

# Digest: Linking life-history evolution and substitution rates in extreme environments

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## Abstract

Weiss & Berv (2025) proposed and tested a resource longevity hypothesis on marine invertebrates in deep-sea ecosystems. They found that organisms in ephemeral environments have faster substitution rates, whereas those in stable environments have slower rates. The study confirmed that evolutionary rates differ across habitat types, a pattern the authors attributed to habitat longevity. Notably, there was no significant association between species body size and evolutionary rate. This suggests that resource variability drives evolutionary rates in these extreme environments.

**Keywords:** body size, molecular evolution, mutation rate

Uncovering the tempo of molecular evolution, and identifying its determinants, is a fundamental research area in evolutionary biology. The pace of new mutations in a genome, or the mutation rate, is influenced by the varying effects of mutagens and DNA repair efficiency. However, measuring the germline mutation rate, or the number of new mutations in sperm or egg cells per generation, is complex and challenging (Bergeron et al., 2023). An alternative is to infer and study the rate at which mutations become fixed within a clade (usually species or populations), known as the substitution rate. As substitution and mutation rates are interdependent, both are influenced by species-specific factors that affect new mutation frequency and fixation, as well as a genome's repair efficiency (Bromham, 2009).

Metabolic rate, generation length, and fecundity are important life-history traits affecting mutation accumulation over time (reviewed in Bromham, 2009). For example, high metabolic rates can increase the production of free radicals, which can cause mutations (Sohal & Allen, 1985). Shorter generation lengths and higher fecundity increase genome replication, raising the likelihood of mutations occurring and becoming fixed. Longevity and body size influence genome repair efficiency, potentially decreasing substitution rates (see Bromham, 2009). Hence, long-lived and large-sized species tend to invest more in repair mechanisms to ensure longevity and growth (Nabholz et al., 2007). These factors interact, and various biological and ecological processes that covary with or influence these traits may also predict molecular evolutionary rates.

In a recent study, Weiss & Berv (2025) propose a resource longevity hypothesis in which variation in the temporal availability of resources influences the life-history traits of animals, affecting their rates of molecular evolution (Figure 1). The authors tested their resource longevity hypothesis by analyzing substitution rates of invertebrates inhabiting deep-sea chemosynthetic ecosystems, such as cold seeps, hydrothermal vents, and organic falls. These environments vary greatly in their temporal stability: cold seeps are long-lived habitats, often persisting for millennia, where fluids rich in methane or other hydrocarbons gradually escape from subsurface reservoirs into the ocean floor; hydrothermal vents are transient systems associated with tectonically active regions, and when superheated, mineral-laden water is released through seafloor cracks; and organic falls, including decomposing wood or whale carcasses, are short-lived and support communities for only a few years to decades.

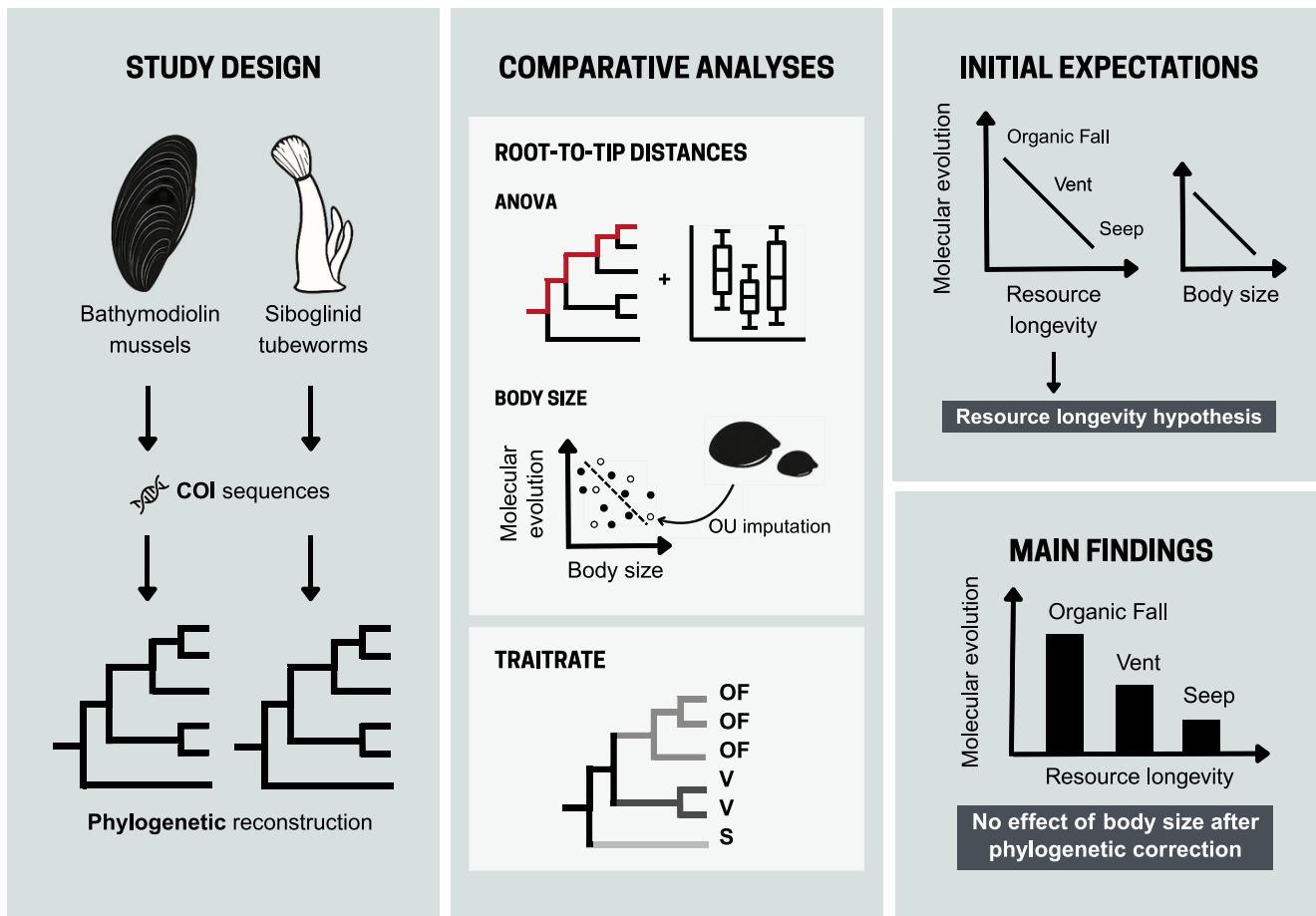
The study focused on mussels (Mytilidae: Bathymodiolinae) and tubeworms (Siboglinidae). For each clade, the authors used publicly available mitochondrial CO1 (cytochrome c oxidase subunit 1) sequences to reconstruct maximum-likelihood gene trees and extracted root-to-tip branch lengths as a proxy for substitution rates. The focus on CO1 stemmed from current data limitations, as other mitochondrial and nuclear markers for these taxa are underrepresented in GenBank. Additional sampling or sequencing would require considerable logistic and financial resources, making CO1 the most broadly available option at present.

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**Figure 1.** Study design and comparative analyses of rates of molecular evolution in deep-sea invertebrates across different habitats. COI sequences were used to estimate substitution rates in Bathymodiolin mussels and Siboglinid tubeworms, which were analyzed separately. Another complementary approach was used to estimate evolutionary rates, the *traitRate* method, which does not rely on root-to-tip distances. Rates of molecular evolution were expected to correlate negatively with resource longevity. The authors found support for the resource longevity hypothesis in both clades, but no effect of body size on molecular evolution after accounting for phylogenetic signal in body size.

Their results revealed an inverse relationship between habitat longevity and COI rate: organic-fall specialists had the highest rates of evolution, vent taxa showed intermediate rates, and seep dwellers showed the slowest rates. In other words, organisms in areas with more ephemeral resources tended to have faster substitution rates, possibly due to resource availability constraining lifespan and ultimately resulting in rapid growth and reproduction. Importantly, the study employed two complementary approaches to estimate evolutionary rates: root-to-tip branch lengths and the *traitRate* method, which is a model-based approach relying on molecular clocks (Levy Karin et al., 2017). Both mussels and tubeworms showed similar results across methods, emphasizing the robustness of the observed pattern for these two distinct phyla. The *traitRate* analyses, which jointly model discrete habitat states and local molecular clock variation, supported the resource longevity hypothesis over competing explanations (e.g., mutagen-avoidance or whaling-driven bottlenecks).

The authors found no evidence supporting an expected correlation between proxies of animal size and substitution rates. They compiled body-size data and imputed missing values under an *Ornstein-Uhlenbeck* model within a phylogenetic framework (Figure 1). Although organic-fall

taxa were generally smaller than vent or seep relatives, regressions that account for phylogenetic signal in body size showed no residual effect of size on COI rate—a surprising result, as smaller size (and presumed shorter generation time) often correlates with faster evolution in other taxa (see Bromham, 2009). Substitution-rate differences were largely due to synonymous codon changes, suggesting a neutral mechanism, though a few nonsynonymous sites hinted at habitat-specific selection. Furthermore, traits other than body size might have a stronger influence, considering the diverse life-history strategies of these marine invertebrates. Overall, these findings suggest that ephemeral habitats favor *r-selected* strategies (small size, rapid maturity) that increase the germline divisions per unit of time, thereby elevating the mutation rate. Moreover, accelerated mitochondrial evolution in short-lived environments may facilitate rapid genetic exploration and ecological divergence, potentially driving speciation in transient deep-sea resource patches.

Although the use of a single mitochondrial gene (CO1) in Weiss & Berv (2025) might limit broader evolutionary inferences, it also suggests new research prospects. While mitochondrial protein-coding genes like CO1 show conserved rate variation in large groups, such as vertebrates (Broughton & Reneau, 2006), considerable rate variation

across the mitogenome is common (Borges et al., 2025; Duchêne et al., 2011), meaning patterns in one gene may not generalize to others. Different coding regions might exhibit distinct evolutionary dynamics, and overlooking such heterogeneity risks biasing substitution rate inferences. Future work could expand genomic sampling to include multiple mitochondrial and nuclear genes to test whether habitat-linked rate patterns are genome-wide or gene-specific.

Furthermore, while mussels and tubeworms belong to phyla that diverged hundreds of millions of years ago, broader taxonomic sampling across diverse lineages and habitats (including those outside the deep sea) will further test the universality of the resource longevity hypothesis. Integrating structural and functional analyses of mitochondrial genes to disentangle selective pressures (e.g., sulfide resistance in CO1) from neutral processes is another interesting future avenue. Addressing these limitations will deepen our understanding of how environmental stability shapes genome evolution across the tree of life.

## Author contributions

F.S.C. and M.M.A.S. wrote the first draft; all authors wrote and revised the final version.

## Conflict of interest

The authors declare no conflict of interest.

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