Key innovations and the ecology of macroevolution

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The origin or evolutionary 'success' of taxa is often attributed to key innovations – aspects of organismal phenotype that promote diversification. Different ways of delimiting taxa and measuring 'success' (i.e. number or longevity of species, morphological variety or differential control of energy) give rise to different ideas of how key innovations might operate. Key innovations may enhance competitive ability, relax adaptive trade-offs or permit exploitation of a new productive resource base. Recent key innovation studies comparing species richness in extant sister clades may miss important observations possible only with consideration of the fossil record, traditional higher taxa and phenotypic diversity.

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Key innovations are aspects of organismal phenotype important to the origin or subsequent success of a taxonomic group. This concept is controversial, however, because it is difficult to test hypothesized key innovations[1] and because researchers understand the concept in different ways (see Box 1). Nevertheless, the various definitions of key innovation share the basic idea that some attributes of organisms have been important over evolutionary time. The concept links autecology and macroevolution, or more specifically, the summed performance of individuals and the performance of a taxonomic group to which the individuals belong. When properly investigated (Boxes 2 and 3), key innovations can potentially link evolutionary processes acting on different hierarchical levels. Nevertheless, key innovation hypotheses are not attempts to reduce the causes of biological expansion down to a single factor.

Historically, researchers have measured evolutionary 'success' by the appearance of higher taxa, the proliferation of species or the generation of new morphologies. Each measures a different aspect of expansion in the use and control of energy[2], and key innovations may promote this expansion. Recent investigators have tended to focus on taxonomic diversification, usually the number of species in a group, whereas older literature was more concerned with major adaptive shifts recognized by the appearance of higher taxa. Here, I outline how the key innovation concept has itself evolved, explain what can be learned from older approaches, indicate problems in current analytical methods, and offer some alternatives.

Key innovations and higher taxa

The key innovation concept has always been linked to the origin of higher taxa[3,4], specifically to explain how higher taxa arise in terms of population level processes. Miller[3] used the origin of ground-foraging thrashers from among tree-foraging mockingbirds as a case study of a taxon (genus *Toxostoma*) originating from within another (genus *Mimus*) and described the differentiation in digging ability among thrashers as a possible 'genus in the making'. The acquisition of simple, but functionally important, changes in beak form makes possible the appearance of sets of birds (thrashers and mockingbirds) with different functional abilities and ecological tendencies. Traditional systematicists would recognize the adaptive and ecological distinction between these birds by placing them in different taxa.

These taxa are, of course, those of evolutionary systematics. The differences between such taxa can be large, whereas Miller saw natural selection as capable of only incremental change and felt that extinction is insufficient to account for the distinctiveness of major groups[3]. Instead, small changes in form can have a large functional significance (i.e. key innovations) and bring a lineage into a new ecological sphere where it can diverge free from competition with related incumbent species[3].

This connection between key innovations and the origin of higher taxa made biological sense to early workers. Invasion of new adaptive zones (i.e. a set of related ecological niches) was seen to precede the origin and diversification of (and within) higher taxa, and key innovations were seen to facilitate a transition into a new adaptive zone. Historically, studies of key innovations have focused on characters that diagnose higher taxa and set them apart adaptively from their close relatives[5] as opposed to characters that promote diversification *per se*. For example, among mammalian orders, the Tubuliden-tata (aardvarks) are not and probably never have been particularly diverse either morphologically or taxonomically; nevertheless, aardvarks possess key characters that have essentially committed them to eating colonial insects, a way of life quite different from other 'subungulates'[5]. Traditional ('evolutionary') systematists would recognize the distinctiveness of aardvarks by placing them in their own order. If macroevolution is concerned with such 'character-state transitions that diagnose evolutionary differences of major taxonomic rank'[6] (e.g. between the order Tubulidentata and other mammalian orders), then key innovations should occupy a central place in the study of macroevolution.

Historically, the rug might have been pulled out from under the key innovation concept with the decline of evolutionary systematics and the rise of phylogenetic systematics. When systematists began to group species into holophyletic (monophyletic *sensu stricto*) clades rather than higher taxa, investigators of macroevolution shifted their focus from the biological differences between groups to the differential performance of clades, most easily measured as numbers of species. Because many traditional higher taxa are paraphyletic, unacceptable within phylogenetic systematics, many macroevolutionists viewed the biological distinctiveness of higher taxa as a partial result of an arbitrary classification[7]. On the other hand, differences in the number of species between clades could be investigated as the result of

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Box 1. Contrasting definitions of key innovation

Miller (1949): '... key adjustments in the morphological and physiological mechanism which are essential to the origin of new major groups'[3].

Van Valen (1971): 'A key *character*, in the adaptive sense, is a structure or element of physiology that makes a taxon more or less committed to a way of life different from, or appreciably more efficient than, that of its ancestors'[5].

Levinton (1988): 'key innovation is necessary, but not sufficient for a subsequent radiation'[6].

Baum & Larson (1991): '... a trait that greatly modifies the selective regime of the lineage in which it evolves'[15].

Rosenzweig & McCord (1991): 'A key adaptation is a change in the mathematical rule governing a trade-off constraint so that after the change, the trade-off is less severe'[13].

Erwin (1992): '[K]ey innovations characterize particular clades and are both necessary and sufficient to explain diversification within the clade'[39].

Heard & Hauser (1995): 'an evolutionary change in individual trait(s) that is causally linked to an increased diversification rate in the resulting clade (for which it is a synapomorphy)'[9].
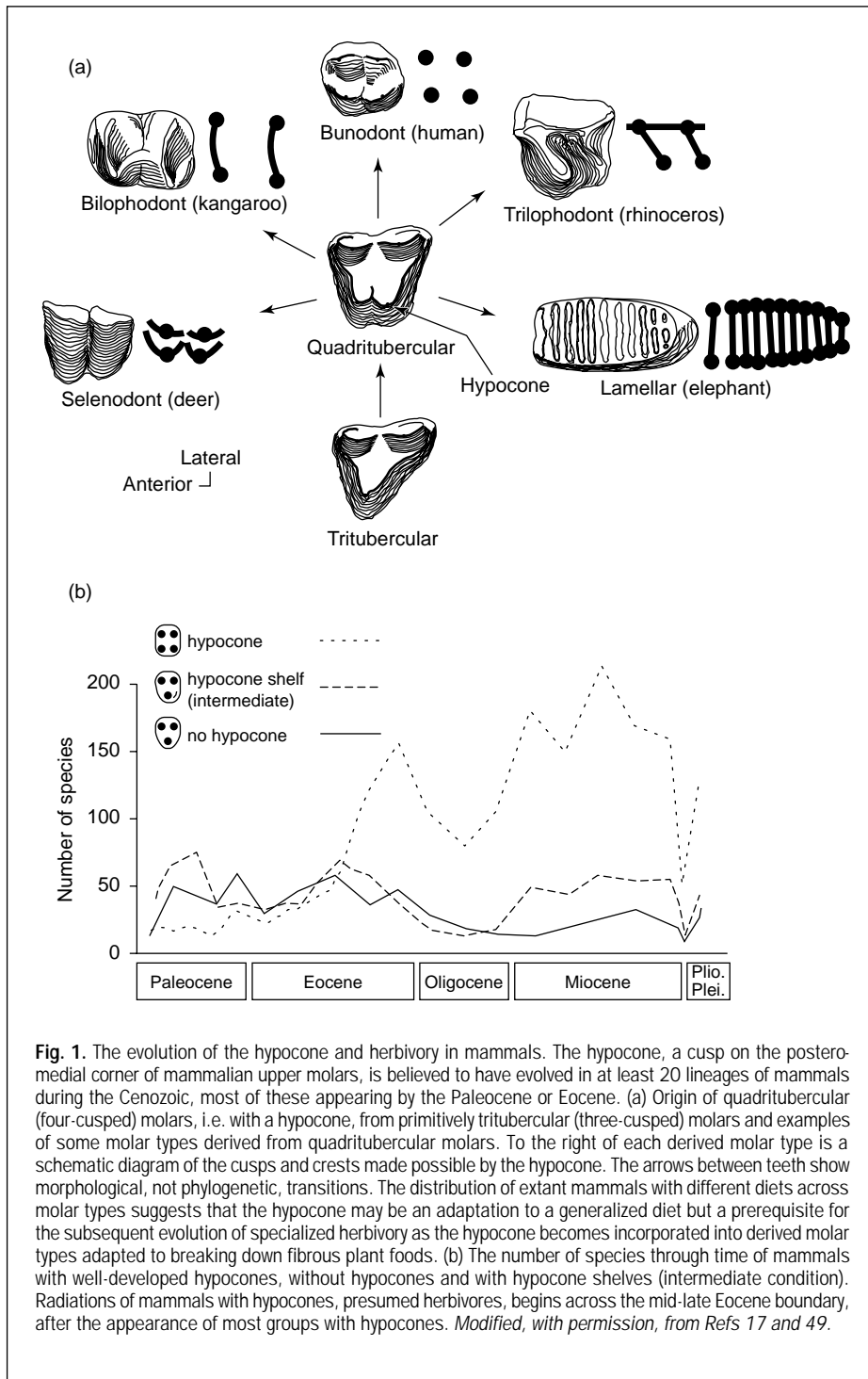

Fig. 1. The evolution of the hypocone and herbivory in mammals. The hypocone, a cusp on the postero-medial corner of mammalian upper molars, is believed to have evolved in at least 20 lineages of mammals during the Cenozoic, most of these appearing by the Paleocene or Eocene. (a) Origin of quadritubercular (four-cusped) molars, i.e. with a hypocone, from primitively tritubercular (three-cusped) molars and examples of some molar types derived from quadritubercular molars. To the right of each derived molar type is a schematic diagram of the cusps and crests made possible by the hypocone. The arrows between teeth show morphological, not phylogenetic, transitions. The distribution of extant mammals with different diets across molar types suggests that the hypocone may be an adaptation to a generalized diet but a prerequisite for the subsequent evolution of specialized herbivory as the hypocone becomes incorporated into derived molar types adapted to breaking down fibrous plant foods. (b) The number of species through time of mammals with well-developed hypocones, without hypocones and with hypocone shelves (intermediate condition). Radiations of mammals with hypocones, presumed herbivores, begins across the mid-late Eocene boundary, after the appearance of most groups with hypocones. *Modified, with permission, from Refs 17 and 49.*

different net rates of diversification (origination minus extinction). Adopting a phylogenetic classification would obviate the need to explain how a higher taxon might arise from another, because, in a phylogenetic classification, taxa do not arise from one another but instead are nested within each other. If the origin of higher taxa were to become a non-issue, so too might the evolutionary role of key innovations.

Key innovations and the proliferation of species

One way to rescue the key innovation concept and incorporate it into recent discussions on macroevolution is to link key innovations to the rate of taxonomic evolution (e.g. the change in number of species within a clade over time). If the evolutionary performance of groups is measured using net rates of diversification, then perhaps key innovations operate by increasing either the rate at which species form or the probability that species will survive to speciate again (not all workers would accept the latter as key innovations[8]). In fact, recent research on key innovations has focused mainly on taxonomic diversification[9]. Accordingly, a substantial literature has developed on how to detect changes in the rate of taxonomic diversification on phylogenetic trees[10].

In some cases, the connection between innovation and taxonomic diversification is direct, in others less so. If speciation results from divergence in the same characters on which natural selection acts, as in ecological[11] or competitive[12,13] speciation, then a key innovation that facilitates ecological divergence might also directly influence taxonomic diversification as well. Evidence for these controversial speciation modes, however, is rare in nature. In theory, ecological or competitive speciation should be most common at the base of adaptive radiations[11,12] or during biotic replacements[13] when key innovations may have most influence on diversification rate[14].

In other cases the connection between innovation and taxonomic diversification is indirect or unclear. Heard and Hauser[9] hypothesized that on an ecological time scale key innovations might work by one of the following three mechanisms: (1) by allowing escape from competition via invasion into a new adaptive zone, (2) by decreasing the probability of extinction by increasing population density via increased individual fitness, or (3) by favoring reproductive or ecological specialization.

Invasion of a new adaptive zone may result in a change in the selection pressures acting on a lineage[15], which may result in evolutionary changes of a magnitude that traditional systematists would recognize by naming a new taxon for the derived forms[4,6]. Whether the change in adaptation also results in a proliferation of new species depends as much on the adaptive zone itself as the lineage invading it. Adopting herbivorous habits seems to offer many opportunities for new species among insects[16] and mammals (Fig. 1)[17], whereas adopting parasitic habits offers fewer opportunities[18].

Do key innovations impart resistance to extinction? It is easier to imagine how key innovations might improve survivorship of peripherally isolated populations than increase chances of forming isolates in the first place. Longer lived isolates are more likely to attain reproductive isolation, be sampled in the fossil record and speciate again. Evidence from the fossil record, however, is equivocal. Extinction rates in a variety of organisms have been observed to remain constant for long periods of time or to vary in ways unrelated to diversity equilibria or steady states in the number of species[19,20] (apparent resetting of diversity equilibria to higher levels is often attributed to key innovations[14,17]). Thus, diversity equilibria tend to be regulated by origination rate alone rather than extinction rate or an interaction between the two. Accordingly, the effects of key innovations have been sought in origination rates[21].

It is important to note, however, that originations in the fossil record are not

speciations *per se*: a decrease in the extinction rate of populations in ecological time might be detected as an increase in the origination rate of taxa in paleontological time[17] because longer-lived populations are more likely to be sampled in the fossil record or themselves to undergo speciation. Thus, key innovations can still increase the number of taxa, or even origination rate, through a decreased extinction rate at a lower hierarchical level.

Do key innovations favor reproductive specialization? The evolution of multiple nectar spurs in the columbines purportedly has contributed to their radiation; nectar spurs presumably reduce the time to reproductive isolation by favoring greater specificity in columbine-pollinator coevolutionary interactions[22]. Similarly, the specialized syrinx of passerine birds, used in vocalizations, may increase the potential for rapid divergence in mate-recognition systems[7,23,24].

Traits such as nectar spurs and the syrinx of passerines might produce proliferations of species by favoring the formation of isolates, but it is not known whether an increase in species richness is always accompanied by other aspects of biological expansion. For example, do reproductive key innovations also produce, by themselves, evolutionary changes of a sufficient scale to be distinguished at high taxonomic rank (i.e. by an evolutionary systematist)?

Are such reproductive key innovations of macroevolutionary significance? If evolutionary trends are driven ultimately (and not merely proximately) by selection or sorting among species, then reproductive key innovations might provide the variance among species in speciation and extinction probabilities (species 'fitness') upon which species selection can act. It is unclear, however, how different those species arising from the action of reproductive key innovations would be from each other; ruminant artiodactyls for all their horns and antlers are fairly homogeneous in their teeth[25], as are passerine birds in locomotor strategy (Fig. 2)[26]. Species selection in this case might be analogous to natural selection in a population with extremely low additive genetic variance; that is, there must be heritable variation in species phenotype for there to be a response to species selection. Furthermore, divergence between higher taxa in nonreproductive characters, for example those affecting resource use, would have to occur secondarily to the proliferation of species.

Do key innovations foster ecological specialization?[9] The labroid (cichlid) pharyngeal jaw apparatus may have been instrumental in the evolution of trophic adaptations allowing sympatric species to coexist in East African lakes[27–29]. Is the eco-
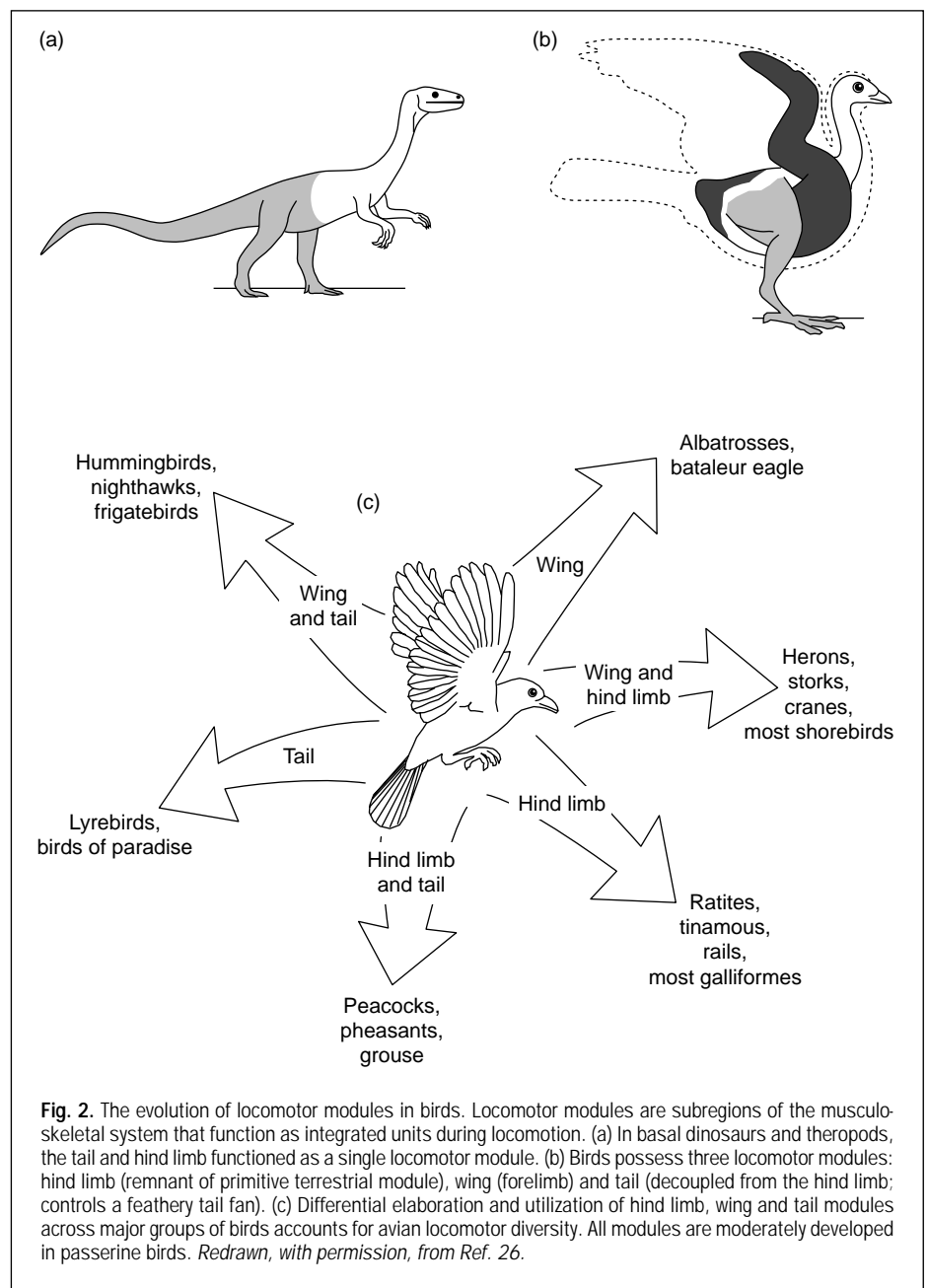

Fig. 2. The evolution of locomotor modules in birds. Locomotor modules are subregions of the musculo-skeletal system that function as integrated units during locomotion. (a) In basal dinosaurs and theropods, the tail and hind limb functioned as a single locomotor module. (b) Birds possess three locomotor modules: hind limb (remnant of primitive terrestrial module), wing (forelimb) and tail (decoupled from the hind limb; controls a feathery tail fan). (c) Differential elaboration and utilization of hind limb, wing and tail modules across major groups of birds accounts for avian locomotor diversity. All modules are moderately developed in passerine birds. *Redrawn, with permission, from Ref. 26.*

logical process at work here expansion or specialization? Specialization implies that a comparable amount of energy is allocated among more species, lowering the average population density of each species. This constraint would impose limits on the morphological evolution of a group because the most specialized species with the lowest population density would become vulnerable to extinction by stochastic factors[30]. According to one view, some key innovations increase the number of species that can coexist in communities by making it possible for species to survive at lower population densities, e.g. the transition from wind to insect pollination[31,32]. (Contrast this with key innovations that promote higher population density, discussed above.) But, it is not known whether cichlids today utilize the same amount of energy as the ancestral cichlid, the sis-

ter group of cichlids or some group that cichlids replaced (the last is probably irrelevant as the East African lakes are young geologically).

Key innovations that promote further evolutionary change

Another way to rescue the key innovation concept is to hypothesize that the appearance of a traditional higher taxon represents an interesting biological phenomenon that one can investigate directly. Such higher taxa may not be the preferred unit of phylogenetic systematists, since they do not group species solely according to genealogy. Nevertheless, the differences between higher taxa do seem to represent important differences in way of life, organismal construction and functional biology. Analysis of higher taxa and their properties has provided numerous insights into

the evolution of the Earth's biota largely based on the assumption that the number of higher taxa reflects diversity in other aspects of biology as well[33]. The validity of this assumption is currently under quantitative empirical investigation[25,33,34].

In the absence of a clearly defined relationship between taxonomic and morphological evolution, some workers, particularly functional morphologists, have asked whether some putative key innovations are evolutionarily versatile[35], that is, have some traits facilitated evolutionary change irrespective of their effects on the number of taxa[6,36]? One can understand evolutionary versatility in terms of trade-offs. Response to selection for one function may be limited by, among other factors, selection for other functions. Key innovations may reduce the cost associated with the trade-off among functions[13], as would also increasing the amount of energy available to organisms[2,17,18]. Evolutionary versatility may be high in a lineage of organisms possessing many parameters controlling form[35]. Decoupling previously linked structures or functions may be the most common way of increasing the number of these parameters[37].

The best known decoupling event resulting in enhanced evolutionary versatility is the case of the jaws of cichlid fish. Diversification in diet by cichlids has been accompanied by adaptations of the oral jaws for capturing different kinds of food. Evolution of the pharyngeal jaw apparatus may have made these specializations possible. Pharyngeal jaws appear to have co-opted the task of processing food, thereby freeing the oral jaws from costs associated with both procuring food and processing it[1,27,28]. Moreover, the initial step in the acquisition of the cichlid pharyngeal jaw apparatus may itself have been a structural decoupling of the upper pharyngeal jaws from the rest of the branchial skeleton (including the lower pharyngeal jaws)[29].

Another example of decoupling may be found in birds. Birds occupy a narrow range of body sizes compared to theropod dinosaurs but are arguably more diverse in locomotor adaptations; for example, adaptations in the hind limb for specialized diving, paddling, wading, trunk climbing or perching did not evolve in dinosaurs[38]. Flight arguably freed the avian hind limb from the full-time demands of weight-bearing in terrestrial locomotion[26].

Furthermore, reduction of the caudofemoralis muscle (the major hind limb retractor) and with it the bony tail seems to have decoupled the tail functionally from the hind limb (Fig. 2)[26]. The relatively independent tail, forelimb and hind limb of birds each constitute a separate 'locomotor module' that can respond somewhat independently to selection or form novel associations with other modules; for example, an integrated wing–tail flight apparatus seems to be a novelty of the first birds, whereas elaboration of the wing–tail association at the expense of the hind limb characterizes hummingbirds[26]. Patterns of locomotor diversity in birds remain to be quantified, but locomotor diversity and species richness in birds seem to be somewhat independent; the species-rich passerine birds appear not to have elaborated novel combinations of locomotor modules to the same extent as other birds (see Fig. 2)[26].

In the two cases described above, it appears that the decoupling of previously functionally linked elements results in evolutionary versatility. In cichlids, the resulting evolutionary changes are accompanied by an increase in species richness, but in birds, they are not. In both cases, however, the evolutionary changes are of a magnitude that a traditional systematist would recognize by distinction at a high taxonomic rank. Interestingly, pharyngeal jaw characters also diagnose the family Cichlidae as well as its constituent genera[28], and locomotor strategies characterize some higher taxa of birds.

The key innovation concept in evolutionary biology

The concept of key innovations touches upon many aspects of evolutionary biology (Box 4), but the largest single contribution that this concept can make is to focus the questions of macroevolution on individuals. This attention to individuals does not imply, however, that only the attributes of organisms are important to the performance of taxa or that key innovations are both necessary and sufficient for the origin or diversification of a taxonomic group[39]. Key innovations can never by themselves be considered a sufficient reason for biological expansion, since evolution always occurs in a context. Rather, key innovation explanations merely keep the organism, the primary object of natural selection, in the center of macroevolutionary inquiry[27].

Future work must not focus exclusively on comparisons between extant sister clades in Recent species richness (see Box 2). Historical trends in taxonomic richness, rates of taxonomic diversification and patterns of phenotypic diversity as observed both today and in the geological past can all contribute to the understanding of how key innovations might operate (Boxes 2 and 3). Sister clades are not the only comparable groups: the diversity of a taxon with an innovation can also be

Box 4. Key innovations and evolutionary theory

Convergence

A feature that has evolved in numerous lineages provides many examples for study[17]. In addition, such repeated evolution suggests that the trait might have adaptive significance. For example, multiple origins of heterospory (production of spores of two sizes) in vascular plants suggests that heterospory itself may have importance apart from being a precursor to the seed habit[44].

Escalation

Escalation hypothesizes that adaptation to enemies (competitors, predators or prey) has brought about long-term evolutionary trends[45]. An 'arms race' can occur when a lineage of organisms adapts to its enemies, which in turn evolve counteradaptations and force the original lineage to adapt to new, more-efficient enemies[45]. Escalation predicts the observed radiations in land plants with defensive structures, such as latex and resin canals[42], freeing them temporarily from insect predation. Escalation also predicts the observed radiations in insects with enzymes for metabolizing plant defensive compounds allowing them to exploit previously unavailable plants[46].

Correlated progression

An alternative to the key innovation model of the origin of groups is correlated progression. If the key innovation model supposes that individual traits promote subsequent evolution in other traits, then correlated progression proposes that a group of functionally related features evolves together in response to selection[47]. Positive feedback may occur, as change in one feature allows changes in others, and these affect the evolution of the original feature[48]. The distinction between these two models is subtle, and any correlated progression also can be seen as a series of key innovations. The models do differ, however, in their treatment of morphological integration – does large evolutionary change occur when selection acts upon features that are functionally integrated and respond as a unit (correlated progression) or features that are functionally decoupled and respond individually to selection (key innovation)[13,35]?

compared to that of its paraphyletic ancestor[40] or to the group that it seems to replace ecologically[13] (Box 2). These kinds of comparison nearly always require a fossil record documenting the biotic replacement. Diversity can also be compared within morphological groupings that have ecological but no taxonomic meaning in both extant and extinct biotas[17] (Fig. 1). Explicit consideration of ecological factors can reveal in what circumstances a particular innovation might be expected to promote diversification (it would be naïve to expect that an innovation would have the same effect on every lineage)[41] (Box 2). This kind of comparison can be carried out on extant taxa, as well as on extinct taxa if their palaeoecology is well enough understood.

Armed with these techniques and possible comparisons, one can proceed to address some of the following unanswered questions surrounding key innovations:

Do innovations that seem to promote the diversification of species also promote adaptive evolutionary change and the differentiation of traditional higher taxa? Does greater species diversity imply ecological specialization or expansion? Is evolutionary change promoted by structural decoupling (key innovation model), by morphological integration (correlated progression model; see Box 4) or by some complex interaction of the two[26]? Answers to these questions will be undoubtedly interesting and perhaps surprising.

Acknowledgements

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Stress response

Global Ecology in Human Perspective

by C.H. Southwick

Oxford University Press, 1996.
£16.50 hbk (xxi + 392 pages)
ISBN 0 19 509867 6

Ecology: A Bridge Between Science and Society

by E.P. Odum

Sinauer Associates, 1997.
£17.95 pbk (xiv + 330 pages)
ISBN 0 87893 630 0

There is an old adage that one shouldn't judge a book by its cover. Eugene Odum's revision of *Ecology and Our Endangered Life Support Systems* displays a tranquil scene of the Marshes on Sapelo Island (Georgia) – a watercolour by his late wife, Martha. Charles Southwick's image is not so arresting. Southwick has chosen a photograph, rather than a watercolour to portray the stark reality of the lives of the poor in the less developed countries: a kaleidoscope of the suffering and misery that is the fate of more than a billion of humankind. Yet these works have much the same tale to tell: the earth's ecosystems have been severely abused; the resulting human-caused degradation of ecosystems pose grave threats to our common future; and that a new ethic is needed to close the gaps between the rich and the poor.

Both authors develop this theme from the organizing principles of ecology. The large middle section of Odum's text reviews basic ecological principles, from ecosystem, population and community ecology perspectives. Embedded within this section are the clearly destructive aspects of human activity: the effects of chemical use on the protective ozone layer; the costs to human health and ecosystem health due to the dependence of agriculture on pesticides; soil loss from agricultural activities; mining of aquifers, salinization and other pathologies are besetting the earth's ecosystems. In describing the major ecosystems of the world, Odum adds the human-constructed systems which are now dominant systems in many regions – agroecosystems (where the distinction is made between industrial and traditional agriculture), and urban–industrial techno-ecosystems.

The heart of Odum's message is contained in the Epilogue, where the thorny issues of the global prospect, environmental transformation from human activities, and environmental ethics are addressed. Here, Odum is concerned with how to make the transition from a presently debilitated planetary ecosystem to one that is vital, adaptive, and sustainable – considering not just the 'natural ecology' but the humans within the system as well. His message harks back to the challenge expressed half a century ago by Aldo Leopold – how can humankind occupy the earth without rendering its ecosystems dysfunctional? Odum portrays humanity as a parasite on the earth. A wise parasite protects the survival of the host – and it is here that Odum argues that a new ethic is required for proper servicing of our host (the earth's ecosystems). In his view, the choices facing humankind are to continue in the current mode 'the short-term view', wherein ecosystems are neglected and consequently degraded, while values are placed on individual survival with uncontrolled fertility and an expanding human population or the 'long-term view' in which value is placed on species survival, controlled fertility, and on healthy ecosystems. The consequences of the former are portrayed as 'miserable survival', while the latter as 'favourable survival'.

Southwick begins with the concept of global ecology. The 'big picture' is portrayed in terms of climate change and global warming, agriculture and soil erosion, deforestation, desertification, biodiversity, poverty and health, and population growth. The book aims to set forth an agenda by which to evaluate such issues through specifying principles of global ecology, facts relating to these principles, conclusions to be drawn from the facts, and the options for action.

The stress-response framework or approach to environmental systems[1,2] emerges at the heart of the work. Setting the stage with a scholarly treatment of views through the ages on potential conflicts between humans and nature, Southwick turns to more recent prophecies, contrasting the pessimistic *Global 2000 Report to the President*[3] with the upbeat optimistic response of Simon and Kahn[4] – a response that appears to me to be one of both denial and wishful thinking[5]. Southwick apparently agrees, as he proceeds to muster evidence for the devastation that human activities have already had on the earth's ecosystems. In the interest of balance, he occasionally reverts to a discussion of the benefits of restructuring the earth. However, it is clear that he believes the consequences far outweigh the benefits. Here we might pause again to look at the unsettling scene on the cover – one that is no match, however, for the even greater horrors envisioned in Peter Booth's 'Painting 1982' which 'adorns' (if that is the word) the cover of A.J. McMichael's sobering *Planetary Overload*[6].

Southwick makes his case for the destruction of the earth's ecosystems all the more tangible with abundant photographs and global synoptic pictures of patterns of desertification and deforestation. The case would be all the stronger if the photographs were reproduced at a higher grade, and the data on the global situation were more current, rather than stemming from information compiled in the 1970s and early 1980s. But despite these limitations (and these are not

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