Chapter 10

RATES OF METABOLISM AND EVOLUTION

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SUMMARY

1 The rate of evolution is intrinsically important because a multitude of characteristics, ranging from molecular variation to life histories to taxonomic diversity, are influenced by relative rate differences.

2 The metabolic theory of ecology (MTE) predicts that patterns and processes of evolutionary rates are related to resource uptake from the environment and resource allocation to survival, growth, and reproduction.

3 Although classic studies in evolutionary biology date back to the work of G. G. Simpson and J. B. S. Haldane, consistent patterns for why and how organisms differ in evolutionary rates have not developed nor provided a solid empirical understanding or theory.

4 Recently, advances have been made in more rigorously measuring rates of evolution by synthesizing dated phylogenies with explicit models of evolution.

5 MTE may shed light on some evolutionary rates problems. Organisms with higher metabolic rates appear to have faster molecular rates of evolution, rapid rates of behavioral relative to morphological change, and more rapid diversification rates.

6 Future studies of MTE and evolutionary rates will be exciting as experimental systems are developed, more comprehensive databases are created, and new questions arise as to how the adaptive nature of evolution rates across biodiversity are impacted by global changes.

10.1 INTRODUCTION

In time everything changes; the question is what are the null expectations for change, what are observed differences in rate change, and are these differences consistent across the diversity of life. The metabolic theory of ecology (MTE) provides a basis for tackling these rate issues: the rate at which organisms take up and use energy influences survival, growth, and reproduction. In turn, such allocation will impact how everything changes from ecology to evolution. Here, we look at whether metabolic rates relate to and predict various types of evolutionary rates across taxa including molecular, phenotypic traits, and patterns of diversification.

Rates of evolution are profoundly important because they may underlie "the reasons for the great diversity of organisms on the earth" (Simpson 1953). Although many studies have been devoted to understanding rates of evolution, a consistent body of work remains

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elusive (Gingerich 2009). Reasons for this are many but primarily relate to paucity of complete databases across taxa, lack of reliable time sequence information, methodological problems in measuring rates of evolution, and the panoply of variables relevant to evolutionary rate change. Nevertheless, issues pertaining to rates of evolution have synthesized problem areas. In his seminal work on the topic, Simpson (1953) "executed a brilliant tactical maneuver" (Laporte 2000, p. 129) by using the phenomenon of evolutionary rates to pull together two disparate areas, paleontology and genetics. Today, in similar fashion, questions about evolutionary rates may synthesize new approaches for the MTE.

Differential rates of evolution are well known. For example, mammals have evolved faster than mollusks (Stanley 1973) and, within mammals, carnivores have evolved faster than primates (Mattila and Bokma 2008). In addition to taxonomic differences, rate changes are observed among traits. Quantitative behavioral or ecological characteristics such as social group size or home range size generally evolve at faster rates than morphological traits (Gittleman et al. 1996).

Such observed differential rates are not well understood. This is mainly due to uneven data availability and inconsistent trends across taxa or traits. For example, across mammals, by far the best-known taxonomic group, life-history information has been reported for only around 30% of species and even body size has not been measured in hundreds of species (Jones et al. 2009); this is especially problematic when considering metabolic hypotheses because direct measures of physiological usage or capacity are sparse. Data availability is only part of the problem. In some of the most well-studied systems, empirical trends occur in many directions. For example, morphological evolution in body size across Platyrrhini (monkeys) and Phalangeriformes (opossums) may be significantly faster in large and small species, thus not revealing consistent reasons for rate differences (Cooper and Purvis 2009).

Of course, there is no reason that rates of evolution must occur in the same form across taxa or traits. As Simpson (1953) forewarned, "Evolution involves changes of so many sorts that measurements of its rates must necessarily be complicated if they are to cover important aspects of the subject in an unambiguous and instructive way" (p. 4). Cooper and Purvis (2009) recently summarized factors known to influence rates of evolution (Fig. 10.1). Many of these are iconic relationships in what we know about evolutionary change. For example, small species with faster generation times and shorter lifespans are known to have rapid evolutionary rates and form some of the logic behind *r* and *K*-selection theory (Gould 1983; Calder 1984). However, even when we restrict our attention to morphological evolution, we find that body size, interspecific competition, geographic range, and ecological specialization may be equally influential and, as stated above, may occur in various directions. As Cooper and Purvis (2009) discuss, there are many other important variables which influence rates of evolution and further study is needed to sort out real from artificial patterns due to uneven data.

Generally, the relationship between metabolic rate and evolutionary rate has not received much attention though there is a natural fit between the two rates: differences in behavioral and ecological change, ontogenetic differences at individual levels, and responses to environmental changes are all strongly influenced by metabolism. The focus of this chapter is to consider whether and how some core topics of evolutionary rates – molecular evolution, trait evolution, and macroevolution such as speciation and extinction – are tied to metabolic rates.

10.2 METHODS FOR MEASURING EVOLUTIONARY RATES

There is a surprising variety of methods for measuring evolutionary rates in the literature, and little consensus as to which methods are to be preferred. Here, we present a brief review of methods for quantifying evolutionary rates. We focus primarily on evolutionary rate defined as a change in the value or variance of a trait over a given time interval (e.g., a change in the nucleotide composition of a DNA sequence, or in the value of a morphological trait). We also briefly consider methods for quantifying variation in diversification rates among lineages, and discuss confusion in the literature about the relationship between evolutionary rate and phylogenetic signal.

10.2.1 Measuring rates of sequence evolution

Measuring rates of molecular evolution has become fairly straightforward with modern techniques of

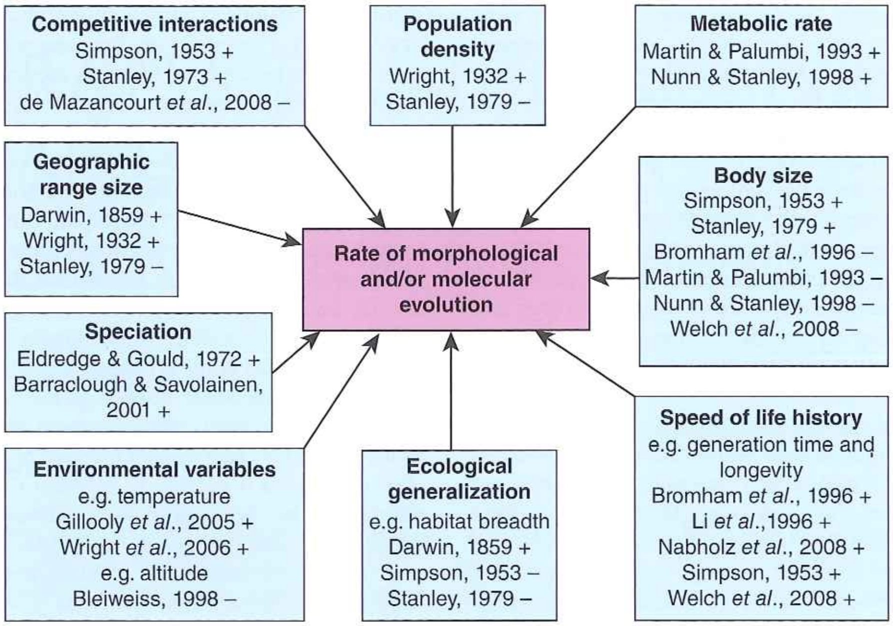

Figure 10.1 Diagram showing the variables which are hypothesized to affect rates of morphological and/or molecular evolution along with selected references for the hypotheses. (+) Hypothesized positive relationship between the variable and evolutionary rate; (–) hypothesized negative relationship between the variable and evolutionary rate. Note that these variables are themselves often interconnected, directly or indirectly, but the relationships between them have been omitted to increase clarity (Darwin 1859; Wright 1932; Simpson 1953; Eldredge and Gould 1972; Stanley 1973, 1979; Martin and Palumbi 1993; Bromham et al. 1996; Li et al. 1996; Bleiweiss 1998; Nunn and Stanley 1998; Barraclough and Savolainen 2001; Gillooly et al. 2005; Wright et al. 2006; de Mazancourt et al. 2008; Nabholz et al. 2008; Welch et al. 2008). Redrawn from Cooper and Purvis (2009) by permission of John Wiley & Sons, Ltd.

molecular systematics. By comparing a molecular phylogeny with branch lengths in units of number or proportion of nucleotide substitutions to a time-calibrated phylogeny (i.e., a chronogram with branch lengths in units of millions of years since divergence), it is possible to derive an estimate of the absolute rate of molecular evolution for a lineage. It is important that an appropriate model of sequence evolution be used when estimating a phylogeny, and there exists some debate as to which model selection procedures are most accurate (Posada and Crandall 2001; Posada and Buckley 2004). There are also a number of competing methods available for estimating a chronogram using molecular sequence data and geological calibration points (e.g., Sanderson 2003; Drummond and Rambaut 2007). However, there is little disagreement that substitution rate is an appropriate measure of rates of sequence evolution. In contrast, the best measure of rates of morphological evolution remains unclear.

10.2.2 Measuring rates of morphological evolution

The classic unit of morphological evolution in past studies of evolutionary rate is the "darwin," first described by Haldane (1949). It is defined as an evolutionary change by a factor of *e* (the base of natural logarithms) per million years (Gingerich 1993). The time interval separating a given change in trait values can be estimated directly from the fossil record, or based on the phylogenetic distance separating species in a time-calibrated phylogeny (Gittleman et al. 1996).

Haldane (1949) described several additional measures of morphological evolution. As an alternative to measuring rate in units of *e* he suggested using the phenotypic standard deviation within a population, since this is the raw variation which will be targeted by natural selection. Gingerich (1993) dubbed this measure the "simpson." Haldane further suggested that number of generations would be a more informative unit of time than years, since generation time scales so differently with absolute time in different organisms. Gingerich defined the "haldane" as a change in trait variance by a factor of one standard deviation per generation. While these measures of evolutionary rate likely more directly reflect the process of evolution than the darwin, they have rarely been used because the information needed to quantify them is often unavailable for a lineage of interest. Generation times for many species, particularly fossil taxa, are unknown. The population variance of a trait is even more rarely known. In contrast, the darwin requires only an estimate of time elapsed and the change in species average trait values.

In 2009 Ackerly introduced a new measure of evolutionary rate, the "felsen," defined as an increase of one unit per million years in the variance among sister taxa of ln-transformed trait values. It is calculated from standardized independent contrasts of a ln-transformed trait estimated on a tree with branch lengths in units of millions of years. The method has advantages over previous methods for measuring evolutionary rates. An *F*-test can be used to see if different clades have significantly different evolutionary rates, and a number of methods can be used to assign confidence limits to a rate estimate (Ackerly 2009).

Finally, Evans et al. (2011) introduced a new measure of evolutionary rate called "clade maximum rate," which is defined as the rate of change in a specified extreme value of a character (either the minimum or the maximum) for a clade within a given time interval. An advantage of this measure over the felsen is that it does not require a resolved phylogeny, only the recognition of distinct clades (e.g., monophyletic taxonomic groups). It is thus more easily applicable to fossil data. In the first empirical application of clade maximum rate, Evans et al. showed that very large (e.g., orders of magnitude) evolutionary decreases in mammalian body mass (such as extreme insular dwarfism) can happen over 1/10 fewer generations than large increases.

10.2.3 Evolutionary rate and phylogenetic signal

In addition to the myriad methods available for quantifying rates of morphological evolution, there exists some confusion about the relationship between evolutionary rate and phylogenetic signal. Phylogenetic signal can be broadly defined as a tendency for the similarity of the traits of species to be inversely correlated with their phylogenetic distance (i.e., more closely related species are more similar). A prevailing hypothesis is that traits evolving more rapidly and/or that are evolutionarily labile will tend to show weaker phylogenetic signal (e.g., Blomberg et al. 2003; Rheindt et al. 2004; Silvertown et al. 2006), and thus that low signal necessarily indicates rapid trait evolution. However, under the most commonly assumed model of character evolution, pure Brownian motion, this assumption is often not valid (Ackerly 2009).

The Brownian motion model is based on models of random particle diffusion in a liquid. It is a widely used neutral model of character evolution under genetic drift, and is assumed by most phylogenetic comparative methods (Felsenstein 1985, 1988; O'Meara et al. 2006). For continuous characters there is no expected relationship between rate and signal under pure Brownian motion (Hansen and Martins 1996; Freckleton and Harvey 2006; Revell et al. 2008; Ackerly 2009). Other models of character evolution such as bounded Brownian motion and the Ornstein–Uhlenbeck model of evolution (Butler and King 2004) have been shown in previous mathematical and simulation studies to potentially produce correlations between phylogenetic signal and evolutionary rate that are negative, absent, or positive (Hansen and Martins 1996; Freckleton and Harvey 2006; Revell et al. 2008; Ackerly 2009). Thus phylogenetic signal is not a reliable indicator of whether trait evolution is rapid or slow unless the mode of trait evolution is known. Phylogenetic signal and evolutionary rate are related but distinct patterns, and researchers wishing to test hypotheses concerning evolutionary rates would do best to quantify them directly using methods discussed above.

10.2.4 Estimating diversification rates

One of the central goals of evolutionary biology is to understand the factors that explain variation in the tempo and mode of evolution among lineages. Until recently, rates of speciation and extinction could only be estimated from the fossil record (e.g., Simpson 1944; Stanley 1979). However, with the rise of molecular phylogenetics, it is now possible to estimate diversification rates using data from extant species. Nee et al. (1992) were the first to estimate diversification rates from a time-calibrated molecular phylogeny, and numerous subsequent studies investigated diversification rates using broadly similar methods (e.g., Baldwin and Sanderson 1998; Rüber and Zardoya 2005; Harmon et al. 2008; Phillimore and Price 2008). One pattern that is commonly documented is a slowdown in diversification rates over time (i.e., a slowing of lineage accumulation towards the present, reviewed in Cusimano and Renner 2010). This pattern is generally attributed to density-dependent rates of cladogenesis and niche filling (Stanley 1979; Nee et al. 1992). However, Cusimano and Renner (2010) argued that apparent slowdowns in diversification rate may be driven by a tendency for systematists to sample phylogenetically distinct taxa, thus resolving a greater proportion of basal than recent divergences. Based on the results of simulations, they argued that diversification rates cannot be reliably estimated from phylogenies that contain less than roughly 80% of all extant species.

Additional concerns have been raised about estimating diversification rates from molecular phylogenies. Ricklefs (2007) argued that the tendency of studies to focus on large (i.e., speciose) clades has produced a distorted view of the process of diversification, and that in reality most clades exhibit much lower rates of diversification than have typically been measured. Rabosky (2009, 2010) criticized the assumption that diversification can proceed indefinitely, and argued that in many cases ecological factors will set the maximum species richness of a clade. If clades generally have a maximum potential species richness, estimates of diversification rates based on modern species richness and clade age can be quite misleading. Old clades would be more likely to have hit their diversity ceiling, causing a slowdown in diversification, regardless of their maximum potential rate of cladogenesis. We note, however, that it seems unlikely that ecological limits on clade diversity are commonplace, given the observation that clade age is generally a strong correlate of clade diversity (McPeek and Brown 2007). If such limits exist, it seems that clades frequently do not reach them.

Liow et al. (2010) criticized both purely molecular and purely fossil-based studies of diversification rates. They showed in a simulation study that estimates of diversification rate based on either will be biased in some circumstances, but that molecular and fossil studies will tend to be biased in different ways; an approach combining both sources of information may be the most appropriate general method for assessing diversification rates. The estimation of diversification rates remains an active area of research and debate.

10.3 PROBLEMS AND HYPOTHESES

Although MTE is relatively new, some interesting questions have already explicitly developed in relation to evolutionary rates. The following examples seem especially relevant because they integrate various phylogenetic and macroecological approaches, synthesize data at broad spatial and temporal scales, and have received enough attention that hypotheses are more focused on specific causal mechanisms. Until now, few studies that are promising for MTE have explicitly used the analytical methods for measuring rates (i.e., those described above), thus providing opportunities for future research.

10.3.1 MTE and rates of molecular evolution

One of the major features of molecular evolution is that rates of sequence divergence vary considerably among different lineages. Differences in mutation rate and generation time are both commonly invoked to explain this variation (reviewed in Bromham and Penny 2003; Rand 1994), and metabolism has a clear potential link to mutation rates. Mutagenic byproducts of the metabolic process, such as oxygen radicals, would be expected to reach higher concentrations in species with higher mass-specific metabolic rates, potentially producing faster mutation rates through higher rates of oxidative damage to DNA (Shigenaga et al. 1989; Rand 1994). Numerous studies have shown that smaller animals generally have higher rates of sequence evolution (e.g., Bromham et al. 1996; Nunn and Stanley 1998; Bromham 2002), which Bromham and Penny (2003) interpreted as evidence of the influence of metabolism. However, generation time also shows strong allometric scaling, so this observation alone cannot be taken as strong evidence of the effects of metabolic rate.

Further evidence comes from studies that have compared endotherms and ectotherms across a similar range of body sizes, which generally show that ectotherms have much slower rates of molecular evolution for their size (Martin and Palumbi 1993; Martin 1999; but see Seddon et al. 1998). Comparison of Foraminifera that occur at different latitudes also showed that the rate of sequence evolution was directly proportional to the temperature at which Foraminifera occur, and thus presumably their metabolic rate (Allen et al. 2006). Finally, a recent study showed that equations based on

MTE and the neutral theory of molecular evolution can accurately predict variation in the rate of sequence evolution among species with different body sizes (Gillooly et al. 2005b). As opposed to the somewhat more controversial links between metabolic rate and rates of diversification and morphological evolution, the importance of MTE for understanding variation in rates of molecular evolution among species seems well established.

10.3.2 MTE and trait evolution

Intuitively, behavioral characteristics such as group size or home range movements should evolve faster than morphological or physiological traits. Variation in traits at population and individual levels along with relative heritability measures suggest more rapid behavioral than morphological evolution. Indeed, the remarkable, long-term domestication experiment by the Russian geneticist, Dmitry K. Belyaev, demonstrated over a 40-year period of trait selection in 45 000 silver foxes (*Vulpes vulpes*) that behavioral changes such as fear or shyness occur much earlier than morphological or physiological changes (reviewed in Trut 2001). Direct selection for domestication in silver foxes shows that, in a unique population of 100 foxes bred between 30 and 35 generations, changes in behavioral development occurred earlier than morphological change. Importantly, the developmental changes in behavior were related to physiological and hormonal effects. Over the years, others have hypothesized that behavioral and ecological traits evolve at faster rates than morphological rates (see Brooks and McLennan 1991). Nevertheless, despite considerable theoretical discussion (see West-Eberhard 1987), few empirical tests have shown actual differences in rates of evolution among traits, especially while controlling for phylogenetic differences across taxa and using accurate methods for rate measurements.

Comparing relative rates of evolution among traits suggests that MTE is important for observed differences in trait evolution. Using comparative data of six morphological (body and brain size), life-history (gestation length, birth weight), and behavioral/ecological (home range and population group size) traits, Gittleman et al. (1996) calculated darwins for all of these traits using dated molecular trees (see Fig. 10.2). Given expected trends for quantitative trends in other studies (see above discussion of darwins) three findings were consistent: (1) traits reveal an expected inverse relationship between evolutionary rate and timescale; (2) slopes are more negative with group size than body weight, though the values are shallow; and (3) "instantaneous" rate change is greater in group size than body weight. All of these findings are consistent with the

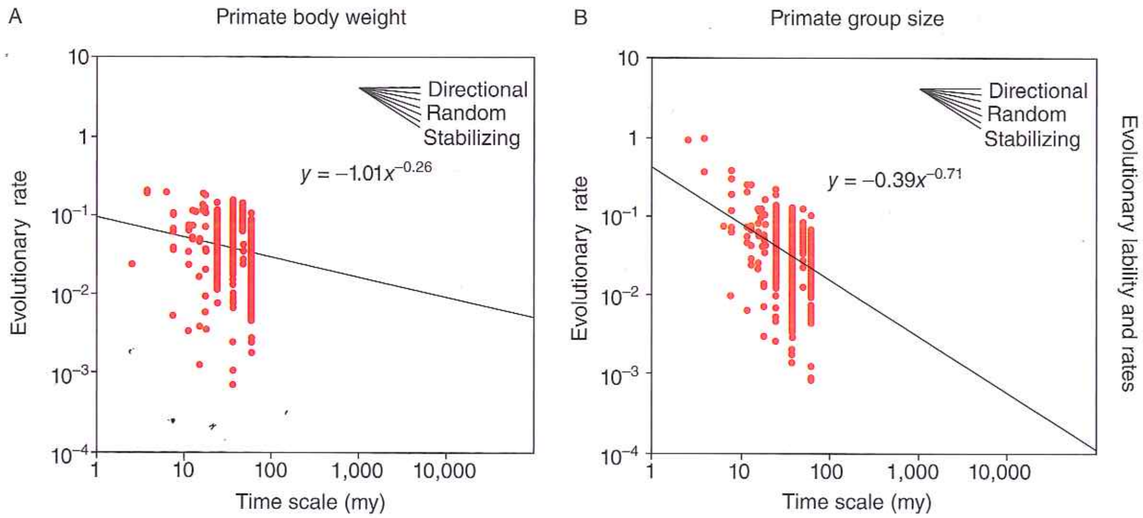

Figure 10.2 Log evolutionary rate ("darwins") versus log time interval (million years ago) observed across Primates for (A) body weight and (B) group size. Values of slope represent directedness of evolution and values of intercept represent rates over a million years of evolution. Redrawn from Gittleman et al. (1996).

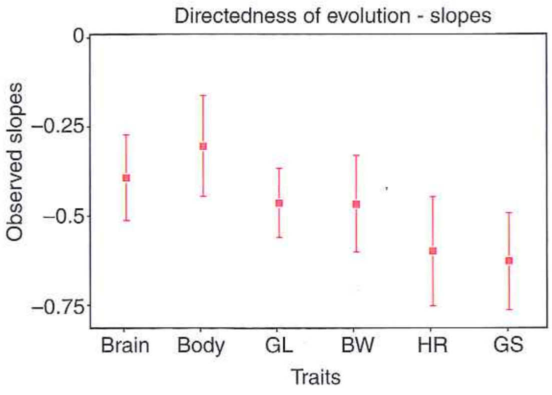

Figure 10.3 Combined values of slopes across eight mammalian taxa (Primates, Ceboidea, Carnivora, Canidae, Bovidae, Cervidae, Certacea, and Arvocolinae) observed for each quantitative trait. Traits are denoted by the following: Brain, brain weight; GL, gestation length; BW, birth weight; HR, home range; GS, group size. Means and standard errors are included for each trait. Redrawn from Gittleman et al. (1996).

intuitive prediction that behavior evolves differently from morphology. Specifically, evolutionary change in the behavioral traits of home range movements and group size is more of a random walk and relatively more directional in the morphological traits (see Gingerich 1993, for discussion of evolutionary rate models). The important observation here related to MTE is that comparing the slopes of rate change across variables the morphological traits (body size, brain size) approximate three-quarter values in contrast to the more plastic behavioral and life-history traits (Fig. 10.3). This study, however, involved small sample sizes (<40 species) and did not standardize timescale among phylogenies. Clearly, examining other behavioral and morphological traits in a greater diversity of taxa would give a more complete view of evolutionary rates.

Another promising area for future research is the relationship between metabolic ecology and rates of behavioral evolution. Organisms with a metabolic surplus may be free to evolve more complex behaviors than organisms with more constrained energy budgets. For example, shrews have such a high mass-specific metabolic rate that they are forced to spend almost all of their time foraging just to support basic life functions. By contrast, frogs, though often of similar size to shrews, as ectotherms do not need to spend as much time foraging to support basic metabolism. This may explain why costly display behaviors to attract mates are widespread in anuran species, but are absent in shrews. We note, however, as a counter-example that hummingbirds have both extremely high mass-specific metabolic rates and costly display behaviors.

Conversely, many types of complex behavior, particularly certain types of social behavior, require relatively large brains. Brain tissue is metabolically extremely expensive to maintain (Leonard et al. 2007), and it could be that only endothermic organisms that have large energy budgets are likely to evolve large brains. This could in turn explain why complex social behavior and learned behavior are so much more common in mammals and birds than in other animal groups. The relationship between metabolism and rates of behavioral evolution is a potentially rich area of inquiry that has rarely been considered.

10.3.3 MTE and diversification rates

Allen et al. (2002) first proposed that MTE could explain global diversity gradients such as the "latitudinal diversity gradient" that occurs in many groups (see Storch, Chapter 11). MTE predicts that, due to metabolic effects on rates of evolution, diversification rates will be directly proportional to temperature. This theory is similar to Rohde's (1992) "evolutionary speed" hypothesis, but makes more explicit predictions. One of the predictions of MTE is that diversity (log species richness) should scale with temperature with a slope of approximately −0.65, and Allen et al. (2002) presented preliminary analyses demonstrating that this relationship roughly holds across a range of groups. Subsequent studies have tested for this relationship in a diversity of organisms, with mixed results. While some studies have demonstrated the scaling between environmental temperature and diversity predicted by MTE (e.g., Allen et al. 2006; Wang et al. 2009), other studies have failed to find it (e.g., Algar et al. 2007; Latimer 2007; McCain and Sanders 2010). For example, Hawkins et al. (2007) looked at temperature and diversity relationships across 46 groups and found that the predictions of MTE were only borne out in, at most, five of them. In a response to Hawkins et al., Gillooly and Allen (2007) noted that a scaling relationship between environmental temperature and diversity is only one of the predictions of MTE, that the prediction only applies to ectotherms, and that differences in water availability have the potential to diminish or even reverse expected relationships between temperature and diversity. Cassemiro and Diniz-Filho (2010) further argued that pure MTE is too simple to explain the majority of global diversity patterns, but showed that minor derivations of it can explain a much wider range of patterns.

One clear prediction of MTE, as well as Rohde's evolutionary speed hypothesis, is that diversification rates should be higher in warmer areas. While many studies have examined the relationship between diversity and temperature (reviewed in Cassemiro and Diniz-Filho 2010), surprisingly few have explicitly considered diversification rate. Negative correlations between latitude and diversification rate, or differences in diversification rate between temperate and tropical lineages, have been shown in birds (Ricklefs 2006b), amphibians (Wiens 2007), and angiosperms (Jansson and Davies 2008). Allen et al. (2006) also showed that speciation rate scales with temperature in marine Foraminifera. It remains to be seen how general the relationship between diversification rate and temperature is, and we suggest that this represents an important avenue of future research.

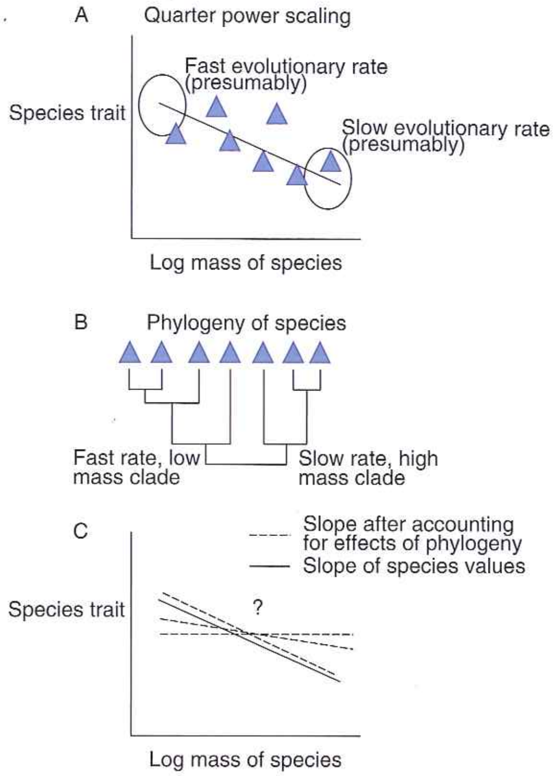

Figure 10.4 How do phylogeny and evolutionary rates relate to metabolic scaling? When species exhibit quarter-power scaling (A) can this drive differences in rates of molecular or morphological evolution (B) among clades? Conversely, when the influence of phylogeny is taken into account (C), does the scaling exponent remain similar or change?

10.4 CONCLUDING COMMENTS

Just as Simpson integrated genetics and paleontology by developing concepts and methodologies around questions of evolutionary rate (Laporte 2000), so too may rates questions serve as an integrative approach to questions about metabolic ecology. In this chapter we have summarized some theoretical problems, emphasizing certain methods that are useful for problems of why some taxa and traits seem to have divergent rates of evolution.

A few areas seem especially interesting for future work. First, as described in this chapter, most studies to date have considered evolutionary rates and MTE from macro perspectives. It will be increasingly important to adopt experimental studies to pinpoint causal mechanisms. For example, selection experiments for metabolic rate and its influence on body size or behavioral development, similar to early experiments on inbred strains of rats to study brain–body size evolution (Atchley 1984), may be instructive. Second, more comprehensive databases that provide data on metabolic rate, morphology, and behavior with rates tests in mind will be informative. Applying a phylogenetic perspective will be particularly valuable to incorporate into future studies of scaling and MTE (see Fig. 10.4). For example, Symonds and Elgar (2002) and White et al. (2009) both showed deviations from quarter-power scaling of metabolic rates in some cases when influence of phylogeny was taken into account. Last, considerable attention is appropriately being directed at problems of humanity's increasing "ecological footprint." How quickly can organisms adapt to increases of global climate change of 2 °C, which species will adapt, what genetic-phenotypic characteristics will allow for greater adaptation? These issues inherently involve rates of evolution and, as developed in this chapter, MTE is an important hypothesis for getting at these questions.