Opinion

Life histories are not just fast or slow

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Life history strategies, which combine schedules of survival, development, and
reproduction, shape how natural selection acts on species' heritable traits and
organismal fitness. Comparative analyses have historically ranked life histories
along a fast–slow continuum, describing a negative association between time allo-
cation to reproduction and development versus survival. However, higher-quality,
more representative data and analyses have revealed that life history variation
cannot be fully accounted for by this single continuum. Moreover, studies often
do not test predictions from existing theories and instead operate as exploratory
exercises. To move forward, we offer three recommendations for future investiga-
tions: standardizing life history traits, overcoming taxonomic siloes, and using
theory to move from describing to understanding life history variation across the
Tree of Life.

Life history diversity

Any individual organism is born, survives, develops, possibly reproduces, and ultimately dies.
The organism's resulting life history is the pathway it takes on this journey and comprises key
life history traits (see Glossary; e.g., age at maturation or death, rate of growth or reproduction).
There are countless pathways through life, so the Tree of Life boasts an astounding diversity of
life history strategies (Box 1), defined by allocations of limited resources to the competing
needs of survival, development, or reproduction. Selection on these trade-offs should maximize
fitness within the constraints of body size, lifestyle, resource availability, and environmental con-
ditions. Central aims of evolutionary ecology include quantifying life history strategies, identifying
ecological and evolutionary patterns in strategies across species, and understanding the evolu-
tion of life histories in a rapidly changing world [1].

Increasing numbers of studies use comparative methods to address these central aims because
life history databases are rapidly growing in number, volume, taxonomic cover, and accessibility
[e.g., 2–4]. This rapid increase has taken place thanks to contributions from citizen science and
remote sensing, novel monitoring technologies, and open science. Although welcome, these
new developments are not without challenges. The first two central aims of quantifying life histo-
ries and identifying patterns among species are often addressed, but choices of data and analyt-
ical approaches vary, often between taxa, thus precluding reliable comparisons between studies.
Moreover, the third central aim of understanding life history evolution is often not addressed, be-
cause approaches are mostly correlative rather than rooted in testing hypotheses from the
existing theory.

We propose a roadmap for future enquiries into life history diversity across species. We include
several theoretical, empirical, and analytical recommendations to move toward research
underpinned by testable hypotheses rooted in current evolutionary theories rather than exploratory

Highlights

Life history studies support the fast–
slow continuum as the dominant but
not unique axis structuring life history
variation.

Other important axes of life history varia-
tion associated with development and
reproductive tactics exist, and explora-
tion of further axes, clusters, and bound-
aries of life history variation is needed.

Existing life history analyses are venturing
far from theory and could benefit from a
stronger focus on hypothesis testing
rather than exploration.

We make recommendations to identify
the structuring axes of life history varia-
tion through data choices and analytical
methods of dimensionality reduction
with recourse to a comprehensive
model of life history.

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Box 1. Life history strategies

Are carrots (*Daucus carota*) similar to blue-ringed octopuses (*Hapalochlaena lunulata*) (Figure I)? They both start life small and grow fast, but few survive to adulthood, produce many offspring in one breeding event at around 2 years old, and are semelparous. By contrast, humans (*Homo sapiens sapiens*) and blue whales (*Balaenoptera musculus*) grow slowly and mature late but are likely to survive to adulthood, usually produce one offspring every 2–3 years, and have remarkably similar lifespans: The oldest known living human, Jeanne Calment, reached 122 years of age, and blue whales may live up to 110 years [58]. The sacred fig tree (*Ficus religiosa*) and giant barrel sponge (*Xestospongia muta*) are like carrots and blue-ringed octopuses in that they start life small, are unlikely to survive to adulthood, and, once mature, produce many offspring. *X. muta* and *F. religiosa* are also like humans and blue whales, however, because they are iteroparous over long lifetimes: One sacred fig 'Jaya Sri Maha Bohi' in Sri Lanka is the oldest known human-planted tree, which at around 2300 years old is similar in age to the oldest known Caribbean giant barrel sponge [59].

Although distantly related organisms may share similar life history strategies, closely related organisms can show remarkably different life histories. The Dasyuridae family, to which the Tasmanian devil (*Sarcophilus harrisii*) belongs, is one of the most diverse marsupial families [60], with dasyurid species showing different life history strategies, despite being closely related. Maturity usually occurs at ~11 months, but, although in some species all males die by 12 months old following a single synchronous mating, others reproduce many times annually and live for several years [61] . Plant life history strategies are often even more labile than animal strategies: pine trees (*Pinus* spp.) vary vastly in lifespan, despite having similar morphology and physiology: The Virginia pine (*P. virginiana*) rarely lives over 150 years [62], whereas the bristlecone pine (*P. longaeva*) holds the record of nonclonal longevity at 4850 years old [63].

The Tree of Life abounds with examples of distantly related organisms sharing convergent life history strategies, despite divergent body size and lifestyle, and *vice versa*. Evolutionary ecologists seek to understand, across broad taxonomic groups, how and why diverse life history strategies, such as those exemplified here, are distributed across phylogenies, space, and time.

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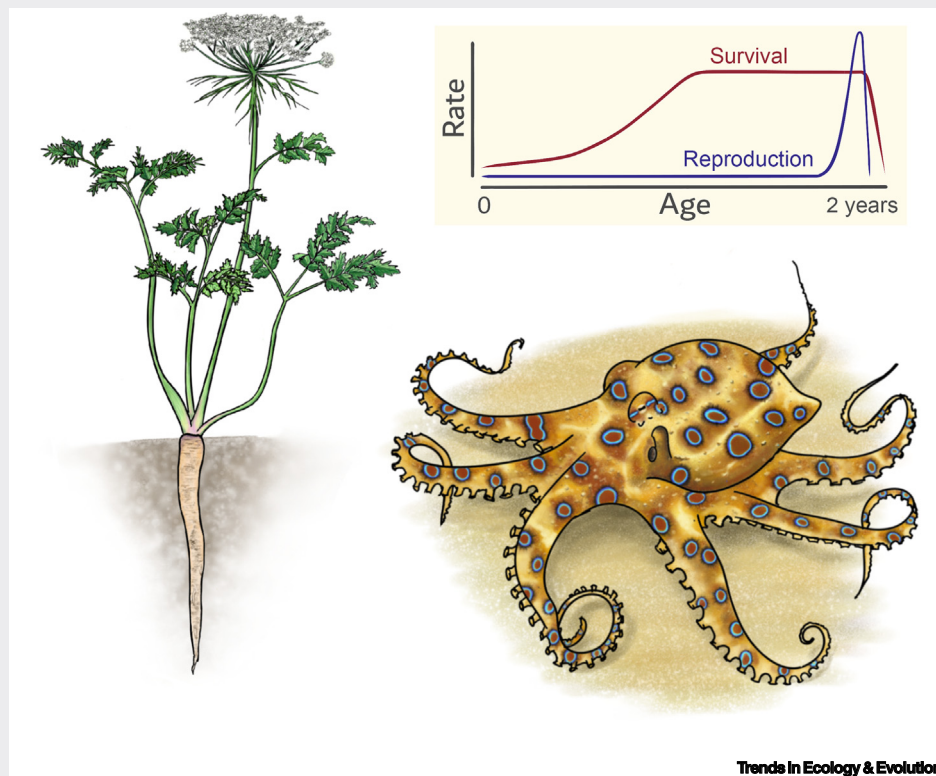@X: @iainmstott (I. Stott); @Rob_SalGo
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Figure I. Carrots (*Daucus carota*) and blue-ringed octopuses (*Hapalochlaena lunulata*) are distantly related organisms with very different forms and functions. Yet, these organisms have very similar life history strategies: As illustrated on the inset graph, relative rates of survival (red) start low but increase with size into adulthood, and, at around 2 years of age, both organisms die following a single reproductive event.

approaches to data analysis. In this context, we overview evidence that the **fast–slow continuum** [5] remains the main structural axis describing life history diversity, providing a useful context for identifying and explaining novel patterns describing substantial life history variation. However, we also argue that life histories are more than just fast or slow.

The fast–slow continuum

Life history strategies are defined by covariation, and therefore trade-offs, among life history traits. For instance, an organism that allocates a lot to growth or reproduction early in life will likely pay a toll on future survival [5]. Across species, life history strategies are typically structured along an axis defined by the trade-off between allocation of time to reproduction and development versus survival. This trade-off underpins the ubiquitous fast–slow continuum, which is usually the dominant axis structuring life history variation across species, including in mammals [6–8], birds [6], insects [9,10], fish [11], and plants [12].

There is evidence that the fast–slow continuum is strongly associated with ecological and environmental patterns and processes, with a frequently observed association being that slow species have higher risk of extinction, on average, than fast species. For instance, slow fishes have higher sensitivity of population growth to sea temperatures [13], slow mammals and birds have higher extinction rates [14], and slow species display more negative responses to human disturbances than their fast counterparts [15,16]. On the other hand, fast species are more sensitive to certain projected environmental outcomes of climate change [17]. These findings are key to protecting future ecosystem function [14] and helping develop cost-effective conservation plans [18]. Even in community ecology, the fast–slow continuum explains interspecific patterns in trophic ecology better than established trade-off theories [19], and integration of the fast–slow continuum into models of disease ecology has recently been advocated to provide more mechanistic explanations [20].

Multiple axes to grind: beyond the fast–slow continuum

The fast–slow continuum alone is not an adequate universal pattern of species' life history strategies: Many extant life history strategies fall outside its predictions. Marine turtles and most trees illustrate a common outlier: species characterized by long lives, late maturations, high survival, and high reproductive outputs (where fast–slow would predict low) [21]. More generally, organisms with **vital rates** closely linked to size and development but weakly to age can be exceptions to the fast–slow 'rule' [22]. A growing body of evidence shows that life history strategies are also defined using an axis of variation involving developmental or reproductive patterns. Such axes include **altricial** versus **precocial** offspring [8], high to low recruitment rates [23], or **semelparity** to **iteroparity** [6,10,12]. In some cases, axes other than reproduction or development explain substantial life history variation, such as age-specific distributions of mortality and reproduction [24]. However, the exact meaning of additional axes is hindered by the vast heterogeneity of life history traits analyzed in this context [25].

A key research priority of ecology and evolution is to understand life history variation where survival and reproduction are closely linked to factors other than age. These factors include body size, especially in species with **retrogression** [26]; life stage, especially in species with **diapause** [12]; and metabolic rate [27]. Another key research priority is to identify potential clusters of life history variation [28] and the limits of the variation among viable life histories [12]. A strong theoretical steer is important in the process of identifying and explaining life history patterns; indeed, even theoretical understanding of the origin and maintenance of the fast–slow continuum has room for improvement.

Glossary

Altricial: species where newborns are helpless and require parental care.

Bauplan: the generalized structural body plan that characterizes a group of organisms and especially a major taxon. Includes the set of anatomical and physiological structures that allows living functions to acquire energy from the environment, to assimilate that energy, and to transform assimilated energy into tissues.

Diapause: spontaneous interruption of development in some animals, marked by a strong reduction in metabolic activity.

Fast–slow continuum: axis of variation in species' life history strategies structured along two extremes: 'fast' species develop fast, mature early, reproduce a lot, and die young, whereas 'slow' species develop slowly, mature late, reproduce little, and live a long life. We use the popularized 'fast–slow' form; however, Stearns originally conceived it as 'slow–fast.'

Fitness: how good a particular genotype is at leaving offspring in the next generation relative to other genotypes in the same population.

Generation time: mean age of reproduction in a population. Other definitions exist, such as the average time between two consecutive generations.

Genotype: the genetic makeup of an organism.

Indeterminate grower: an organism whose Bauplan is not genetically determined, so it continues to grow after it has achieved sexual maturity (e.g., all plants, some mushrooms, fish, amphibians, reptiles, and many mollusks).

Iteroparity: reproductive schedule whereby multiple reproductive events occurs during the life cycle of an organism.

Life expectancy: the average time period that an organism of a given age may expect to live in a population. Life expectancy at birth corresponds to the mean age at death in a population.

Life history strategy: Life history strategies are defined as covariations among life history traits (e.g., long life, late maturity, and long development usually display a strong positive covariation and correspond to a strategy displayed by slow-living organisms).

Life history trait: key moments along the life cycle of an organism describing

Life history theory and the fast–slow continuum

To look for meaningful life history patterns beyond the fast–slow continuum, we need a clearer theoretical understanding of how the fast–slow continuum fits into wider life history theory. An organism's life history strategy determines its fitness, because life history reflects the rates of survival and reproduction that determine numerical representation in future generations [29]. The associations among traits that define a life history strategy not only result from selection acting on heritable phenotypic traits but also filter how selection contributes to the phenotype (Box 2). This idea is underpinned by the canonical Euler-Lotka identity, which comprises age-based schedules of survival and reproduction, from birth to oldest age [1], and characterizes how survival and reproduction over the life course determine a population's growth rate and long-term viability. However, the identity's simplicity masks the diversity of combinations of vital rate schedules that can achieve the same population growth, does not include temporal or spatial variation in vital rates, and does not account for life histories with size- or stage-dependent vital rates [22].

Theory based on the principle of allocation of limited resources [30] predicts life history variation both among species (via allometric constraints and macroevolutionary processes) and within species (via natural selection in fluctuating or heterogeneous environments). Trade-offs between lifespan and growth/reproduction are more likely among species because resource allocation is more variable than resource acquisition at this level, whereas within species, the reverse is true [31]. Species are therefore arranged along a fast–slow continuum as a result of interspecific trade-offs, whereas positive associations between lifespan and reproductive output often define the primary axis of variation among individuals within species, at least for birds and mammals [32]. In many clades, resource allocation theory may oversimplify trade-offs that act on complex suites of (co)varying traits underpinning vital rates, which could further depend on population density, nonresource environmental factors, and phylogenetic constraints [32].

The macroevolution of life histories of species in fluctuating environments could follow similar principles to evolutionary models of heritable trait variation among individuals within populations. Models of density-dependent selection in fluctuating environments conclude that life history strategies are selected to maximize a function of both rate of increase and **lifetime reproductive success** [33]. This prediction resonates with a fast–slow axis, depending on fluctuating environmental pressures, instead of settling to either extreme. The stochasticity of rates of survival will further influence selection on life cycle 'speed': Uncertainty in adult survival is likely to favor early reproduction, whereas uncertainty in juvenile survival will favor iteroparity, higher-quality offspring, and longer life [34] or alternatively favor bet-hedging and seed-bank strategies [17].

Several unique life history strategies could achieve the same lifetime reproductive success. This perhaps explains frequent observation of the second axis of variation, focused on distribution of reproduction over age. Selection to optimize survival, development, and reproduction involves a sequential series of traits over ages or states, which has to date been overlooked (Box 2); therefore, if selection acts on a combination of rates of survival and reproduction, tensions exist among multiple strategies for producing offspring. Yet, our current theories of life history evolution, including the Euler-Lotka identity, do not tell us how organisms should achieve maximum fitness.

Different life stages may be under different selection pressures on their vital rates. Not all stages of any given life history should be equally fast or slow, especially given organisms usually grow in size toward reproductive maturity, and in some cases past, such as in **indeterminate growers**. Future analyses should test whether some stages are consistently faster or slower

survival, development, and/or reproduction functions. Examples include times to events such as age at maturity or life expectancy and rates such as growth or reproduction.
Lifetime reproductive success: cumulative number of offspring recruited over the lifetime of an individual. It is a dimensionless number but provides an approximation of the population growth rate (and thereby gets a time dimension) when divided (on a log scale) by generation time.
Precocial: species where newborns have an advanced state (e.g., with open eyes at birth in mammals) and are able to feed themselves and move independently almost immediately.
Retrogression: the ability to regress to a smaller, younger, or less developed stage with time.
Semelparity: reproductive schedule whereby a single reproductive event occurs during the life cycle of an organism. In fatal semelparity, death occurs right after reproduction.
Vital or demographic rate: key demographic process that shapes the dynamics of a population. At minimum, these rates include survival, development (in stage-based models), and reproduction but can also include dispersal, dormancy, etc.

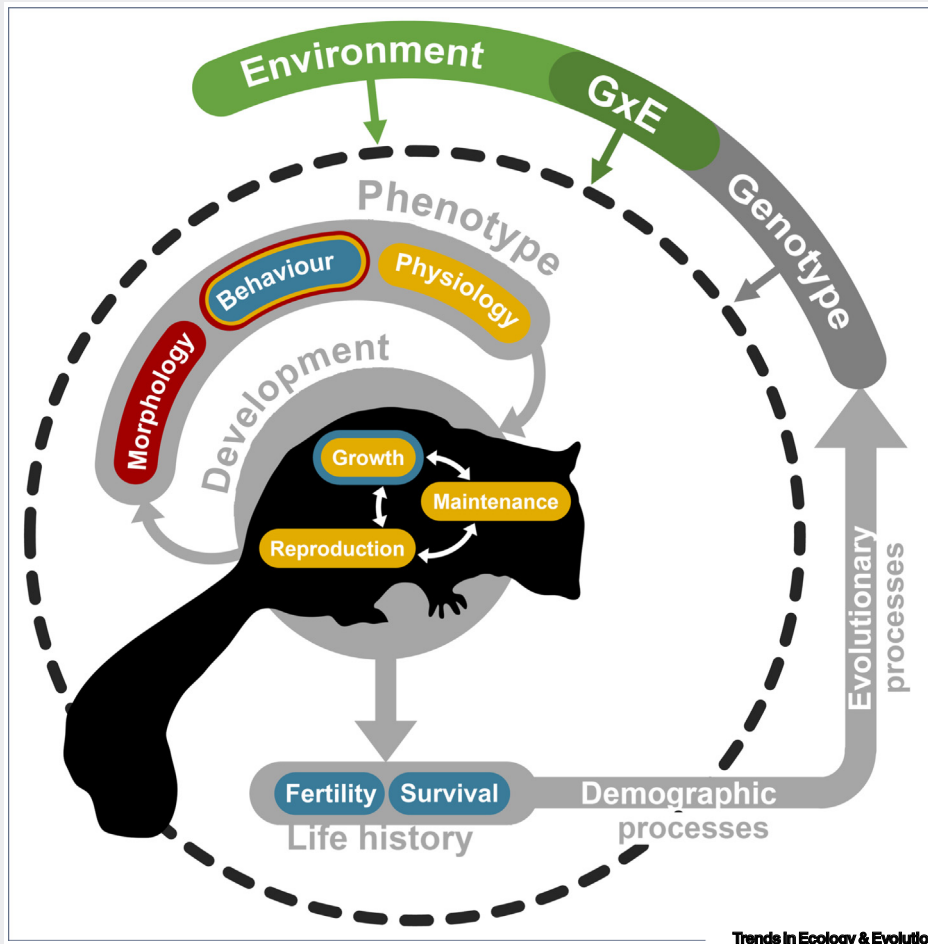**Box 2. A model life history: from resource acquisition to allocation and fitness**

Figure I. A schematic view of a framework to examine and quantify life history strategies, showing the relationships between different trait types. Colors illustrate what currencies traits are measured in: energy (orange), space (red), and time (blue).

An organism's life history strategy is shaped by interacting traits, which fulfill different needs of the life history and which are measured in different ways (Figure I).

At the core of the life history strategy is resource allocation to competing developmental traits: supporting survival (somatic maintenance) versus reproduction (the germline) versus growth in either [64]. The key unit of measurement, or currency, of developmental traits is amounts and rates of energy allocation.

Processes of resource allocation can be difficult to measure directly, but the results of resource allocation are often evident in the phenotype. Phenotypic traits encompass any observable organismal traits, often part of the morphology, behavior, and physiology of the organism. Phenotypic traits may be measurable using many currencies; we identify key metrics of use of space, such as home range size (behavioral) or specific root length (morphological); expenditure of energy, such as metabolic rate (physiological) and foraging efficiency (behavioral); and time provides a means to track these as rates, such as body mass growth. Other types of phenotypic traits and currencies may exist. Phenotypic traits are responsible for acquiring resources and so will also counterinfluence developmental traits [65].

The consequences of resource acquisition and allocations is the ability to survive and reproduce across the lifespan. Survival and fertility distributions determine life history traits, which are almost exclusively measured in time. Life history traits can be durations (e.g., average age at maturity); rates (e.g., number of offspring per year); or temporal probabilities

linked to survival, development, and reproduction (e.g., probability of surviving to maturity). Life history traits are often converted to expectations at population or species level, especially where this makes it possible to measure average phenotypes (e.g., mean **life expectancy**) for events that occur only once in an organism's life cycle (e.g., death).

Life history traits ultimately govern an organism's fitness and its population size, structure, and dynamics [1] by removing or adding individuals to future generations. Demographic and evolutionary processes act together to mold **genotype** frequencies in populations and species in future generations, given constraints imposed by evolutionary history. Genotype naturally influences all organismal traits (assuming some heritability). Traits can all covary with and feed back on one another directly or indirectly and are subject to constraints imposed by evolutionary history, physical laws, **Bauplan**, and the environment [33]. Natural selection acts to favor those life history strategies that maximize the organism's fitness in its environment, given those constraints [1].

than others or whether the time spent in a given stage depends on species features and/or environmental context.

Vital rates could be selected to promote population resilience alongside long-term rate of increase. In stochastic environments, fitness will depend on selection for life histories that confer resilience, incorporating resistance to and/or recovery from numerical change following demographic disturbances [35]. Slow life history traits may result from selection for resistance through allocation of resources to defend against typical disturbances. Fast life histories may result from selection to quickly recover from disturbances. If a negative association between resistance and recovery exists, certain disturbance regimes might help to explain the fast–slow continuum, but other patterns of covariation, dependent on disturbance regimes, could select for different interspecific patterns in life history.

Challenges for measurement and analysis of life history traits

The choice of trait data used to evaluate interspecific life history patterns and theories is nontrivial, with important consequences for the interpretation of analyses. Life history trait data vary greatly in abundance, accessibility, and quality (Table 1) [36]. Quantifying life history traits requires significant effort to collect high-quality longitudinal data in order to observe events, especially when rare, and infer population-level rates (Table 1). The gold standard is detailed schedules of age- or stage-specific vital rates reliably estimated from long-term individually based monitoring of populations in the wild [37], so available trait data are taxonomically biased [36]. Common sets of life history traits can be derived from these schedules across species (Table 1). However, because the traits derived from these schedules are mathematical functions of the same underlying schedules of survival, development, and reproduction, correlations among traits are a combination of the real and the artefactual [38].

To help standardize the trait sets used to describe life histories, we identify three key ways (currencies; Box 2) to quantify life history data, although other currencies will exist. Many studies use dimension-reduction approaches to capture information that defines life history strategies, which condense trait sets into fewer, usually orthogonal, composite variables (Box 3). Past comparative analyses have been performed on heterogeneous life history trait currencies. Mixing currencies confounds the interpretation of the structuring axes of life history variation because orthogonality can emerge from having different units. Single-currency suites of life history variables may aid in interpretation of dimension-reduction analysis. An awareness of how each trait is measured and consequences for analytical outcomes is important. Even within currencies, the units of measurement vary; for example, demographic measures mix rates, durations, ages, and frequencies. Currencies can also be confused by measuring traits in one currency as proxies for another, such as using morphological or behavioral sexual displays as proxies for allocation of energy to reproduction [39]. Using trait sets with common currencies, alongside appropriate analytical approaches, will yield optimal results.

Table 1. Comparison of different types of demographic data in the context of life history strategy comparative analyses.

Data type	Strengths	Weaknesses	Source(s)	Examples/Refs
Simple traits, based on expert natural historian knowledge and opinion	• Easy to measure • Available for most widely known species	• Difficult to verify • Often missing measurement types (e.g., mean, median or mode) • Usually lack measures of variation • Terminology and meaning is often taxon-specific	Field guides, books	Typically lifespan, age at maturity, gestation interval, clutch size, frequency of reproduction, mass at birth and at maturity
Simple traits, derived from published measurements	• Verifiable using primary literature • Often available in open databases • Often include population-level replicates or estimates of variation	• Available for fewer species, especially in more charismatic taxa • Verifiable sources may be difficult to find	Primary literature, open databases	Databases containing many thousands of species for mammals, fish, reptiles, birds, amphibians, flowering plants (e.g., [4,52])
Life cycle models with age- or stage-based schedules of survival and reproduction (e.g., life tables, projection matrices, integral projection models)	• Quantifies whole lifespan • Popular for both plants and animals • Verifiable using primary literature • Often available in open databases • Often include population-level replicates or estimates of variation • Large toolbox of methods to derive diverse life history trait measurements • Can generate derived life history traits (see below) • Can also be used to generate measures of population performance and resilience (e.g., [35,55])	• Not available for most species, mostly concerns tetrapods with many broad taxa neglected • Data labor-intensive to collect • Often synthesized from multiple sources (sometimes even interspecific) • Vital rates measured with variable precision and often contain errors in inference or parameterization • Vary in length/dimension • Require expertise to handle data and calculate derived measures (usually programming)	Primary literature, open databases	Databases available for plants and animals [2,3,53], and detailed data for humans [54]
Life history traits derived from life cycle models using algebraic and computational methods	• Benefit from all advantages of life cycle models as above • Overcome the issue that models vary in length/dimension • Standardized sets of measurements amenable to comparative analysis • Measures include entire life cycle • Measures include many which are not observable (e.g., life expectancy, generation time)	• Suffer from disadvantages of life cycle models as above: taxonomic breadth, data requirements and sources, measurement error • Often assume conditions not met in real systems (e.g., density-independent population growth, stable age/stage structure) • Possible to conflate life history and demographic traits derived from models (e.g., asymptotic or transient population growth)	Derivation from life cycle models	[56]
Selection pressures on traits, describing the 'importance' of vital rates to fitness using the derivative of the latter with respect to the former (e.g., elasticity or sensitivity)	• Infer the filter that converts vital rates into fitness and imposes selective outcomes • Provide well-established framework for life history variation in plants	• Selection pressures are not life history traits *per se* • Often assume the same conditions as life cycle models as above • Elasticities usually have some constraints across vital rates; hence, life history trade-offs are inevitable	Derivation from life cycle models	[57]

Towards a hypothesis-driven, empirically sufficient era of life history theory

To overcome the contemporary challenges concerning life history data and analyses, we make the recommendations outlined in the following sections.

Agreeing on a universal set of life history traits, derived from schedules of survival, development, and reproduction

Such data can implicitly be measured in a single currency of rates per unit of time [40]. This time-unit harmonization will strengthen the links between life history, demography, and fitness [1], given their explicit treatment of time in the Euler-Lotka equation. Such rates still need credible transformation during statistical analysis [41] (Box 3). We further encourage the development of theories of life history evolution using state variables linked to other currencies, with energy being a primary candidate. Empirical analyses should first be restricted to traits measured in

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Box 3. Statistical methods for comparative analyses of life histories

A set of measurable, correlated traits can be described using a smaller number of emergent, orthogonal variables representing dominant axes of life history variation, such as the fast–slow continuum. Principal component analysis (PCA) is one common statistical method to achieve this goal (e.g., [3,7,9]). PCA is fairly naive in that it does not model measurement error or nonlinearities among traits, but some guidance exists regarding how many dimensions explain meaningful amounts of variation [66]. It is less clear how to compare dominant axes across independent analyses with data sets comprising different traits, taxa, and sampling methodologies.

Relationships between two different multivariate data sets (e.g., climatic and life history data) can be explored using canonical correlation analysis (CCA), which yields two sets of emergent uncorrelated variables by calculating axes with highest correlation between variable sets. This approach recognizes that dominant axes of variation (e.g., fast–slow) may not yield strong relationships with other ecological or evolutionary processes.

Unlike PCA and CCA, factor analysis (FA) [56] treats measured variables as functions of latent variables, with associated measurement or residual error. Because FA does not require latent variables to be uncorrelated, it offers solutions to some problems of PCA and CCA [56], although it comes with issues including occasional emergence of spurious latent variables. We suggest that FA, and broader structural equation models, of which FA is a special case [67], are better suited to the testing of hypothetical rather than data-driven axes of variation.

Rather than measure axes of variation, cluster analyses (CAs) measure multidimensional boundaries of life history variation. CA may help understand, after standardizing for rankings on the fast–slow continuum (using, e.g., **generation time**), which life history strategies do not exist and why, as much as the clustered patterning of those that do. Hierarchical CA has been used to identify substructure in life history variation [68] and could prove useful to apply more widely in comparative life history theory.

Depending on the researcher's perspective, a given environmental, phylogenetic, or morphological variable may drive life history variation or be a nuisance covariate to deal with statistically [69]. Comparative analyses must account for nonindependence due to shared evolutionary history [12]. Phylogenetic methods exist for PCA [69] and FA [70] but not yet for CA. Correlates of traits (e.g., organism size) can be included in analyses, although this risks deriving axes defined by non–life history traits, or regressed against life history to yield residuals for analysis, but this can introduce statistical biases [71].

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the same currency, then multivariate analyses (e.g., canonical analyses) could be used to look for covariation among dimension-specific axes of life history variation.

Filling gaps in life history trait data, including for microbes, fungi, nonvascular plants and invertebrates, and especially marine species

There are challenges inherent to this recommendation; for many organisms, we lack good working definitions of life cycles, let alone what constitutes an individual, reproduction, or even death. Variation in lifestyle (e.g., sedentary versus mobile), Bauplan (e.g., modular versus unitary), growth pattern (e.g., determinate versus indeterminate), and reproductive modes (e.g., sexual versus asexual) further complicate the comparative landscape. Attempts to fill data gaps should prioritize measures to facilitate broad comparisons of life history across all taxa. Concurrently, there is a need for data on vital rate variation within species across all taxa [32]. Time series of vital rate data exist for relatively few species and are necessary for comprehensive assessments of, for example, density-dependent mechanisms driving vital rate variation [32].

Embracing comparative analyses covering broad taxa and levels of biological organization

Besides some exceptions [42,43], multivariate studies seeking to understand axes of life history variation across kingdoms of life emerged only recently [17,44,45]. Previous studies encompassing a broad taxonomic range were limited to bivariate analyses [43]. Naturally, taxon-specific inquiry will still play an important role, especially in data-rich taxa. However, limiting analyses to separate groups of organisms implies a perceived wisdom that gross differences in morphologies, physiologies, and lifestyles of different groups inevitably create different selection pressures on their life history strategies. This presumption should be backed up with empirical

analyses of whether and how the dominant axes of life history variation change among taxa. Existing evidence is they do not [17].

Achieving consensus regarding evolutionary ancestry across all species to implement robust phylogenetic analyses

Recent phylogenetic advances have yielded trees encompassing ever-larger taxonomic groups [e.g., 46,47]. The details of ancestral relationships in many parts of these trees, particularly in deeper evolutionary time, remain debated, however, with multiple gaps to fill. We require better consensus on the best way to analytically incorporate phylogenetic covariance. The classic assumption of Brownian trait evolution is often not supported, and more realistic models such as Ornstein-Uhlenbeck [48] do not solve the need to incorporate evolution toward trait optima and account for shifts in trait optima across taxa [49]. There is a strong potential to find patterning in life history strategies common across all species, but we anticipate being surprised by deep-rooted differences in how natural selection has shaped strategies in particular clades.

Adopting analytical approaches that infer explicit links between life history traits and emergent axes of life history variation

We see a role for the wider use of factor analysis (FA) [50] to help discover life history axes as latent factors of observed vital rates. Further development of FA algorithms will be key to help test hypotheses derived from life history theory, particularly phylogenetically controlled confirmatory FA methods. We also urge the development and application of canonical correlation analysis to reveal associations between the multivariate life history traits of species and their multivariate suites of demographic, phenotypic, and ecological features.

Advancing theoretical frameworks for the macroevolution of life histories

Great theoretical progress has been made in our understanding of selection on rates of survival and reproduction in stable, stochastic, and fluctuating environments [51]. To understand variation in lifetime schedules of vital rates, there is now a need to focus more on both age and stage structuring in these models. Necessary advances include incorporation of resource allocation to growth, investigation into whether multiple life histories can maximize fitness under some circumstances, exploration of life history structure within discrete life stages, and the consideration of new theoretical frameworks such as selection for demographic resilience.

Concluding remarks

The fast–slow continuum is the major structuring axis of life history variation but not the only one. More hypothesis-driven research should guide the study of multivariate life history traits and the ecological and evolutionary drivers and limits. Likely candidates include different reproductive or developmental tactics (see Outstanding questions). We argue that more time spent on theory and hypothesis development will lead to more targeted efforts to better understand how life history strategies are shaped by the environment, ancestry, and Bauplan.

Outstanding questions

Is there a universal characterization of life histories across the tree of life?

Does the fast–slow continuum explain the majority of life history variation across all taxa? It cannot, because it captures patterns across life history trajectories and does not account for age- or stage-specific variation in traits. It provides the broad picture in tetrapods (especially mammals and birds), which are relatively well studied, and only in recent years has the fast–slow continuum been shown to be important in sessile and clonal organisms (vascular plants, corals). Whether the fast–slow continuum is the major structuring axis of life history variation at the trajectory level has not been studied in most invertebrates other than insects, where the fast–slow continuum has been identified, but seems to be less structuring than in tetrapods.

Are other axes of life history variation consistent among taxa? Traits relating to reproductive or developmental tactics have repeatedly emerged as the second most important axis of life history variation. However, heterogeneity in the set of traits analyzed so far prevents us from concluding taxonomic universality.

Are there clearly defined clusters and boundaries of life history variation across taxa that occupy distinct spaces in multidimensional life history trait space? Biomechanical constraints limit the range of covariation among life history traits. Intuitively, certain life history strategies should not exist if they defy physical or evolutionary laws.

How sensitive are examinations of life history trait variation to particular choices of data and analytical approaches? If the impact of these choices on research outcomes is significant, cognizance of such consequences is of paramount importance.

Declaration of interests

The authors have no interests to declare.

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