

Opinion

The ecology and evolution of key innovations

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The idea of ‘key innovations’ has long been influential in theoretical and empirical approaches to understanding adaptive diversification. Despite originally revolving around traits inducing major ecological shifts, the key innovation concept itself has evolved, conflating lineage diversification with trait-dependent ecological shifts. In this opinion article we synthesize the history of the term, clarify the relationship between key innovations and adaptive radiation, and propose a return to the original concept of key innovations: the evolution of organismal features which permit a species to occupy a previously inaccessible ecological state. Ultimately, we suggest an integrative approach to studying key innovations, necessitating experimental approaches of form and function, natural history studies of resource use, and phylogenetic comparative perspectives.

Key innovations: ecological novelties in an evolutionary framework

Key innovations (see [Glossary](#)) have long been considered important in the evolution of ecological diversity. The concept was first introduced in 1949 by Alden Miller [1], who suggested that a phenotypic feature might arise which allows a lineage to exploit the environment in a novel way, and thus enter a ‘new ecologic sphere’. George Gaylord Simpson expanded upon this idea, proposing that the acquisition of a novel trait can be critical to occupying a new ‘adaptive zone’ [2]. Both workers considered that the evolution of such traits could potentially be a core component of **adaptive radiation**: once a key innovation provided access to new resources, natural selection would favor increased **adaptation**, and subsequent speciation would provide the opportunity for descendants to diversify and specialize on different resources owing to ample **ecological opportunity** [3].

However, since Miller’s original paper, discussion of the evolutionary role of key innovations has drifted [4,5]. A widespread emphasis on the role of character evolution in promoting speciation (or diminishing extinction) has come to dominate the study of key innovations ([Box 1](#)), while the central ecological aspect of the concept is now often neglected [5–7]. In turn, this focus on diversification dynamics has precluded exploration of more a detailed understanding of how key innovations induce major ecological shifts.

Here, we review historical and current trends of key innovation research, discuss why a focus on diversification dynamics is misguided, and propose a return to a more integrative approach to key innovation biology.

Tests for key innovations

In the three decades following Miller’s seminal article, key innovations were widely considered to be adaptations central to accessing previously unobtainable portions of the ecological spectrum ([Figure 1A](#)) (e.g., [2,8–10]). Discussions focused on identifying plausible case studies aimed at understanding how the evolution of novel morphological traits could explain shifts to new ecological niches [11,12]. However, as evolutionary biology became increasingly quantitative with the rise of phylogenetic approaches, the largely qualitative idea of a ‘key innovation’ proved difficult to address in a hypothesis-testing framework. As a result, beginning in the

Highlights

The concept of ‘key innovations’ – the evolution of phenotypic traits that permit shifts into previously inaccessible ecological spheres – has been a powerful idea in evolutionary biology.

The expectation that key innovations should result in increased species richness or adaptive radiation is conceptually problematic.

The roles of behavior and physiology in major ecological shifts characteristic of key innovation evolution needs more research attention.

Studies of key innovations that integrate experimental performance and evolution approaches, measures of ecological resource use, and novel phylogenetic comparative methods pose great promise for conceptual and empirical advances.

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Box 1. How have biologists defined key innovations?

We examined three decades of published studies (1995–2021) to review how biologists have interpreted the key innovation concept, and how this interpretation has translated into operational tests. We filtered an initial set of evolution and ecology studies ($n = 206$; see online supplemental material for methods and data) retrieved from a Scopus literature search for 'key innovation' to 118 studies which explicitly defined key innovations (see Table S1 in the supplemental information online).

We found the conceptual basis of identifying putative key innovations consistently fell into one or more of five categories (Table I), demonstrating that the role of key innovations in prompting lineage diversification (resulting from increased speciation, decreased extinction, or both) has become the common meaning of the term in operation. Half of the sampled studies defined key innovations as traits that lead to increased net species diversification rate (50.0%), whereas more than three quarters (78.0%) considered outcome or increases in species richness as one of several criteria.

Table I. What evidence has been used to determine whether a trait constitutes a key innovation?

Measure by which key innovations were identified	% of published studies	Example case studies	Refs
Increased species richness or net species diversification rate	78.0	Floral nectar spurs in angiosperms, the mammalian hypocone	[14,39]
Increased net species diversification rate	71.2 (50.0 ^a)	Axial skeleton modifications in cetaceans, ectomycorrhizal symbiosis in fungi	[76,77]
Increased ecological diversity	31.4 (12.7 ^a)	Hypsodonty in ruminants, anemone cnidocyte resistance in clownfish	[78,79]
Increased phenotypic diversity	10.2 (0.8 ^a)	Pharyngeal jaw apparatus in cichlids, nectivory in songbirds	[80,81]
Increased species richness	10.2 (5.9 ^a)	Cribellar threads in orb-weavers; grasp-suction feeding in electric fishes	[82,83]
Increased fitness	8.5 (5.1 ^a)	Marginal spikes in Venus flytraps	[84]

Published studies may be included in more than one group.

^aWhere proportion was calculated using only studies considering solely that criterion. When no superscript is present, any study that includes that measure – alone (e.g., species richness) or in combination with other categories (e.g., species richness and increased fitness) – is included in calculating the proportion.

Glossary

Adaptation: a character shaped by natural selection for its current function.

Adaptive radiation: evolutionary divergence of members of a single phylogenetic lineage into a variety of different adaptive forms.

Diversifying trait: a trait whose evolution leads to increased species diversification in the clade that possesses it.

Ecological opportunity: the availability of ecologically accessible resources that may be evolutionarily exploited.

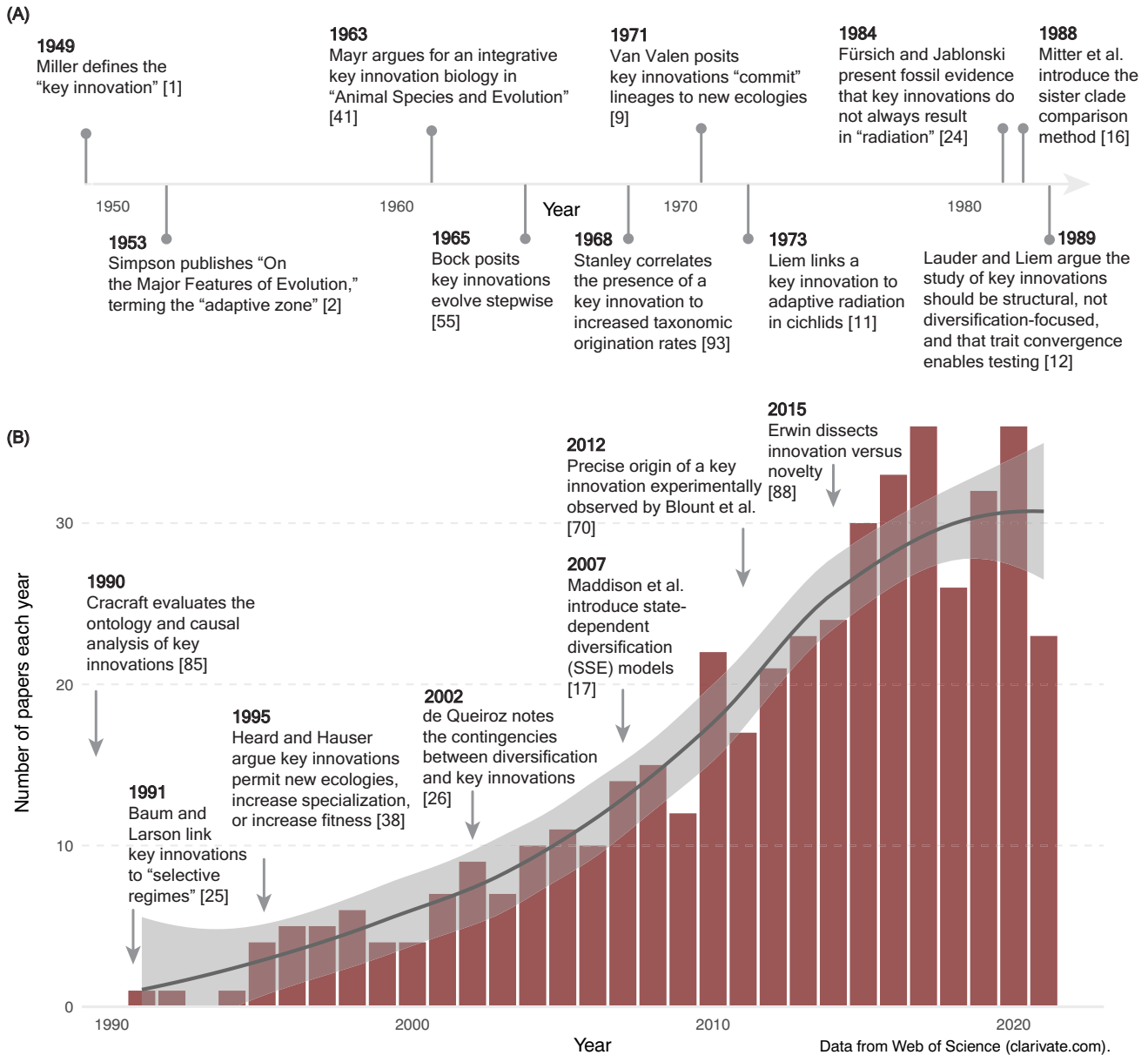
Key innovation: an organismal feature that enables a species to occupy a previously inaccessible ecological state.

Novelty: a newly evolved organismal feature that is absent in the ancestral species.

1980s, the field essentially redefined what constitutes a key innovation in a way that permitted straightforward statistical testing [13]. Specifically, key innovations were reconceptualized as traits which directly enhance diversification (Figure 1B) (e.g., [14]). The rise of tree thinking during this period [15] led to the development of quantitative, phylogenetically informed methods focused on comparing species richness [16]. Eventually, practitioners transitioned from tabulating species counts to inferring precise, state-dependent rates of speciation and extinction (e.g., [17]) (Figure 1B).

We view this redefinition as problematic because it conflates two distinct evolutionary phenomena: diversification in species richness, and shifts in ecology. Clades can become speciose for many reasons unrelated to novel ecological shifts, such as the evolution of traits that affect sexual selection [18] or that reduce dispersal and so diminish the homogenizing effect of gene flow [19,20]. Conversely, even if the evolution of a trait leads descendants to diverge to occupy many different ecological niches, there is no guarantee that the resultant adaptive radiation will have particularly great species richness [21–23].

For this reason, we advocate a return to the classical and ecologically focused conception of key innovations as 'the evolution of an organismal feature that permits a species to occupy a previously inaccessible ecological state'; by 'inaccessible ecological state' we mean the habitats, resources, or other parts of the environment that previously could not be used. While the evolution of a trait



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Figure 1. The evolution of the key innovation concept. (A) Timeline of major conceptual landmarks in the early history of key innovation biology. (B) Trends in annual use of the term 'key innovation' and 'key evolutionary innovation' in evolution and ecology literature registered in the Web of Science ($n = 454$ papers from 1991 to 2021; see Table S2 in the supplemental information online), including loess-smoothed line with 95% standard error. The 21st century has been marked with a steadily increasing availability of well-sampled molecular phylogenies and new phylogenetic methods for estimating macroevolutionary dynamics (e.g., [17]), coincident with a climbing popularity of studies on 'key innovations' and the operational redefinition of the term by many. See [1,2,9,11,12,16,17,24–26,38,41,55,70,85,88,93].

may lead to species diversification, this represents a separate hypothesis to be tested, rather than an integral part of the definition of a key innovation [8]. For the purposes of terminological clarity, we propose the term '**diversifying trait**' for a trait whose evolution leads to increased species diversification in a clade. Of course, these terms are not mutually exclusive; a trait could qualify as both.

The relationship between key innovations and adaptive radiation

From the outset, whether adaptive radiation is an integral part of key innovation evolution has been unclear. Here, we discuss two primary reasons why key innovations may not lead to subsequent adaptive radiation [3,24–26].

First, adaptive radiation requires both speciation and ecological diversification, neither of which intrinsically results from the evolution of a key innovation [26]. Lineages that evolve a key innovation, but which are not prone to speciation – for example, due to high levels of gene flow [27,28], or occurrence in a region with limited opportunity for geographic isolation of populations – are less likely to undergo adaptive radiation [5].

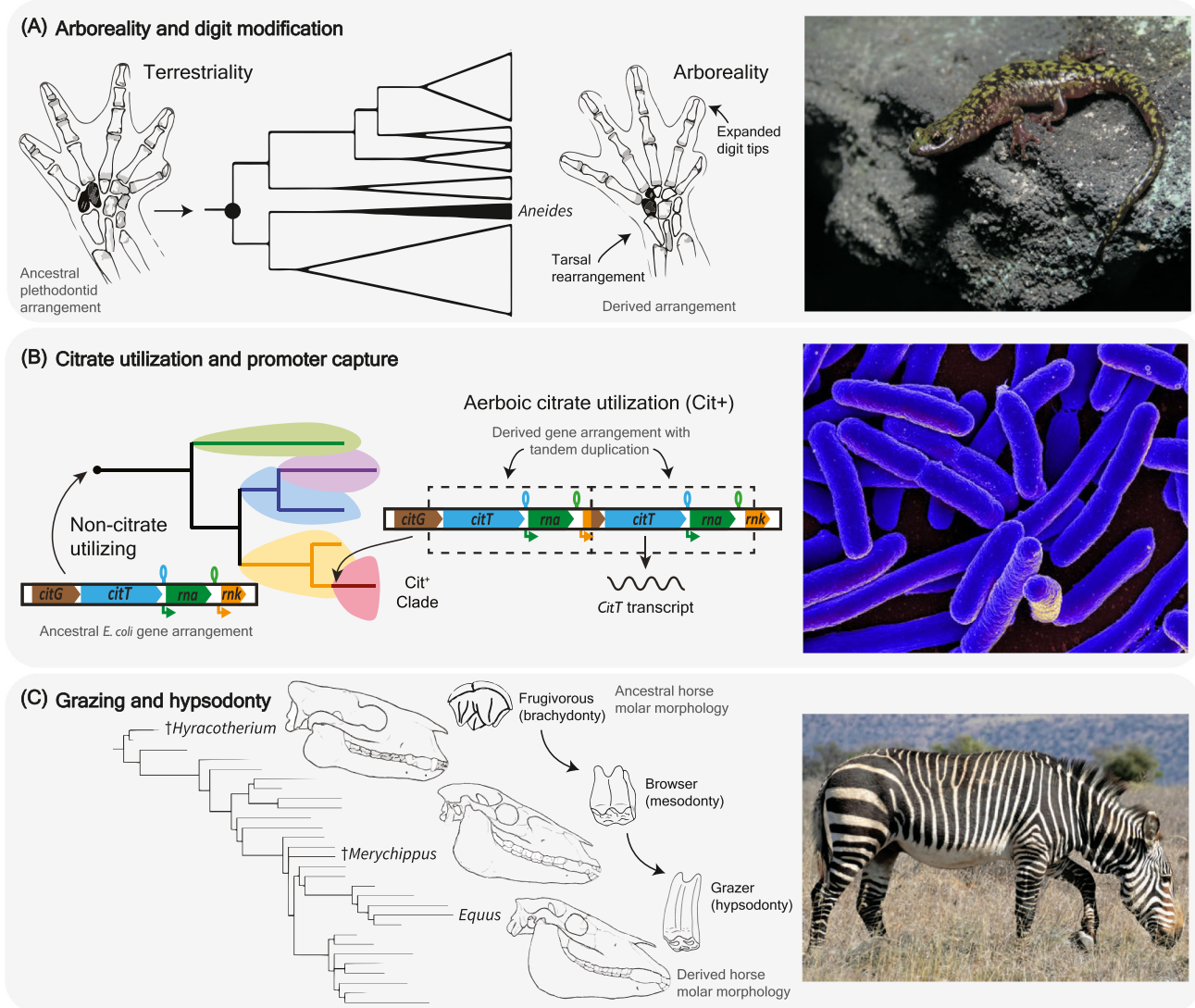
Second, adaptive radiation could be hindered by lack of evolvability [29] in which the lineage bearing the key innovation does not possess, and cannot gain, the heritable variation necessary for further adaptive diversification [5]. Such a lack of evolvability could be attributed to underlying genetic or developmental constraint [30,31], including negative epistasis or pleiotropic interactions [32–34].

Key innovations are integrative organismal features

Traditionally, most key innovations have been identified as morphological features that facilitate access to novel ecological states, such as shifts in dietary or defense regimes [35,36], or occupancy of a different physical space in the environment [6,11,13,37,38]. Famous case studies include the hypocone in herbivorous mammals [39], adhesive toepads in arboreal lizards [40], and resin canals and floral nectar spurs in angiosperms [14,35].

Access to new ecological states, however, often requires behavioral or physiological change as well as morphological evolution [41–43]. For example, some arboreal frogs in Southeast Asia (*Rhacophorus* spp.) have evolved skin flaps and extensive webbing between the toes that provide the capacity to glide from tree to tree in tropical forests [44]. However, biomechanical studies revealed that these morphological modifications in themselves were weak predictors of gliding ability; only when coupled with appropriate behavioral changes – a bent limb position – did these morphological features provide superior gliding ability relative to that of other arboreal frogs [44]. An analogous example exists in C₄ plants, where reconfiguration of the enzymes phosphoenolpyruvate carboxylase (PEPC) and ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) enables more efficient photosynthesis and tolerance of hotter temperatures, but only when coupled with an initial anatomical modification (an increase in the bundle sheath cell-to-mesophyll cell ratio) [45].

Behavioral and physiological changes can be central to key innovation evolution in two ways. First, they can lead to new selective pressures, thus prompting morphological evolution [10,41]. For example, grass-eating behavior in both horses and elephants preceded the evolution of specialized hypsodont grazing dentition by several million years (Figure 2C) [46–48]. Similarly, the origin of air breathing in amphibious mudskippers led to a suite of morphological adaptations for life on land [49]. Second, behavioral or physiological shifts can repurpose pre-existing morphological structures, deploying them in entirely new ways [8,41,47,50,51]. For example, crassulacean acid metabolism, a biochemical syndrome found across plants, inverts the timing of stomatal opening from daytime to nighttime, mitigating water loss and permitting survival in arid climates [45]. A comparable example exists in snakes, where strong, elongate axial musculature initially evolved for limbless locomotion [52] but was subsequently integral to constricting prey items [51].



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Figure 2. Examples of iconic key innovations. (A) The evolution of a key innovation can allow a shift in habitat use: for example, the evolution of specialized skeletal structure in the wrists of climbing salamanders (*Aneides* spp.) enabled the lineage to shift from an ancestral terrestrial ecology to increased arboreality [25]. Illustrations modified from [90] with permission. Photo: *A. aeneus* (Justin L. Lee). Gene arrangements and phylogeny adapted with permission from [70]; *Escherichia coli* gene arrangements and phylogeny provided by Zachary D. Blount; scanning electron micrograph of *E. coli* from Wikimedia Commons (Daniel Mletchen; CC BY 2.0). Horse phylogeny reproduced from data in [91]. Horse skull illustrations (*Hyracotherium* sp., *Merychippus* sp., *Equus* sp.) modified with permission from [92]. Horse dentition illustrations modified with permission from [46]. Cape mountain zebra (*Equus zebra zebra*) photo by Bernard Dupont (Flickr; CC BY-SA 2.0). (B) Key innovations may also provide access to previously inaccessible resources in the same microhabitat. For example, the ability to grow aerobically on citrate evolved in an experimental *E. coli* population founded by an ancestral clone that lacked the ability to do so. This innovation was immediately caused by the expression of a transporter previously inactive in the presence of oxygen owing to a tandem duplication mutation [70]. (C) Key innovations may also evolve via modification of a previous structure. For example, in browsing hoofed mammals, the evolution of high crown tooth height (hypsodonty) permitted a major dietary shift to grazing on abrasive, silica-rich grasses that came to dominate the Miocene [46].

This interrelated role of morphology, behavior and physiology exemplifies how key innovations are integrative organismal features (cf. [53]). Of course, the relative importance of any one factor (e.g., behavior) in driving key innovation evolution may vary dramatically across lineages [54]. Understanding the circumstances under which different types of combinations of traits serve as key innovations is an important question awaiting further research.

This integrative approach enables researchers to best understand how organisms access new ecological states, but a terminological question still remains: for a trait to qualify as a key innovation, how distinctive does the new ecological state need to be from the previous one? Previous definitions highlight the role of such traits in major ecological transitions (e.g., ‘new adaptive zone’ [2]; ‘different way of life’ [9]; ‘new habitat’ [55]; ‘interact with the environment in novel ways’ [56]; ‘access to novel resources’ [6]). But where do we draw the line between a key innovation and an unexceptional adaptive change that promotes a minor ecological shift? Surely, the evolution of a trait that allows a lineage to fly constitutes a key innovation, whereas a trait that allows birds to eat slightly larger seeds is not. But what to do about intermediate cases is not so clear cut. Similar questions arise with concepts like adaptive radiation [23] and keystone species [57]. One option is to accept that the concept is more heuristic than quantitative. Alternatively, the development of methods to explicitly quantify and compare ecological shifts may allow identification of those that are truly exceptional in magnitude (cf. [58] for similar approaches to adaptive radiation). Such approaches are inherently comparative. What is needed is a method for quantifying the extent of ecological change so that the shifts occurring across different lineages can be compared and examined in a statistical framework that identifies those changes that are substantially greater than those experienced by most lineages. Of course, the degree of ecological change is unlikely to be bimodal, but rather a continuum such that dichotomization is artificial (cf. [59]). Nonetheless, development of quantitative methods will enable a more rigorous approach to operationalizing largely qualitative conceptual hypotheses (e.g., [59–62]).

The future of key innovation biology

If the ultimate goal of key innovation research is to understand how the evolution of novel organismal features permits access to previously unattainable ecological states, then an integrative approach unifying ecology and evolution is necessary. As such, testing the hypothesis that a trait constitutes a key innovation requires two central points: a mechanistic understanding of how evolution of the trait altered the way in which individuals interact with the environment, and actual demonstration of the corresponding shift in ecology.

Mechanistic studies will vary in approach depending on the trait in question, but they share the common goal of elucidating how the trait alters functional capabilities [63]. Such tests can occur by directly comparing or modeling variation among individuals which differ in possession of the putative innovation [25,64]. Another approach is to experimentally alter the trait of extant individuals to mimic the ancestral state [65]. For example, experimental removal of specialized toe-fringes in sand-dwelling lizards (*Uma scoparia*) significantly reduced acceleration and velocity on sand relative to those with intact toe fringes [66]. Alternatively, if the genetic architecture of the key innovation is well characterized, it may be feasible to conduct targeted genetic manipulation using CRISPR-Cas9 gene editing to examine how trait variation ultimately affects performance [67].

Ecological studies, in turn, should focus on whether the enhanced capabilities conferred by the trait actually lead to alteration in ecology [64]. That is, how does the key innovation transform an organism’s propensity to access a new ecological state which was inaccessible in the ancestral state? By comparing resource use patterns of individuals with and without the key innovation [64], the association between character state and ecological shift can be illuminated. This integrative combination of mechanistic and ecological studies can test the validity of a putative key innovation among extant taxa, even if it has only evolved once. When a putative key innovation evolves multiple times, however, the power of the comparative approach can be leveraged to test for a statistical association between evolution of a trait and shifts in ecology [37,68].

Building upon this, we recently developed a new phylogenetic comparative framework that jointly infers the history and dynamics of ecology and phenotype across phylogeny, enabling tests of a conceptual model describing a set of hypothesized key innovation macroevolutionary signatures [61]. Specifically, by synthesizing large morphological and ecological trait databases with a global phylogeny of lizards, we illuminated the evolutionary dynamics between a putative key innovation trait (adhesive subdigital toepads) and the ecological state in which it provides enhanced performance (arboreal specialization). We observed that toepads are correlated with the evolution of arboreal specialist lizards: toepads are rarely lost in arboreal lineages, and nonpadded lineages transition from arboreality to terrestriality far more frequently than vice versa [61]. Together, these results suggest that toepads may be a key innovation to unlocking evolutionary access to the arboreal zone.

Our key innovation analytic framework provides the basis to understand the eco-evolutionary dynamics of many putative key innovations. Specifically, this approach explicitly allows tests of (i) the rate at which a key innovation is lost or gained in the presumably adaptive ecological state, (ii) the propensity for innovation-bearing lineages to transition to alternative ecologies, and (iii) the likelihood that the key innovation originated as an adaptation. Together, the phylogenetic comparative framework, in combination with detailed mechanistic studies of form and function with respect to ecology, represents a powerful approach to advancing key innovation biology [35,69].

The study of key innovations is largely retrospective (Box 2), attempting to understand whether and how past evolution of a trait led to historical ecological shifts. An exciting and relatively new approach to the study of key innovations is to observe them in real time as they arise. This approach has been pioneered through long-term laboratory studies in which key innovations

Box 2. On the evolution and identity of key innovations

It has long been recognized that many proposed key innovations represent complex, multivariate phenotypes that likely evolved in a stepwise fashion, sometimes spanning millions of years [55,85]. Examples include the wings of birds [85], biochemical herbivory defense in angiosperms [36,86], and macrophyllous leaves of plants [87]. During the early assembly of such key innovation phenotypes, many incipient steps may not directly lead to ecological shifts but instead may 'enable' [87] or 'potentiate' them [70] (see discussion in [62,88], including a review of the terms 'innovation' and 'novelty').

Whether a key innovation evolves in such a stepwise manner – each change furthering adaptation to a new ecological state – or whether the ecological shift does not occur until the key innovation is fully assembled probably varies from case to case. Understanding the origin and evolution of key innovations is thus complicated [62,88]; some even contest whether key innovations are discrete entities appropriate for evolutionary analysis [85].

In multistep key innovations, distinguishing those early steps that were critical in setting the stage for trait evolution – the enablers or potentiators – from those that were not may be difficult. Experimental evolution studies have shown how the effect of such traits can be established in laboratory settings [70,71]. Of course, retrospective macroevolutionary studies cannot conduct such experiments, but detailed functional, developmental, and genomic studies (e.g., [87]) can sometimes make a compelling case for trait origin.

Broadly, key innovations can evolutionarily originate through several pathways (e.g., duplication or decoupling [32]). However, these pathways may only comprise mechanisms facilitating the evolution of the key innovation phenotype [89] and so do not represent key innovations themselves. This distinction between key innovations and the preceding steps that pave the way for them has important implications for how we consider some iconic evolutionary case studies. For instance, the evolution of pharyngeal jaws in cichlid fish is often considered a key innovation [11]. However, in themselves, pharyngeal jaws do not provide access to new ecological resources. Rather, these ecological shifts occurred in subsequent evolutionary steps, when oral jaws, freed from functional constraints, took on many new functions. The evolution of pharyngeal jaws may have triggered adaptive radiation, but not in the sense of a key innovation. Rather, they did so by releasing a functional constraint, permitting many subsequent ecological shifts as a plethora of new oral jaw morphologies evolved, each of which might be considered a key innovation. This reasoning applies equally to evolutionary duplication of any sort, be it of structural elements or genomes.

fortuitously occurred [69]. For example, in studies of rapidly evolving *Escherichia coli*, the long-term evolution experiment (LTEE) allowed dissection of the precise sequence and mechanisms of key innovation origin (Figure 2B) [70].

These experimental evolution approaches are biased toward organisms amenable to laboratory investigation, with traits such as short generation times and small body size, as well as rich knowledge of their genomics. Microbes, in particular, have been a highly informative model system for studies of key innovation origin [69–71]. However, approaches inspired by the LTEE, in which a population is placed in an environment that contains a resource that the population ancestrally does not use, may be effective in studying the origin of key innovations. Several laboratory studies have since taken this approach (reviewed in [72]), but more such work is needed. Of course, long-term studies of this sort in the wild are difficult in comparison to rapidly evolving laboratory microbes; as a result, documenting the origin and sequence of key innovation evolution in real time in nature remains a largely unexplored frontier worthy of further investigation.

More generally, in studies of key innovation evolution through nonexperimental approaches, investigators should leverage alternative, indirect sources of information when direct fossil evidence is absent. For example, if the key innovation is largely physiological, but co-evolves with osteological attributes that fossilize, these fossilized characters can be used as proxies to infer the timing and rate of key trait evolution (e.g., semicircular canals of the inner ear as proxies for the evolution of endothermy [73]).

Alternatively, if the biology of a key innovation implies the ancestral availability of a particular aspect of the environment (e.g., a biome, an obligate mutualist, or interactions with other species), incorporating available paleontological evidence of the existence of that component could prove informative about the ecological context in which the key innovation emerged [47]. For instance, the recent development of joint inference phylogenetic models incorporating both fossil biome and biogeographical data has shed light on the deep time evolution of *Viburnum*, revealing that associated cold climate adaptations arose *in situ* in North America following the spread of cold temperate forests [74].

Concluding remarks

The study of key innovations has expanded greatly over the last 75 years, even as our understanding of the concept has taken twists and turns. To continue developing our understanding of the ecology and evolution of key innovations (see Outstanding questions), studies should become more integrative, pairing analyses that explore evolutionary patterns using phylogenetic comparative approaches [25] with empirical form–function analyses that investigate relationships between trait evolution and resource acquisition [25,64].

This integrative approach – applicable to studies in both the lab and the field – positions natural history information as essential to the study of key innovations. After all, natural history observations inspired Miller's original concept of key innovations [1]. As such, by revolving research around organismal evolution and ecology in nature [75], we anticipate fruitful empirical and theoretical advances.

Acknowledgments

We thank Allan Larson and George Zug for fruitful discussion on the evolution of key innovations and adaptation, Zachary Blount for kindly providing *E. coli* illustrations, and three reviewers for insightful comments.

Declaration of interests

No interests are declared.

Outstanding questions

Adaptive radiation and the evolution of key innovations: under what ecological and phenotypic circumstances do key innovations promote adaptive radiation?

Why do some key innovations evolve several times and others only once? What factors modulate the propensity for a particular key innovation to evolve? Are convergent key innovations the product of similar or different genetic architecture? Why do some convergent traits serve as a key innovation in some cases (i.e., promote the ecological shift), but not others?

Divergent outcomes of convergent key innovations: when the same key innovation evolves multiple times, why does adaptive radiation happen in some lineages but not others?

Why do some lineages with key innovations have greater longevity than others? The fossil record suggests that some lineages with key innovations appear and disappear very quickly, whereas others have lasted for tens or hundreds of millions of years. How might a key innovation enable a lineage to evade extinction? Do key innovations confer greater extinction risk in some circumstances?

How do key innovations originally evolve? Traditionally, key innovations are typically identified after they evolve, but laboratory 'replay' experimental evolution studies allow us to anticipate their origin. Can these same experiments inform us on the predictability and contingencies of key innovation evolution in nonexperimental evolution systems?

What is the role of ecological interactions in driving or impeding key innovation evolution? How do dynamics of ecological communities impede or hasten the origin of key innovations?

Behavior and key innovations: what role does behavior play in the evolution of key innovations? How often does behavior 'lead' versus 'follow' in the evolution of key innovations?

Supplemental information

Supplemental information associated with this article can be found online at <https://doi.org/10.1016/j.tree.2022.09.005>.

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