Heredity (2007), 1–3

www.nature.com/hdy

NEWS AND COMMENTARY

Evolution and ecological theory

Chance, historical contingency and ecological determinism jointly determine the rate of adaptive radiation

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Heredity advance online publication, 8 August 2007; doi:10.1038/sj.hdy.6801047

Much of the functional diversity of life is thought to have evolved in multiple bursts of adaptive radiation—periods of rapid speciation associated with diversification into a multitude of ecological niches (Simpson, 1953; Benton, 1995). Studying the causes and mechanisms of adaptive radiation is therefore expected to make important contributions to understanding the evolutionary underpinnings of biodiversity and its ecological structure. Distinguishing between effects of chance, historical contingency and ecological determinism, as well as their interactions is of prime importance. Yet, this perhaps is the greatest challenge that investigators of adaptive radiations face when trying to make sense of events in the past. The full complexity of adaptive radiation has eluded analytical and computer-based modeling, although some new approach has recently emerged (Gavrilets and Vose, 2005). Instead, experimental work using the rapid evolution in microbial cultures has taken center stage. Studies of microbial systems have helped to confirm that stable and heterogeneous environments facilitate diversification, and that intraspecific competition in a resource-limited environment can produce negative frequency-dependent selection, which can act as an important driver of ecological diversification (Rainey *et al*., 2000).

These experimental studies support the ecological theory of adaptive radiation, which postulates that diversification is often driven by the combination of ecological opportunity and intraspecific competition (Schluter, 2000). One deficiency of the ecological theory is the difficulty it has in explaining the large variation in occurrence and extent of adaptive radiation between taxa and between localities of the same taxon. There are numerous situations where populations failed to radiate despite inhabiting environments apparently conducive to adaptive radiation and despite belonging to clades that have proven very capable of radiation in other places with apparently similar conditions (for example, Seehausen, 2006). Historical contingency is then usually invoked to rescue the ecological theory.

One element of historical contingency is the presence of other species. The ecological release hypothesis, postulating that taxa radiate when they are released from competition with other species, is probably as old as the concept of adaptive radiation itself (Simpson, 1953). The hypothesis derives from the observation that recent adaptive radiations occurred most often on isolated island archipelagos or in closed lakes. However, the evidence can be ambiguous, and there is evidence too that the presence of other species can have a positive effect on diversification (Emerson and Kolm, 2005). Two experimental microbial evolution studies, both published earlier this year in *Nature*, address facets of this question in adaptive radiation theory: the effects of other species as predators and as competitors.

Meyer and Kassen (2007) investigated the evolution of ecological diversity in experimental populations of the bacterium *Pseudomonas fluorescens*, in the presence and absence of their protist predator *Tetrahymena thermophila*. The authors estimated the frequency-dependent fitness functions of competing niche-specialist genotypes, the broth-colonizing ‘smooth’ and the biofilm-forming ‘wrinkly spreader’ in the presence and absence of predators. They found that competition and predation could both generate diversifying selection, although the effect was weaker under predation—probably because predation reduces bacterial densities, thereby weakening resource competition. In a second experiment, the authors cultured populations of initially isogenic *P. fluorescens* under conditions in which competition does not cause adaptive radiation. The addition of predators caused the emergence of multiple novel ‘wrinkly spreader’ genotypes resistant to predation. Finally, the authors found that, under conditions conducive of competition-driven radiation, predation caused a significant time lag in the diversification of the bacteria, but no difference in the long-term sustained diversity. Interestingly, the predator-free experiments produced the overshooting of diversity typically seen in experimental microbial radiations, whereas final diversity was approached more steadily in experiments with predators.

Meyer and Kassen (2007) conclude that both intraspecific competition and predation can drive adaptive radiation independently, but that the stronger frequency dependence arising from resource competition may limit a primary role of predation to those cases where there are few opportunities for resource specialization (so that disruptive selection on resource utilization is unlikely). Furthermore, they argue that the negative effects of predation on the rates of diversification may explain why diversification rates on islands often appear faster than on continents. Their experiments bear on a long-standing debate about the role of predators in adaptive radiation and may actually help to reconcile apparently contradicting observations. The impact of predation on the adaptive radiations of the East African cichlid fish was the subject of intense dispute in the 1960s. Lowe-McConnell (1993) summarized the debate and concluded that predation appears to inhibit speciation in the absence of predation refugia, whereas it could promote it in the presence of refugia. Among the African Great Lakes inhabited by *Astatotilapia*-related haplochromine cichlids, those with a native community of top predators (*Lates*, *Hydocynus*) harbor less species-rich cichlid radiations than comparable lakes that lack native top predators (Figure 1). The idea that the diversity in these latter lakes is currently in the overshooting phase of radiation and may eventually converge with that in the other lakes to intermediate levels is intriguing. It is consistent with the finding that the species richness in African cichlid radiations correlates negatively with radiation age, after controlling for lake size (Seehausen, 2006).

Fukami *et al*. (2007) used experimental adaptive radiation in *P. fluorescens* to investigate the effects of immigration history, specifically, the relative timing

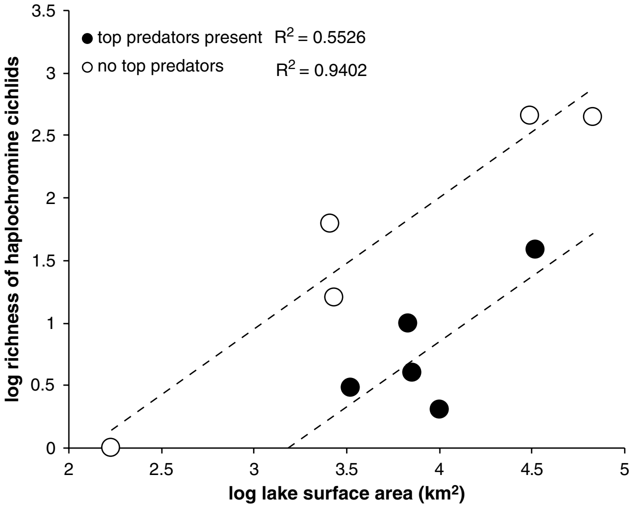

Figure 1 The relationship between lake size and species richness of *Astatotilapia*-related haplochromine cichlids in African Great Lakes without and with native top predator communities. Trend lines are estimated as least-squares regressions on a loglog scale (only lakes that hold *Astatotilapia*-related cichlids included; data are obtained from Seehausen, 2006).

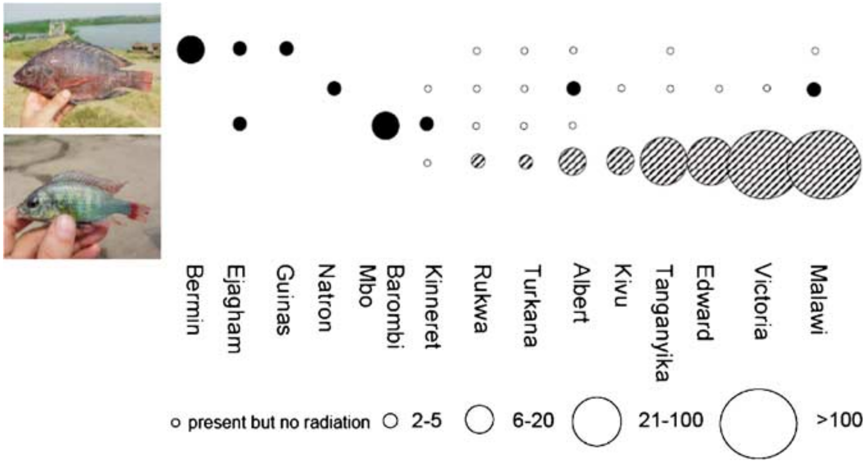

Figure 2 Geographical patterns of adaptive radiation imply the possibility of suppression between unrelated cichlid lineages. Two major phylogenetic lineages are responsible for most of the adaptive radiations of cichlid fish in African lakes, the tilapiines (black circles, three genera from top to bottom *Tilapia*, *Oreochromis*, *Sarotherodon*) and the *Astatotilapia*-related haplochromines (hatched circles; circle size represents number of species). Both groups are widely distributed across African lakes, and often co-occur. However, they very rarely radiate in the same lake: in lakes in which haplochromines radiated, tilapiines did most often not, and most tilapiine radiations occurred in lakes from which haplochromines are absent. It will be interesting to investigate whether the apparent inhibition of tilapiine radiations by the presence of haplochromines is related to arrival order, as the experiments of Fukami *et al*. (2007) predict, or competitive superiority of haplochromines. The case of Lake Kinneret indicates that tilapiine radiations do not necessarily have to be suppressed by the presence of haplochromines. There are also cases where both lineages co-occur and neither radiated, or where only one occurs yet did not radiate, but these cases are not plotted (data are obtained from Seehausen, 2006). Photo insets show representatives of the two lineages: *Oreochromis niloticus eduardianus* (top) and *Astatotilapia elegaus* coexist in Lake Edward but only *Astatotilapia* radiated.

of arrival of competing species, on diversification. When introduced alone into the medium, the ancestral 'smooth' genotype rapidly diversified into a 'fuzzy spreader' and multiple 'wrinkly spreader' genotypes. However, when 'smooth' and a derived 'wrinkly spreader' genotype were introduced sequentially, the timing and order of arrival resulted in striking differences in the extent of diversification. When arriving at least 24 h after 'smooth', 'wrinkly spreader' had no detectable effect on the diversification of 'smooth'. Conversely, it completely suppressed the radiation of 'smooth' when arriving earlier: 6 h after 'smooth', simultaneously or beforehand. Varying the order of arrival among four different *P. fluorescens* genotypes, the authors showed that the suppression of radiation by early arrival of a competitor occurred as a consequence of pre-emptive colonization, rather than unequal competitiveness of different genotypes.

Interestingly, two effects parallel the observations of Meyer and Kassen (2007). First, the treatments converged on an intermediate diversity in the long term. After 30 days, the effects of the immigration treatment on diversity were no longer apparent. Second, the treatments that were conducive to early rapid diversification generated an overshooting effect, which the others did not.

Fukami *et al*. (2007) hypothesize that subtle differences in immigration history may explain the otherwise puzzling variation in diversification observed across replicate radiations of the same taxon, such as lizards on the Caribbean Islands, cichlids in African lakes or snails on the Hawaiian Islands. Although this idea is not entirely new, the highly repeatable effects of subtle differences in the timing of arrival are a qualitatively new feature. It will be difficult to test the contribution of this effect in nature. However, molecular phylogeographic approaches in systems with mutiple natural replicates hold some promise (Figure 2). The prediction would be that among multiple taxa in a closed ecosystem, the taxon that is most divergent from its external source population (the oldest colonist) should be the most likely to undergo adaptive radiation.

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Benton MJ (1995). Diversification and extinction in the history of life. *Science* **268**: 52–58.

Emerson BC, Kolm N (2005). Species diversity can drive speciation. *Nature* **434**: 1015–1017.

Fukami T, Beaumont HJE, Zhang X, Rainey PB (2007). Immigration history controls diversification in experimental adaptive radiation. *Nature* **446**: 436–439.

Gavrilets S, Vose A (2005). Dynamic patterns of adaptive radiation. *Proc Natl Acad Sci USA* **102**: 18040–18045.

Lowe-McConnell R (1993). Fish faunas of the african great lakes: origins, diversity, and vulnerability. *Cons Biol* **7**: 634–643.

Meyer JR, Kassen R (2007). The effects of competition and predation on diversification in a model adaptive radiation. *Nature* **446**: 432–435.

Rainey PB, Buckling A, Kassen R, Travisano M (2000). The emergence and maintenance of diversity: insights from experimental bacterial populations. *Trends Ecol Evol* **15**: 243–247.

Schluter D (2000). *The Ecology of Adaptive Radiation*. Oxford University Press: Oxford.

Seehausen O (2006). African cichlid fish: a model system in adaptive radiation research. *Proc R Soc B* **273**: 1987–1998.

Simpson GG (1953). *The Mjor Features of Evolution*. Columbia Univ. Press: New York.

Editor's suggested reading

Brakefield PM, French V (2006). Evo-devo focus issue. *Heredity* **97**: 137–138.

Mallet J (2005). Speciation in the 21st century. *Heredity* **95**: 105–109.

Meyer A (2005). Evolutionary biology: cichlid species flocks of the past and present. *Heredity* **95**: 419–420.

Sinervo B (2005). Evodevo: Darwin's finch beaks, bmp4, and the developmental origins of novelty. *Heredity* **94**: 141–142.

Tobler A, Kapan D, Flanagan NS, Gonzalez C, Peterson E, Jiggins CD *et al.* (2005). First-generation linkage map of the warningly colored butterfly heliconius erato. *Heredity* **94**: 408–417.