

about four letters. If, however, they are instructed to report as many letters as possible from one particular row then, even if the instruction is given just *after* the letters were presented, observers usually manage to report the complete row of four letters. It seems that all of the letters are potentially reportable, but only four can actually be reported. The cue instructs the observer which four to select.

Block [10] emphasises that observers have the impression they see all of the letters even though they cannot report all their identities. He claims that the experience of the unreported items is complete — it is not a matter of seeing ‘blurs’ or generic impressions of letters, but rather seeing all of the letters in the array with equal levels of phenomenal detail despite only able to access the identity of the reported subset. Items can exist that are seen phenomenally but whose identity cannot be reported because the capacities of phenomenal and access consciousness differ.

The contrary position, for example [12], is that experience of the unreported items is incomplete and so there is no dissociation between experience and cognitive access.

For this to occur we need to have, in Block’s own words ([13] p. 573), “unconscious representations that are specific enough to do the task with the observed accuracy... the cue is supposed to promote attentional amplification of the cued unconscious specific representation, which, when combined with the conscious generic representation, results in a conscious specific representation of the cued item.” That is, of course, exactly what Sergent *et al.* [3] have found (except that their subjects do not even appear to report a generic representation of the unseen stimulus).

Sergent *et al.*’s [3] result does not necessarily invalidate the distinction between access and phenomenal consciousness, but it does lend weight to the alternative, and perhaps simpler, position that consciousness is just consciousness.

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Adaptive Radiation: Convergence and Non-equilibrium

The spectacular adaptive radiation of cichlid fish in Lake Tanganyika encompasses extensive morphological convergence and co-occurrence of ecologically similar species, forcing a reevaluation of non-equilibrium dynamics in community assembly.

Rosemary G. Gillespie

The diversity of life is bewildering, but two age-old questions remain: first, is species origination dictated by chance evolutionary events or constrained to follow fairly predictable trajectories? Second, does the observed diversity and composition of species reflect an equilibrium, and if so, over what time period? In terms of species origin, one argument is that evolutionary outcomes are shaped by the whims of immediate events: “The divine tape player holds a million scenarios ... [and] the end results are so different” [1]. The alternative is that outcomes are

constrained such that the appearance of certain forms at a given time and place becomes “very probable, if not inevitable” [2]. With regards to patterns of species composition, the debate concerns the ‘balance of nature’ — the idea that the overall diversity at a site tends toward a relatively steady state. This supposition was questioned with the recognition of the importance of the dynamic nature of biodiversity, and that patterns may be governed more commonly by non-equilibrium processes in which species diversity is inherently unstable and changing over time.

Insights into these long-standing questions, as often in evolutionary biology, have come from insular systems, habitats isolated by surroundings that are inhospitable to the respective organisms, as these provide discrete settings, often replicated over space and time. Moreover, with the advent of sophisticated genomic, isotopic, and visualization tools, it has become possible to understand the detailed history of lineages, and the extent to which patterns of differentiation are linked to shifts in ecology and associated morphology. In a recent issue of *Current Biology*, Muschick *et al.* [3] summarize the results of an extraordinarily comprehensive study of the adaptive radiation of cichlid fish in the African Great Lakes, in which the ecological identity of species, and their occurrence within a given community, is frequently predictable. The study represents the most extensive quantitative analysis to date

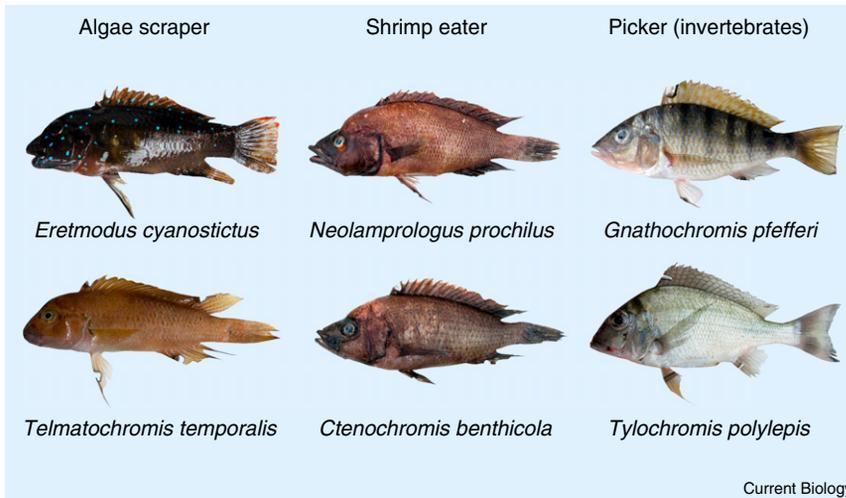


Figure 1. Tanganyika cichlid ecomorphs.

Set of three of about a dozen primary ecomorphological types of cichlid fish; each pair co-occurs within Lake Tanganyika [3]. Photo credits: Moritz Muschick, Adrian Indermaur, Walter Salzburger.

of the ecological underpinnings of adaptive radiation in cichlids.

The authors [3] make two major points: the first relates to how diversity originated, the second to the dynamics of the communities thus generated. In the context of the ecological predictability of species origination, the authors show that morphological characters, including body and jaw shape, are correlated with the trophic niche (as indicated by stable isotopes and gut content). The important point here is that convergence to similar form is strongly associated with the trophic niche of the organisms (Figure 1). This has long been suspected, and has served as the basis for the idea of ‘ecomorphs’, or sets of species that are similar in ecology, morphology, and behavior, but are not necessarily closely related [4]. The repeated evolution of similar functional morphologies has now been illustrated in many other adaptive radiations, including Hawaiian finches, Caribbean *Anolis* lizards [5], *Mandarina* snails of the Bonin Islands [6], Hawaiian spiders [7], and Hawaiian creepers [8], among others (Figure 2).

The detailed ecomorphological work by Muschick *et al.* [3] in cichlids is particularly important in the light of recent advances in genomics which are showing that, when similar traits evolve in an adaptive radiation, the same genetic pathways can be deployed, though often in concert with other genetic changes [9]. There are now many examples showing deployment

of similar genetic changes to allow rapid and repeated adaptive change, including the colonization of freshwater glacial lakes by marine sticklebacks with the repeated evolution of similar benthic and limnetic forms [9], and the establishment of lizards and mice in desert environments of North America with repeated evolution of traits associated with adaptation to the light and dry habitats [10]. Likewise, small changes in a single gene appear to be responsible for the repeated evolution of similar coloration in the mimicry complexes of *Heliconius* butterflies [11]. This kind of recurrent evolution of similar forms controlled by the same genetic pathways can span many taxonomic levels: adaptation to cave environments has been found to involve a similar mutation at the first step of melanin synthesis, in both planthoppers (from Hawaii and Croatia) and Mexican cavefish [12]. While it is clear that use of the same genetic pathways can explain some of the remarkable examples of convergent evolution during adaptive radiation, there are other factors at play. Perhaps most intriguingly, plasticity has been highlighted as having a major role in adaptive radiation: It appears that flexibility in ecology, behavior, or morphology allows organisms to explore the adaptive landscape while being buffered from the effects of novel genetic variants [13]. Here again, cichlids have provided a superb illustration: the jaw shape of neotropical Midas cichlids can

change in response to different diets, placing the animal under a different selective regime; this plastic response may then serve as the basis for subsequent adaptive radiation [14]. Other fish can show similar flexibility. In particular, individuals of anadromous sticklebacks are limnetic when young, becoming more benthic with age: it appears that selection on the timing of this developmentally plastic response has served as the basis for repeated evolution of pairs of benthic and limnetic species as the fish have moved into freshwater lakes [13]. The intriguing point is that actual changes in gene frequency can be achieved through ecological or developmental plasticity, a phenomenon known as ‘genetic accommodation’, and that this flexibility may facilitate rapid adaptation while constraining it to specific trajectories.

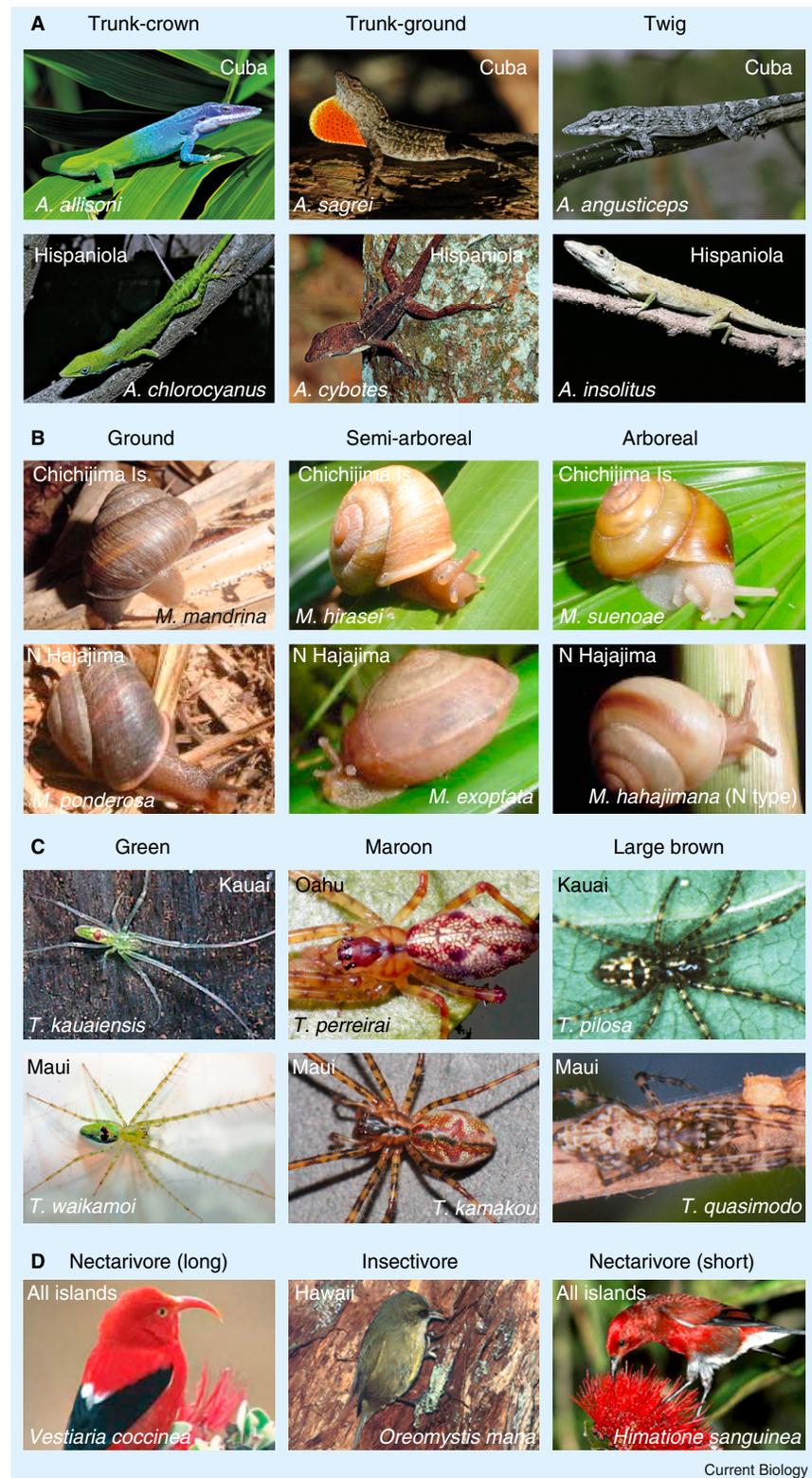
The second major point made by Muschick *et al.* [3] is that similar ecomorphs (though not closely related species) often co-exist in Lake Tanganyika, which might be surprising given that theory predicts competitive exclusion should prevent co-occurrence of taxa that might occupy the same niche. The authors suggest that the relatively advanced age of the adaptive radiation in Lake Tanganyika allows similar ecomorphs from distant lineages to coexist simply because they have accumulated differences in other attributes, and so may occupy slightly different niches. This pattern is reminiscent of the *Anolis* radiation in which co-occurrence of ecomorphs is possible when they differentiate along another (physiological) axis [5]. However, the significance of this finding becomes apparent when considered in the context of the growing number of studies showing that co-occurrence of ecologically equivalent species may be quite common in nature [15]. For example, among select groups of treefrogs and lizards, lineages of an ecological form can readily colonize areas in which a similar form already resides [16]. The corollary is that particular environments may allow many evolutionary outcomes, rather than a fixed equilibrium of defined niches. Indeed, it is not clear as to whether species composition can achieve steady state when speciation, as opposed to immigration, is the

Figure 2. Sets of ecomorphological equivalents for different adaptive radiations.

The examples illustrate first, the taxonomic diversity across which the repeated evolution of ecomorphological similarity is found; second, the same ecomorph in different islands/lakes is not identical, and convergence along one morphological/ecological axis might differ in another; third, while the occurrence of similar ecomorphs on different islands/lakes is frequently due to convergence, as in *Anolis* lizards and *Mandarina* snails, it can involve a mixture of both colonization of multiple islands by a single species as well as convergence to the same ecologies between islands, as in the Hawaiian honeycreepers. (A) *Anolis* lizards — three of six known ecomorphs, from two islands of the Greater Antilles; in each case, the different ecomorphs within islands are more closely related to each other than they are to the same ecomorph on the other island [20]. (B) *Mandarina* land snails — three of four known ecotypes from two of the Bonin Islands in the west Pacific; taxa belonging to lineages within each island are monophyletic [6]. (C) Three of four known ecomorphs of the spiny leg clade of Hawaiian *Tetragnatha* spiders on older (Kauai, Oahu) and younger (Maui) islands [7]; the taxa shown from different ecomorphs on the same island are more closely related to each other than to the same ecomorph on different islands. (D) Hawaiian honeycreepers showing that similar ecomorphs occur on different islands, though it has involved a mixture of colonization of multiple islands by a single species (the two nectarivores) as well as convergence to different ecologies within islands (the insectivore creepers which have evolved independently [8]). Photo credits: A: Jonathan Losos (except *A. insolitus* – Kevin de Queiroz); B: Satoshi Chiba; C: R. Gillespie except *T. kamakou*, Darko Cotoras; D: Jack Jeffrey.

principal contributor to species richness: the protracted rate of speciation may prevent diversity reaching a steady state, with species richness dictated simply by diversification rates and time.

The finding of co-occurrence of ecologically equivalent species is particularly fascinating given recent work on *Anolis* lizards showing that species richness is primarily determined by island-specific limits on total diversification, thus arguing for some form of equilibrium diversity [17]. Meanwhile, studies that have used island chronologies to look at changes in diversity over the course of adaptive radiation have revealed a peak of diversity on islands of intermediate age in the archipelagoes of Hawaii [18] and Macaronesia [19], though only in more diverse lineages [18]. This pattern suggests that there may be some form of steady state, but the rate at which it might be attained differs between taxa.



In the cichlid study [3], the authors find no indication of equilibrium having been reached in the lineage. Further research is clearly required to identify the timeframe over which lineage diversity might reach equilibrium,

if it does, in the context of adaptive radiation. The stage is now set for understanding how convergence might facilitate rapid saturation of communities, and potentially allow 'super-saturation' such that multiple

species can come together within a broadly defined niche.

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Quality Control: Putting Protein Aggregates in a Bind

Asymmetric inheritance of protein aggregates in budding yeast is a fascinating yet controversial area of aging research. A recent study demonstrates that unfolded protein aggregates are confined to the mother by tethering to organelles rather than retrograde transport.

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One of the most intriguing aspects of aging is the ability of cells to asymmetrically distribute potentially harmful protein aggregates during the process of cell division and therefore allow half of the progeny of each division to begin life with a clean slate. Recent studies have investigated the mechanism for this phenomenon in budding yeast [1,2], which undergoes asymmetric mitotic cell division and segregation of aging related aggregates between the mother (aged) and bud (newborn) [3,4]. A debate has centered over the role of the motility of protein aggregates and the contribution of actin in generating asymmetric inheritance. A new study by Spokoini *et al.* [5] now reveals that certain aggregates are asymmetrically inherited due to confinement of their

motility as a result of accumulation in juxtannuclear quality control compartments (JUNQ) or insoluble protein deposit compartments (IPOD).

An earlier study suggested that an active transport mechanism involving actin cables is responsible for the clearance of heat-shock-induced protein aggregates, decorated with the Hsp104 chaperone, from the bud to the mother prior to cytokinesis (Figure 1A, top) [1]. This hypothesis was supported by data showing that disruption of the actin network led to defects in asymmetric inheritance of aggregates and that some aggregates in the bud moved across the bud neck into the mother side. A later study from our laboratory [2] questioned this hypothesis, firstly on the grounds that cell polarity and well oriented actin cables only exist in a limited time window prior to entry into mitosis, well before cell division [6].

It then used quantitative particle tracking analysis of hundreds of protein aggregates to show that aggregates move in a stochastic but confined manner that does not contain any statistically significantly transport component throughout the cell cycle [2] (Figure 1A, middle). This finding led to a mathematical model to explain asymmetric aggregate inheritance based on the study's phenomenological measurements. The model predicted that the observed properties of the confined diffusion of the aggregates combined with the geometry of budding yeast cells were sufficient to yield a very low probability of aggregates entering the bud from the mother during the time span of a cell cycle. Parameters of this model that impact this probability include the cell-cycle duration, the width of the opening between the bud and the mother, the presence or absence of confinement, and the diffusion coefficient of the aggregates.

The above model (referred to herein as 'the stochastic model'), however, was based simply on the experimentally measured diffusion parameters and made no assumptions about the mechanism underlying the observed confined diffusion of the