Wainwright Exam

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1

Jim Brown's metabolic theory of ecology proposes the following universal scaling of all rates:

$$R = B_0 M^{-1/4} e^{-E/KT} \tag{1}$$

where R is the rate of interest, B_0 a normalizing constant, M is body mass E the energy of metabolism, around 62 electron-volts (eV), K is Boltzmann's constant and T is temperature (in Kelvin).

If we wanted to make this question easy for ourselves, we would pretend we never heard of this, make the reasonable assumption that metabolic rate scales linearly with body mass, and consequently assert that the energy ceiling sets a total body mass ceiling. Consequently any change in abundance is balanced by a change in body mass, you would just replace N individuals of mass M with $N/2$ individuals of mass $2M$ to obey the energy ceiling. Too bad Jim had to tell us about quarter power laws and make the question harder.

Anyway, the basic idea is that with a fixed ceiling on the rate energy can enter the system, if you want a species with a larger body mass you better make it less abundant or you'll exceed your energy allocation for the system. The question is how much less abundant? Our first instinct might be to keep the total biomass constant, so we replace 1000 rodents that each have a mass of one kilogram with 500 rodents with a mass of two kilograms.[1] However, Mr. Jim says no, no, its the rate, not the biomass, that we have to keep constant. Bigger organisms are more efficient, energy use doesn't

[1] big rodents, I know, but trying to use SI units and keep the math simple, so the biology of my example has to suffer

increase linearly with mass but instead scales a little less than linearly $M^{3/4}$, so doubling the mass requires only $2^{3/4} = 1.68$ times more energy. This means that by replacing my 1000 small rodents with 500 big rodents of twice the mass, I have some energy left over. Instead of 500 big rodents, I can add $1000/1.68 = 595$ big rodents in place of my 1000 little ones.

2

Decoupling morphological traits that have been previously constrained is one way that some group could substantially increase its diversification rate relative to its sister lineage. Decoupling can occur in a variety of ways. One of the best studied examples is the role of gene-duplication events. A gene may code for a particular protein needed by the organism to survive and perform, thus any changes to the gene are usually detrimental and selected against. For instance, the protein may play an important role in binding oxygen for transport in the blood stream. However, if the gene accidentally becomes duplicated, mutations in one of the genes will not interrupt the necessary biological functions of the other copy. It is possible that one copy receives a beneficial mutation, or series of mutations, that allow it to perform a different function. This may be very related (after all, the protein was already closely designed for a particular task); perhaps we get something a new oxygen carrying protein that binds with the original one, increasing the capacity of both – probably how the two alpha and beta subunits of haemoglobin came to be – or perhaps the protein is co-opted for a different purpose – instead of being an energy-making device powered by protons following in, it runs in reverse as an energy-consuming pump that pushes protons out. A large-scale survey would do well to consider the genes involved in metabolism in various bacterial and archae lineages, from those that metabolize carbon to those that metabolize sulfur, iron, and other diverse compounds.

Duplicating a metabolic gene and then allowing it to mutate to metabolize a different but related compound (move from sulfate to sulfites) would allow that particular lineage to colonize new territories, where it can subsist on a resource unavailable to its sister lineage. The lineage with the duplication may find that its extra copy is transformed to work on different metabolites within different lineages, while the original sister lineage is stuck with its constrained single protein, and cannot explore the diverse morphospace of different niches. Consequently, we would might see rapid speciation along

one lineage, and slow diversification along the other lineage, which we can trace back to a single gene-duplication event that occurred near the node separating the two. This could probably be repeated for many different bacterial and archae clades, as many exhibit radiations onto particular sets of metabolic energy sources. A similar investigation could be conducted more generally across gene duplications in all creatures, to see how often a duplication event in a lineage is correlated with an increased diversification rate.

The best methodology for identifying different diversification rates along a phylogenetic tree owes itself to Brian Moore, relying on topologically based methods outlined in his book chapter (2004). The method is discussed in question 4.

3

Because biological functions are complex, their performance is typically determined by the values of many morphological traits. How fast an animal can run depends not only on its mass and the length of its legs, but the positions of its joints, the strength and speed of its muscle fibers, and its metabolic rates, among other things. More complicated functions, such as survival in face of predation, depend on even more traits – not only running speed, but acceleration vs stamina, and also traits such as camouflage. This complex functional dependence means that there are many morphological combinations that can achieve the same functional performance – two very different morphologies may provide the same running speed, or the same average escape rate in encounters with predators. Such complex mappings of many different morphological combinations to the same functional performance are known as many-to-one mappings. As a consequence, a lineage can diversify extensively in some aspect of its morphology; perhaps one species becomes better and better at camouflage while another species becomes faster and faster at escaping predators, and yet both achieve the same survival metric in predator-encounter experiments.

4

One testable prediction is that an increased net diversification rate would be correlated with an increased rate of trait evolution. For instance, the decoupling of the motor control between tail, leg and pectoral muscles of a lizard (dinosaur) in those lineages that become birds is hypothesized to have resulted in an increased rate of diversification, giving rise to the Aves clade. Along with this rapid diversification creating many new species, we might expect that any given species also experiences rapid trait evolution as it is tuned by natural selection for its new habitat. The decoupling of motor control allows some lineages to evolve powerful grasping feet to take prey, while others to evolve webbed feet for swimming, while before these changes were constrained by any associated changes they would have had on the coupled system with the tail. Reduction of an evolutionary constraint will initially result more rapid trait evolution, a simple consequence of less constrained evolution from population genetics. Because the this more rapid trait evolution explores the morphospace faster, allopatrically isolated populations will drift apart faster, accumulating DMI's and behavioral differences at a proportionally faster rate due to the increased rate of trait evolution. This results in a parallel increase in the rate of speciation, and consequently higher diversification (speciation - extinction) rates.

Brian Moore's (2004) topologically based methods allow us to evaluate an ultrametric tree to determine if the diversification rates differ significantly throughout the tree overall, and across nodes. We might then expect the tree of all herps (lizards, birds, etc., I know its big and not very feasible, but its more fun to think big[2]) to show different rates of diversification across the node separating Aves from lizards. The basic idea of the method is to ask if one side of node is more branched then expected. The probability that the left side of a node has L of the N total species represented while the right side has $R > L$ species represented in an equal rates Markov chain branching process is given by

$$P = \frac{2L}{N-1} \tag{2}$$

[2]parallel examples of decoupling that allow a lineage to increase its rate of trait evolution and diversification might include decoupling primary jaw from the pharengeal jaw in fish, which will occur on a more reasonable size tree to actually do this test, but I'm already going with the birds and dinosaurs.

By considering likelihood ratios of the partition under the equal rates model compared to a model with separate diversification rates along each lineage in the node. This gives a significance test to assert that the rates are indeed statistically different between the lineages. A positive test would let us assert that the lineage with more branching has a statistically higher diversification rate, as expected by the biological argument regarding the decoupling on that lineage.

The next part of our question is analyzed with Brian O'Meara's `Brownie` software, which allows us to ask if the rate of trait evolution differs significantly across different lineages of a phylogeny, provided we have trait values at the tips. The original method assumes Felsenstein's (1985) Brownian motion model for trait evolution, and asks if the Brownian rate parameter differs between two lineages across a node (again across our node of interest, where modern-day lizards meet birds). Our prediction is that again we would find a positive answer.

This procedure could be repeated for many candidate examples of decoupling, adaptive radiations and key innovations, where one might expect a higher rate of trait evolution and subsequently a higher diversification rate. The grand meta-analysis would ask if the outcome of the `Brownie` test was correlated with the outcome of Moore's test.