plants? Is genome size related to organism size in eukaryotes? Such questions are always aimed at eventually trying to tease out cause and effect, but a crucial preliminary scientific step is to determine whether or not two traits are even correlated.

In the "olden days" of biology—by which I mean before the 1980s, which is of course not that long ago—the standard procedure in testing for correlation would simply be to measure the trait values across many species, plot the data, fit a linear regression, and check if the slope of the line was significantly different from 0.

A flaw in this work was exposed in a famous paper by Felsenstein (1985). He noted that, if species shared common ancestry, and thus had shared phylogenetic history, then different species will not be statistically independent samples. Instead, species that are more closely related will tend to have more similar traits. He illustrated this with an imaginary "worst-case scenario" (Fig. 3.1).

In Fig. 3.1 (middle), 20 species in Clade A are equally related to each other, as are another 20 species in Clade B. However, the two sister clades are separated by a long period of independent evolution, indicated by long branches. Imagine we have measured two continuous traits, for example, tree height and seed mass. If we imagine a simple (if no doubt unrealistic) model for evolutionary change in these traits, wherein trait values randomly wander without any directional trend, but with the expected amount of wandering increasing with time, then a lot of evolutionary change can accumulate along those long branches. Even under this simple model, it is likely that the common ancestor of Clade A will have values for Traits #1 and #2 substantially different than the common ancestor of Clade B.

As Node A diversifies into Clade A, and Node B diversifies into Clade B, the traits of each descendant species randomly wander away from their common ancestral
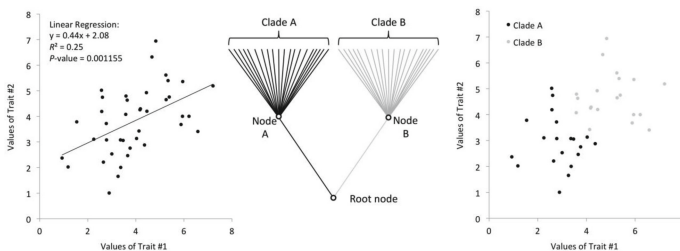

Fig. 3.1 Felsenstein's "worst case scenario" where an apparently strong correlation between two traits across species (left) is due to two sister clades (middle) simply having different averages in the two traits (right). Such spurious correlations are easily generated by simulating the gradual evolution of 2 independent continuous traits on this tree structure. (After Figures 5 and 7 of Felsenstein 1985)

values. When the resulting data are plotted (Fig. 3.1, left), it appears that Trait #1 and #2 are strongly correlated, with a positive slope of 0.44, an R^2 suggesting that Trait #1 explains 25% of the variation in Trait #2, and *P*-value of 0.001155, reassuringly well below the standard $P < 0.05$ cutoff for statistical significance. Excited biologists could publish this correlation and speculate on causal relationships.

Unfortunately, as Felsenstein pointed out, the whole analysis is spurious, because the entire signal of relationship is coming from the different mean values of Traits #1 and #2 in the two clades, and because Clades A and B inherited different ancestral starting values from their respective ancestors at Node A and Node B. Instead of having a sample size of $n = 40$ independent species supporting a relationship between the two traits, in this imaginary study, the real sample size is really just $n = 2$ sister clades with different means. Of course, a relationship can be postulated based on two points, but $n = 2$ is not an acceptable sample size—a straight line can always be drawn between two points!

The problem that Felsenstein identified is just an evolutionary special case of the common problem of statistical non-independence in data. Classic statistical methods and their results (such as estimates of the slope of a relationship, or the *P*-value) assume that data within a group are "IID"—independent and identically distributed. In other words, they assume that each of the data points is an independent sample from the same underlying population or process. However, if the underlying process created correlational structure in the data, and this structure is ignored in the statistical models used, then the statistical results can be badly misleading.

The evolutionary process of descent with modification is just such a process, and the "groups within groups" structure produced by a phylogenetic tree (see the concept "clade" in Table 1.1 of Chap. 1 in this volume) means that lineages' traits will often share a pattern of similarity that mirrors the closeness of the species on the phylogeny. While this pattern of correlations can itself be useful—notably, it can provide evidence of the phylogenetic tree—it is a major hindrance when attempting to determine if traits are correlated for some other, non-phylogenetic reason.

Fortunately, Felsenstein's paper did more than just point out the problem: it also pointed out a theoretical solution. Felsenstein noticed that, while the raw measurements of traits across species will be strongly correlated because of shared evolutionary history, the *differences* between sister clades will be statistically independent because they represent the changes in traits that have accumulated since the clades diverged from a common ancestor. This applies whether the clades are "small" (equivalent to what were traditionally termed species), or "large" (where a clade includes multiple populations/"species").

Felsenstein's method is known as Phylogenetic Independent Contrasts (PICs). While the details of the method involve some math and assumptions (Huey et al. 2019) about the evolutionary process, the method is now implemented in open-source programs, for example in the free computer language R (Paradis 2012). It can be run in seconds, given a data table and an estimate of the phylogeny.

An empirical example is given below. A common, but flawed, intuition is that genome size is tied in some way to organismal complexity, with the "better" or bigger organisms having bigger genomes. After all, bacteria have small genomes
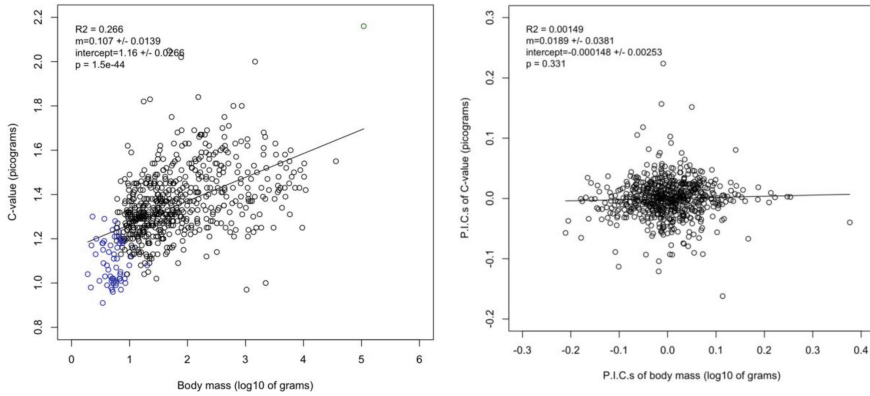
Fig. 3.2 Body mass plotted against genome size, in birds. The raw data seems to show that smaller birds have smaller genomes (left), but this relationship disappears when the autocorrelation due to shared ancestry is removed through Felsenstein's Phylogenetic Independent Contrasts (P.I.C.s) technique (right)

(often about 1 million DNA "letters," or bases), and complex organisms like us have large genomes (humans have over 6 billion bases of DNA in our diploid genomes). What happens when we test this hypothesis?

Data to address these questions are now available in various published databases (Gregory et al. 2007; Jones et al. 2009; Myhrvold et al. 2015; Gregory 2021). Birds are an excellent instructive example. Figure 3.2 was created by plotting the logarithm of body mass (x-axis) against genome size (y-axis), represented by the "C-value," a term for a physical measurement of the mass of the genome in picograms (genomic size has been measurable since the 1950s using techniques from cell biology long before genome sequencing was available).

If we look at the regression in Fig. 3.2 (left), it appears that despite substantial scatter, there is good evidence of a positive relationship. The slope is positive, the R^2 is 0.27, and the *P*-value is an impressive $P = 1.5 \times 10^{-44}$. Conventionally, any *P* less than 0.05 would be considered a statistically significant relationship. However, when we take the *same* data and use the bird phylogeny to calculate the body mass *contrasts* and C-value *contrasts*, the regression of contrasts against each other (Fig. 3.2, right) has a slope indistinguishable from 0, with a nonsignificant *P*-value of 0.33.

It turns out that a lot of what is driving the apparent relationship in Fig. 3.2a is the fact that hummingbirds, indicated by the blue circles, have both tiny body masses and slightly smaller genomes than other birds. However, all hummingbirds share these two traits, which were presumably already present in a common ancestor, so in actuality, this only provides one instance where body size and genome size appear to have shifted together. When this contrast is included with all of the other contrasts across the bird tree of life, no overall relationship is supported.

It is important to note that the PICs method does not always destroy apparent relationships. While relationships between genome size and complexity or body size
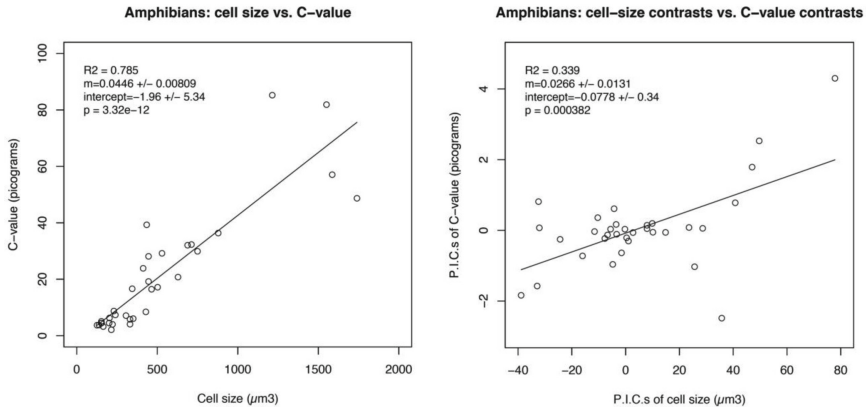
Fig. 3.3 Amphibians show a strong relationship between red blood cell volume and genome size. This relationship is strong both in the raw data (left) and in the phylogenetic independent contrasts (right)

are often not supported in analyses of multicellular clades, some clades show a strong relationship between genome size and the size of their red blood cells (Fig. 3.3). In this case, the apparent relationship in the raw traits is confirmed in the regression of PICs.

Using our random-wandering model for continuous traits evolution, we can estimate, very approximately, the most probable ancestral values of cell size and genome size. These ancestral state estimates can be mapped onto the amphibian phylogeny (Fig. 3.4). Doing so shows why the correlation between the two traits is not merely a product of phylogenetic structure: across the amphibian tree, increases in cell size co-occur with increases in genome size, and these coincident events occur many times across the tree.

When Felsenstein proposed PICs in 1985, the peer-reviewers were skeptical that the technique would be useful because good estimates of phylogeny were usually not available (Huey et al. 2019). However, with advances in DNA sequencing technology, and computer programs to estimate phylogenies from DNA (several of them developed by Felsenstein), phylogenies became ubiquitous in the 1990s. Nowadays, it is virtually impossible to publish a paper in comparative biology without using Felsenstein's Phylogenetic Independent Contrasts, or some more advanced method.

The PICs method has now been around long enough that it is considered conventional. However, it is already clear that more sophisticated methods will come to dominate the science of comparative biology in the future (Uyeda et al. 2018). These more complex methods also rely on phylogeny to account for similarities due to shared evolutionary history.

This vignette is relevant to speciesism because it shows that the shift from species-based thinking to phylogeny-based thinking impacts our general scientific and philosophical understanding of the world and the basic statistical methods that scientists use to test hypotheses. It is worth noting that PICs and related tools can be used to test
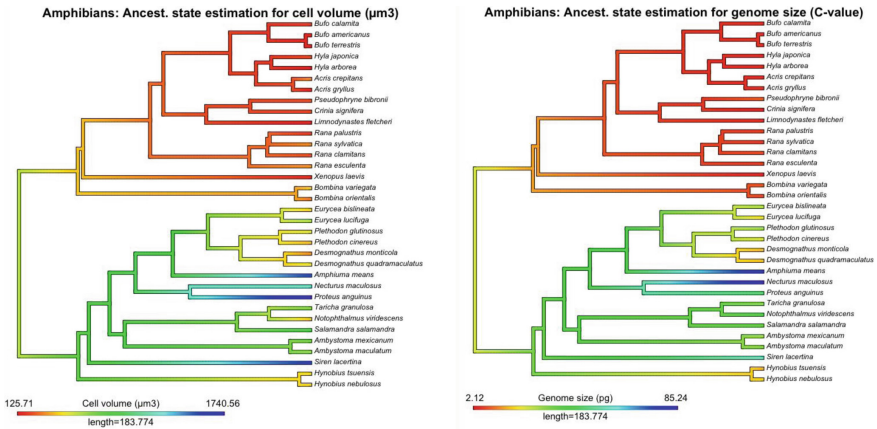
Fig. 3.4 Inferred evolution of red blood cell size (left) and genome size (right) in amphibians, under a simple model known as Brownian motion. Mapping traits onto the amphibian tree of life shows that the correlation between traits does not always result from the bias of phylogenetic relationships. In this case, increases in cell size co-occur with increases in genome size, and these coincident events occur many times across the tree. See the colorized legend illustrating how cooler colors (cell volume, left—vs.—genome size, right) arose multiple times in separate cases

hypotheses whether or not the "Operational Taxonomic Units" at the tips of the tree are considered species, or some other level of lineage. Populations, virus strains, and languages can all be analyzed phylogenetically since they originate through "descent with modification" involving the copying of information and stepwise changes that are themselves copied. Even anti-evolution legislative proposals have been analyzed phylogenetically! (Matzke 2016).

3.2 Biodiversity in Space: Spatial Phylogenetics

Phylogeny-based thinking has also had a major impact in another subfield of ecology and evolution: measuring biodiversity and mapping how it changes in time and space. Traditionally, the dominant measure of "biodiversity" has been simple species diversity: the number of species counted in any particular sampling unit, such as a geographical region or a geological time-bin.

However, knowledge of evolutionary trees means we know that not all "species" are equally distinct. Some species represent very young lineages that have diverged from their still-extant relatives in an evolutionarily short period of time, perhaps hundreds of thousands or even just thousands of years. Other species represent the last surviving members of lineages that have existed for hundreds of millions of years.

Both cases are important and worth preserving, but many people have long felt there is something significant about the last surviving members of ancient lineages.

Although the term "living fossil" has various problems (Casane and Laurenti 2013), it does capture the astounding fact that some lineages (e.g., the living tuatara, the platypus, southern conifers like the kauri and Wollemi Pine, and the ginkgo), would only be known from fossils except for the survival of these species, often in relatively isolated geographies or habitats.

While this "feeling" of significance is worthwhile, scientists like to quantify, and the advent of widespread phylogenies has enabled scientists to apply numbers that capture the uniqueness of extant lineages (Rosauer et al. 2009; Mishler et al. 2014). The measurable quantity is simply: how much of the living Tree of Life would be lost if a particular species (or some other clade) went extinct? In the case of New Zealand's tuatara, something like 250 million years of evolutionary history would be lost. The extinction of humans, in contrast, would result in only about 6 million years lost from the Tree of Life, assuming our closest relatives, the chimpanzees, survived. The extinction of the domestic horse might only cause the loss of about 1 million years of history, due to the existence of close relatives (donkey and zebra; Lippold et al. 2011).

Merely having this measurement does not itself resolve moral or policy questions about where to put conservation efforts and money; these are questions for conservation biology and policymakers. However, measuring the "phylogenetic diversity" or phylodiversity (Kling et al. 2018) represented in a region may be a more stable and useful measurement of the biodiversity of a unit than the species count, which can shift as taxonomic conventions and technology change. Crucially, such measures can be mapped, forming the basis of the nascent science of spatial phylogenetics (see Allen and Mishler, Chap. 8, this volume).

Maps of phylodiversity are useful scientifically because they provide a historical dimension for studying the processes that produced and maintained extant biodiversity and its distribution. Interestingly, some regions of the globe have relatively more neoendemics (endemic lineages that originated recently) and other regions have relatively more paleoendemics (endemic lineages that are the last representatives of ancient groups and persisted or accumulated in a particular region). While the mapping of phylogenetic diversity and neo/paleoendemism is well advanced, attempting to fit models to the observed patterns is still at an early stage, albeit with a promising start.

3.3 Studying Biodiversity in Time: The Challenges Imposed by Ranks

In one sense, paleontology has long done science at something other than the species level. Due to the incompleteness of the fossil record, studying diversification and extinction with only species counts is often statistically dubious. The number of fossil species known in particular regions and time-bins can depend heavily on the amount of fossil-bearing rocks of the right location and age, the quality of preservation,

taxonomic opinion, and even paleontological interest—the number of paleontologists available for a particular clade, region, and time, and the amount of effort they spend discovering and describing fossils (Valentine 1985).

For these reasons, it is common place for paleontologists to study macroevolution using coarser measures of biodiversity, typically higher Linnaean ranks, such as the number of genera or families. While the practice of counting Linnaean taxa—which are fairly subjective groupings—has various plausible critiques (de Queiroz and Gauthier 1994; Hendricks et al. 2014), it remains true that major features of the history of life (e.g., the five great mass extinctions [Barnosky et al. 2011]), were discovered by counting Linnaean ranks. Such studies would probably have been difficult or impossible if species-level data had been insisted upon. "Species-level" macroevolutionary studies of the fossil record remain challenging today, and species numbers are often back-calculated from higher level ranks.

Perhaps stemming from these successes of a rank-based approach, paleobiology has, ironically, been one of the slowest areas to adopt the phylogenetic approach that has swept through other fields of biology. There are several major challenges here.

First, fossils do not retain DNA. Subfossils (younger organic remains of organisms, such as Neandertal teeth or frozen mammoths) are an exception, but they are a minor one since DNA degrades over time. Even under the best conditions (frozen), a recoverable DNA sequence seems to have a limit of about 1 million years. Without DNA, phylogenies must be estimated from morphological characteristics. While DNA phylogenies are routinely built from thousands or millions of DNA characters, vertebrate fossils typically only have a few hundred characteristics that can be used (scored) as phylogenetic data. Other fossils, such as clams, may have only a few dozen scoreable characteristics.

A second challenge is the phylogenetic methods available for fossil data. Scientists want a time-scaled phylogeny that includes fossils, but this requires probabilistic models of the data. Modeling DNA datasets is aided by the large amount of DNA data available and the simple manner in which DNA is assumed to evolve. Thus, DNA models have been developed continuously since the 1980s. In contrast, morphological data have only received serious modeling attention in the last half-decade (Matzke and Irmis 2018), and the models available are essentially modifications of the DNA models, which is suspect given the greater complexity of morphological evolution. These models seem to work well enough, at least with reasonably large and semi-complete datasets (Matzke and Wright 2016). However, many fossil datasets are small and incomplete. Models are imaginable where fossil sampling completeness varies strongly among regions, ecologies, and time-bins, but such models will require the combined expertise of computational biologists, paleontologists, biogeographers, and experts in the evolution of development ("evo-devo") to develop successfully.

A third challenge concerns the different nature of Operational Taxonomic Units (OTUs, the tips of the branches) in living and fossil datasets. Due to the limitations in the fossil record and in the information that fossils retain, it is quite likely that biologists will be able to distinguish OTUs much more finely for living organisms than for fossil ones. Cryptic "species," for example, are typically only recognized based on molecular data and would be indistinguishable in the fossil record. Similarly, species

that are very similar skeletally, but distinguished by different coloration patterns, vocalizations, breeding times, etc., will be indistinguishable in the fossil record. For these and other reasons, there can be a major mismatch between the OTUs available in the recent and those identifiable even with a very complete fossil record.

Finally, apart from the above challenges, a fourth difficulty remains: are the OTUs that are measured in the present "the same kind" of entity as the lineages when a phylogeny goes back in time? It is entirely possible, even likely, they are not. The former are synchronic while the latter are diachronic (Mishler and Wilkens 2018, Fig. 3.1; see also Table 1 in Swartz and Mishler, Chap. 1 in this volume). What I am proposing is something like the process of coalescence that is well-known to population geneticists. Coalescence refers to how gene variants within populations mutate and replace each other rather rapidly on a timescale of millions of years, even with natural selection occurring. For example, all extant human mitochondrial DNA traces to a common ancestor only 250,000 years ago, meaning that in 0.25 million years, the mtDNA of "mitochondrial Eve" took over the entire human population. This process is continually ongoing throughout the genome of sexual species.

With OTUs that we can distinguish in the present (e.g., populations, subspecies, or closely related species), there may be a somewhat analogous process operating. It could be that recently diverged populations are evolutionarily ephemeral, with most of them getting wiped out rapidly by climate shifts, stochastic disasters (major floods or fires, diseases, etc.), competition from nearby relatives (Gutiérrez et al. 2007), etc. Methods that try to learn about the rates of diversification from dated phylogenies typically assume that all the branches of the tree, from the root to the tips, represent the same kind of entity such that the phylogeny could be sampled at any time-point. But what if the tips of the phylogeny consist of ephemeral clades with short evolutionary lifespans, and the deeper branches of the tree represent more stable entities, for example, a group of populations that occupy a distinct region or ecological niche? In this situation, it would be difficult to make accurate inferences about the rates of diversification, let alone extinction (Marshall 2017). The divergence events detectable deep in the tree would represent relatively rare events (e.g., successful colonization of new areas or niches), but the divergence events near the tips would mostly represent a more common and trivial process of partial genetic differentiation of populations on a landscape.

Biologists are hard at work attempting to address these issues. One avenue to try and address the issue of alleged "incomplete speciation" (we should note in passing the almost teleological speciesism assumption here) is to develop models that include heterogeneity in the diversification process. For example, so-called "extended speciation" models postulate not only rates of lineage splitting and extinction, but also a process of "speciation completion," which assigns a rate at which an already-separated population becomes a "fully distinct species" (Sukumaran et al. 2021). Given this postulate, the speciation-completion process can be incorporated into a large joint model that delineates species and estimates the number of distinct species.

3.3.1 A Rank-Free Suggestion for Studying Biodiversity in Time

Even assuming terminal clades have been successfully identified in the present, the major challenge of a major mismatch between living OTUs and fossil OTUs remains. One "solution" is to essentially declare them incommensurate. In this case, inferences based on phylogenies of living species would provide information about speciation rates at the tips of a tree, fairly reliable signatures of processes just below the tips (Upham et al. 2021), and the fossil record would be used for information about larger clades in the deeper evolutionary past.

I suggest that the "science without species" paradigm might provide an alternative that is worth exploring when studying biodiversity over time. DNA-based phylogenetics can provide a more finely-resolved tree than can the fossil record, but the fossil record provides information about extinct lineages that is (at best) very difficult to recover from DNA phylogenies. How can these two data sources be combined, rather than merely analyzed separately and compared?

There is room for many approaches here, but one that seems underexplored is a multiscale analysis of phylogenetic diversity. By this I mean that any phylogenetic timetree can be queried not only for the number of lineages, N, recorded at any timepoint t—let's call this N_{t+0}—but also for the number of lineages *of a given age* recorded at each timepoint. For example, the number of lineages recorded 1 million years before any given timepoint t would be N_{t+1}, and the number of lineages recorded 5 million years before any given timepoint t would be N_{t+5}. The advantage of this approach is that a metric like N_{t+5} is likely to be much more robust to the above-identified vagaries of fossil sampling, such as fossil species and genus diagnosis, and species delimitation identified above. A combined DNA + fossils phylogeny might well serve as the basis for providing good inference of the rates of processes affecting N_{t+5} through time, however difficult it might be to study N_{t+0} through time.

But there is no need to pick any single time-resolution to study diversification. This would just impose another rank as the one true unit of analysis. Given a phylogeny that includes thorough fossil sampling, the metric is easily calculated at various time-depths. Instead of just relying on a Lineages-through-time (LTT) plot to represent diversification history, LTT curves calculated at a series of time-depths, for example, N_{t+0} through N_{t+20}, could be calculated. Evolutionary models appropriate to shallow-time or deeper-time processes could then be fit, with the expectation that the latter are likely to be easier for time periods before the Recent.

3.4 More Science Without Species

I have outlined above where the phylogenetics revolution in biology can deemphasize, and perhaps totally dispense with the rank of "species" as the key unit of analysis in comparative biology, biogeography, and macroevolutionary diversification.

However, there are other major research topics where the phylogenetics revolution has already thoroughly supplanted the species paradigm.

3.4.1 Gene Trees

In "first-generation" phylogenetics, roughly into the early 2000s, it was common for biologists to assume that if they sequenced three genes from each of 20 species, they should expect that all of those gene trees would be congruent—meaning that the phylogeny of each gene should show the same relationships between species. Disagreement between gene trees was annoying and was termed "incongruence." Generally, the "solution" was to combine all the gene sequences into one large alignment and estimate the phylogeny from the combined dataset, providing a best-estimate phylogeny supported by the majority of data. Unresolved parts of the tree could, hopefully, be resolved by sequencing more genes and adding them into the analysis.

While this "concatenation" procedure was not crazy (and yielded reasonably accurate phylogenies), it left out the fact that genes evolve in populations, and recombine in each generation as chromosome segments are shuffled around. As a result, population genetics *predicts* that many individual genes will have phylogenies slightly different from the overall phylogenetic divergence history of the population, particularly if population sizes are large and the time between population-divergence events is small (Ashman et al. 2018). New phylogenetic methods jointly estimate individual gene phylogenies along with the population phylogeny.

3.4.2 Virus Trees

Viruses have never fit well into the "species" paradigm—it is even debated whether viruses are technically "alive." Whatever the case, it is clear that viruses evolve through descent with modification, and thus phylogenies can be good models to represent their evolutionary history. Viral phylogenetics is a fascinating example showing the benefits of "pure science," basic research that is done to advance scientific understanding rather than practical application, yet which nonetheless turns out to have tremendous application. The field of phylogenetics was largely developed by morphological taxonomists and molecular biologists who wanted to better understand the evolutionary history of their study organisms. One particularly important figure, Willi Hennig, is considered the father of phylogenetic systematics, but his taxonomic expertise was on Micropezidae, a family of flies. However, from humble roots, phylogenetics has grown to be a crucial tool in acute life-and-death situations, namely, viral outbreaks. I used to make this point at meetings by citing a *Science* paper tracing the 2014 Ebola Virus Disease (EVD) outbreak in West Africa (Gire et al. 2014), which concludes with: "Tragically, five co-authors, who contributed

greatly to public health and research efforts in Sierra Leone, contracted EVD and lost their battle with the disease before this manuscript could be published."

In the 2020s, of course, what was previously shocking now seems almost quaint, with the entire globe battling SARS-CoV-2, currently credited with over 6 million deaths, which is certainly a vast undercount. Every day, scientists are sequencing new variants of our opponent and adding them to an international phylogenetic database so we can watch when and where new strains emerge and spread (https://nextstrain.org/ncov/gisaid/global). Phylogenetics supplies the structure upon which we base the namings of new strains ("Alpha," "Delta," etc.). In the case of New Zealand, where I reside, for the first several waves of infection, every new COVID case was sequenced and added to a comprehensive phylogeny used to track viral incursions in real-time (Douglas et al. 2021; Geoghegan et al. 2021; see also https://nextstrain.org/community/narrat ives/ESR-NZ/ GenomicsNarrativeSARSCoV2/aotearoa-border-incursions). It was common to hear the nation's Director-General of Health, Ashley Bloomfield, discuss phylogenies and clades before the national media in the daily 1 pm COVID briefing.

3.5   Conclusion

In summary, we have seen that a major challenge in modern studies of diversification and extinction concerns the units of analysis and how they are defined and recognized. Both "genus" and "species" are human-defined ranks imposed on the phylogenetic tree. The phylogenetic tree is the more fundamental reality that is produced by the macroevolutionary process, and it could include every level of gradation of genetic and morphological divergence. Once ranks are imposed upon it, a variety of methodological problems are created as scientists attempt to make these ranks standardized and comparable across different datasets and timescales.

The only figure that Darwin put in his 1859 *Origin of Species* was a (hypothetical) phylogenetic tree. While his title put focus on how the entities people call species originated, and this concern dominated evolutionary science for many decades, a careful reading of the *Origin* indicates that the whole point was to undermine the permanency of species in favor of a phylogenetic view. We can trace a clear path from his phylogenetic speculations in 1859 to the phylogenetics revolution of recent decades (Fig. 3.5) and the real-time global tracking of deadly pathogens today. While showing the impermanence of species was one of Darwin's major revolutionary advances, it may be that phylogenetic thinking, which in time may allow "science without species," could, in the end be the bigger of the two revolutions.
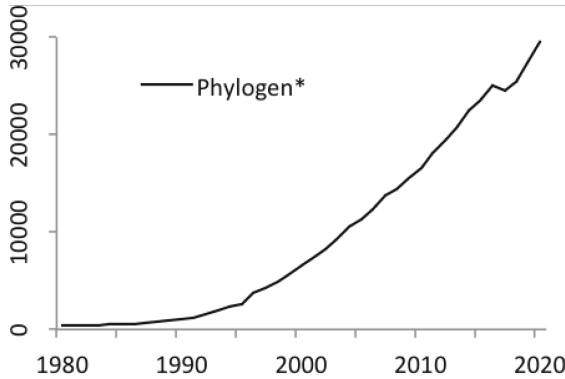
Fig. 3.5 Number of scientific publications using the word "phylogeny" and cognates, 1980–2020, according to the Scopus database (searched August 2021). By 2013, phylogenetics articles accounted for ~ 1% of all published science (David Hills, personal communication), and publication counts have grown 50% in the following 7 years

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