Beyond the Fast-Slow Continuum of Life Histories

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HIGHLIGHTS

* Open-access life history data have proliferated dramatically in recent years and macro-ecological studies are using these data to examine patterns in life histories across the tree of life.

* These studies support the fast-slow continuum being the dominant – but not unique – axis structuring life history variation: other important axes associated with development, reproductive tactics, and demographic buffering have emerged.

* Here, we make recommendations for characterising life history through data choices and analytical methods of dimensionality reduction, with recourse to a clear model of life history.

* We use our framework to advocate that future empirical studies of life history evolution take hypothesis-driven approaches that investigate classical and emerging life history theories, to reveal novel axes, clusters, and boundaries of life history variation across all taxa.

ABSTRACT

Life history theory is key to understanding Earth's diverse life forms. Indeed, schedules of survival, development, and reproduction are the filters through which natural selection acts on species' heritable traits to shape fitness. Prevailing wisdom places species' life history strategies along a fast-slow axis of variation. Challenges to the unicity of this axis are increasingly frequent, given proliferation of life history databases and availability of sophisticated multivariate statistical techniques. However, these empirical approaches often lack concrete theoretical or hypothetical foundations. We advocate for using standardised traits, targeting data gaps and overcoming focus on taxonomic siloes, to facilitate a hyopthesis-driven approach in future examination of drivers of life history variation across the whole Tree of Life.

MAIN TEXT

Any individual is born, survives, develops, possibly reproduces, and ultimately dies. There are countless pathways through life, and as such there is a tremendous diversity of **life history strategies** (see Glossary) across species. However, such strategies are not always associated with species' evolutionary history or environment (Box 1). Central aims of evolutionary ecology include describing and explaining the diversity of life histories across the Tree of Life [1]. In this context, the **fast-slow continuum** [2] has become the standard framework. Indeed, the fast-slow continuum describes a high amount of life history variation across species in most taxonomic groups studied so far [3–9]. However, beyond this fast-slow continuum, many comparative studies have identified various other important axes of variation, often linked to developmental or reproductive tactics.

Around the inception of the fast-slow continuum, Stearns [2] suggested that there was not yet a *"general and reliable theory of life history evolution"* and that the field was not *"empirically sufficient"* to test life history theory. With the emergence of large global databases of demographic and trait data [10–18], we are now much closer in several taxonomic groups to the required sufficiency to test general theories of life history evolution. However, the challenges of identifying, quantifying, explaining, and inferring life history diversity has quickly become lost in a fog of data types, trait currencies, statistical confounds, non-independence, mathematical artefacts, and eco-evolutionary feedbacks.

So although the fast-slow continuum is the main structuring axis of life history variation across species studied to date, it is not by itself an adequate *universal* theory of life history, and there remains little consensus on how to measure life history [19] and which interspecific patterns deserve explanation. As such, we still lack a *"general and reliable"* [2] understanding of life history diversity.

Here, we reflect on the state-of-the-art in life history theory and the potential for general theories in the context of further axes of life history variation beyond the fast-slow continuum. We identify several empirical challenges that must be overcome to properly test such theories across the Tree of Life. These challenges include filling taxonomic and biogeographic data gaps, standardising trait units and developing novel ana-

lytical techniques to facilitate moving toward hypothesis-based over exploratory analyses. Without universal benchmarks, it will be difficult to determine whether the life history strategies we currently observe in the wild are shaped by allometry, relatedness, physiologies, **bauplan** , behaviours, lifestyles, trophic levels, or biogeographic realms.

LIFE HISTORY THEORY AND THE FAST-SLOW CONTINUUM

The life history of an organism determines its fitness, as life history dictates the numerical representation of future generations [1]. Life history is therefore the filter via which selection on phenotypic traits operates, and via which environmental variation generates population, community, and ecosystem dynamics. This idea is underpinned by the canonical Euler-Lotka identity $1 = \int_{x=1}^{\omega} \lambda^{-x} l_x m_x \mathrm{d}x$, with fundamental components describing the schedules of survival (l_x) and reproduction (m_x) to the maximum age $x =$[1]. This identity characterises how survival and reproduction over the life course ($x =$ age) determines population growth (λ). However, this equation tells us nothing about potential covariation between survival and reproduction, between early-life and late-life reproduction, or whether age is the best predictor of fitness; indeed, it has been recently argued that size is a better predictor in many species [20]. A comprehensive theory of life history strategies must at the very least describe measurable directions and strengths of these potential trade-offs, but in reality, life history is much more complicated (Box 2).

Schedules of survival and reproduction can be measured in many ways. Examples include **life expectancy** , longevity, age at first reproduction, **lifetime reproductive output** , measures of **actuarial** and **reproductive senescence** , and **generation time** . Although some of these demographic metrics often do a good job as proxies for life history continua [21], no single one of these **life history traits** adequately captures every characteristic of the demographic schedules l_x and m_x. Therefore, comparative studies often use several life history traits and apply methods of dimension reduction to yield emergent, composite measures. The nonlinearity of these schedules, together with the influence of density dependence and stochasticity [22], complicate measurement of their covariance. These complications remain even if the conceptual framework describing life history structures and competing processes of energy allocation is relatively well known (Box 2).

The fast-slow continuum [2] remains the standard framework for understanding life history diversity across the Tree of Life and is characterised using various life history traits mentioned above. 'Fast' creatures tend to have quick development and early-life allocation of resources to profuse reproduction over survival. 'Slow' creatures have protracted development, delayed maturation, and allocate resources to survival over reproduction. The fast-slow continuum continues to emerge as an important explanator of eco-evolutionary dynamics across taxa, and more recently in the fields of trophic [23] and disease ecology [24] too.

As well as being a canonic ordination of life history variation, the fast-slow continuum predicts species' response to global change. Compared to fast-lived species, slow-lived species show higher sensitivity of population growth to sea temperatures in fishes [25], higher extinction rates in mammals and birds [26], and more negative responses of mammals to human disturbances [27]. These characteristics render long-living species less resilient than fast-living species to environmental insults, making the populations of the former more likely to decline (the so-called "malediction of long-lived species" [28]). However, fast species are more sensitive to increases in temporal autocorrelation of the environment [29]. Such patterns have wider implications for future ecosystem function [26] and conservation success [30].

MULTIPLE AXES TO GRIND

The fast-slow continuum is almost consistently supported as the dominant but by no means the sole factor structuring life history variation, including in mammals [3–5], birds [3], insects [6,7], fish [8] and plants [9] (although the extent of support is sensitive to the life history traits analysed [31]). Exceptions to the fast-slow 'rule' exist, with species having strategies characterised by both high survival and reproduction, such as marine turtles or trees [32], being especially common. Many such organisms have vital rates closely related to size and development, for which age is a poor predictor [20]. These life history strategies are instead defined using a second reproductive axis of variation: *how* species allocate to reproduction, rather

than their reproductive output *per se* . The second most dominant axis of variation thus usually relates to reproductive and developmental tactics, such as from **altricial** *vs.* **precocial** offspring [5]; from high to low recruitment rates [33], high to low frequency of reproduction [7] or from **semelparity** to **iteroparity** [3,9]. In some cases, axes other than reproduction explain substantial life history variation, such as age-specific distributions of mortality and reproduction [34]. The exact meaning of additional axes is hindered by the vast heterogeneity of life history traits analysed in this context [31].

Additional axes may be required to explain additional peculiarities in post-maturation distributions of age-specific survival and reproduction, such as species that reverse development using shrinkage or **retrogression** , or pause development using seed banks or diapause [9].

LIFE HISTORY DATA SOURCES

Quality data for quantifying life histories takes much effort to collect as life histories cannot be described simply by observing static phenotypes. Measuring life history traits can be challenging: some infrequent, brief life history events can be at best rarely observed. Examples include reproduction in semelparous perennial species, or mortality in long-lived species. Much effort has been devoted to the inference of unobserved or imperfectly detected life history events in population studies [35]. The demographic context of traits like generation time and life expectancy means that they must be measured using samples of individuals within populations or species. Hence, life history trait data vary greatly in their abundance, accessibility, and quality (Table 1) [12,36], even among charismatic species [12].

The gold standard in demographic data is detailed schedules of age- or stage-specific **vital rates** . These rates of survival, development, and reproduction are becoming increasingly available through open databases of demographic data (e.g., [10,11,16–18,31,37,38]). Despite the diversity of model dimensions and complexity, life history traits can be derived from these schedules, yielding a set of common traits across species. This derivation overcomes some of the issues with simple trait data outlined in Table 1. Demographic quantities such as stationary [39] and transient [40] population dynamics can also be calculated from life history schedules, as can selection pressures [41]. However, although these databases are accessible, models vary in quality and data remain taxonomically biased [36]. Moreover, the traits derived from these models are mathematical functions of the same underlying schedules of survival, development, and reproduction, hence correlations among them are a combination of the real and the artefactual [42].

CURRENCIES OF LIFE HISTORY TRAITS

We identify four key ways to quantify life history data (Box 2). These ways are often linked to hierarchies of biological organisation and the researcher's own perspective. These four life history *currencies* define how an organism acquires and allocates resources [43], and the consequences for its vital rates. Evolutionary ecologists typically see the world through an adaptive lens and might study selection strength by measuring how schedules of life history traits affect fitness. In contrast, behavioural ecologists perceive evolution of life history in light of an organism's use of energy or space in acquiring resources, whereas developmental biologists focus on energy allocation to ontogenetic cellular and organic processes. From a demographer's perspective, life histories consist of events measured in time or frequency, as these events capture or directly affect survival and/or reproduction over age or stage. However, even within these broad perspectives and currencies, the units of life history trait measurement often vary. For example, demographic measures can be confused by mixing rates, durations, ages, frequencies, and times-to-events. Currencies can also be confused by measuring traits in one currency as proxies for processes in another. Examples include using morphological or behavioural sexual displays as proxies for allocation of energy to reproduction [44], or body size as an allometric proxy for survival, reproduction, metabolic rate, and use of space [3,5,45,46]). Past comparative analyses have often been performed on rather heterogeneous life history trait currencies, including the very first one published by Stearns 40 years ago. The mixture of currencies confounds the interpretation of the structuring axes of life history variation across the Tree of Life. As such, we urge to standardise the currency in future analyses to enable cross-study, cross-taxonomic fair comparisons.

STATISTICAL ANALYSIS OF LIFE HISTORY TRAIT DATA

We argue that alternatives to popular analytical approaches in life history theory should be considered more often [47], and judiciously applied. Tractable generalisations of life history variation frequently require analyses to collapse multivariate trait datasets and associated covariates into a smaller set of latent variables. Common statistical means of reducing dimensionality have both strengths and drawbacks (Box 3). The most popular approach in this context is the Principal Components Analysis (PCA). Although PCA is a well-established exploratory tool, it should not be used naïvely [48].

First, researchers should be aware of their own interpretations and biases when interpreting dimension reduction analyses. Prior to analysis, careful consideration should be given to the aim of the study: for example, PCA informs on correlative rather than causative relationships between variables. Interpreting results of multivariate analyses can be challenging, as composite axes are combinations of underlying traits. Second, careful consideration should be given to how the chosen data may affect outcomes. Indeed, sets of life history traits that are derived algebraically from vital rate schedules may be correlated due to mathematical relationships as much as natural covariation [49]. If a trait set includes measures that are a function of multiple vital rates (*e.g* ., generation time), or that are measured in different units (*e.g* ., energy for metabolic rate and time for mortality), structuring axes from PCAs (principal components) may be challenging to determine. Even if the multivariate trait set is carefully chosen, it is likely to be difficult to draw fair comparisons between studies that use different trait sets and therefore have component axes with different orientations. Third, the statistical shortcomings of analyses must be carefully considered. In particular, a weakness of PCA is that, in its simplest form, it does not consider measurement errors (but see [50]). Fourth, PCAs do not account for non-linearities among life history traits [45]. Finally, and perhaps most importantly, inquiry should be hypothesis-driven: PCA is designed to inform on how variation in multivariate data is partitioned, rather than to test associations between specific traits (Box 3).

RECOMMENDATIONS FOR AN HYPOTHESIS-DRIVEN, EMPIRICALLY SUFFICIENT ERA

Recent increases in available life history trait data unlock our ability to further understand the prevailing patterns of global variation in life history strategies, their evolutionary and ecological drivers and constraints, and their consequences for the extinction risk, invasiveness, and ecosystem functioning. We expand on Stearns' [2] original conditions to identify a number of contemporary challenges concerning life history data and analyses, as we strive to attain the "empirical sufficiency" required to test modern theories of life history evolution.

Moving towards universal life history traits, derived from demographic schedules of survival, reproduction *and* development. Such data can be implicitly measured in a single currency of rates per standard unit of time [51]. This unit harmonisation will strengthen the links between life history, demography, and fitness [1], given their explicit treatment of time in the canonical Euler-Lotka equation. Such rates still need credible transformation during statistical analysis [52]. We further encourage the development of theories and methods to drive our understanding of life history evolution using state variables that are *not* measured using time but linked to other currencies, with energy being a primary candidate.

Filling gaps in life history trait data across the Tree of Life, especially for microbes, fungi, and invertebrates . There are challenges inherent to this recommendation, since for many organisms we lack a good working definition of life cycles and life histories, let alone what constitutes an individual, death, or reproduction. Variation in lifestyle (*e.g.,* sedentary *vs.* mobile, diet, habitat), bauplan (*e.g.* , modular *vs.* unitary, degree of mobility, brain development), growth pattern (*e.g.,* determinate *vs.*indeterminate growth) and reproductive modes (*e.g.,* sexual*vs.* asexual) further complicate the comparative landscape. Attempt to fill data gaps should prioritise measures that will facilitate broad comparisons of life history across taxa. As information gaps across species fill in, it is worthwhile to consider the need for data on vital rate variation within species [53]. Moreover, time series vital rate data exist for a relatively small number of species, and so comprehensive assessments of density-dependent mechanisms driving vital rate variation remain rare.

Embracing life history traits comparative across broad taxa and levels of biological organi-

sation . Besides some exceptions [54,55], multivariate studies seeking to understand axes of life history variation across kingdoms of life emerged only recently [29,56,57]. Previous studies that have encompassed a broad taxonomic range were limited to bivariate analyses [55]. Naturally, continuing taxon-specific lines of enquiry will play an important role, especially in taxa with rich data quality. However, limiting analysis only to separate groups of organisms implies a perceived wisdom that gross differences in the morphology, physiology, and lifestyle of different groups will 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 [29].

Achieving consensus regarding evolutionary ancestry across all species to implement robust phylogenetic analyses. Recent advances in phylogenetics have yielded trees describing the relationships among species across ever larger taxonomic groups [58–60]. Despite these advances, the details of ancestral relationships in many parts of these trees, and particularly in deeper evolutionary time, remain debated and with multiple gaps to fill. We require better consensus on the best way to deal with phylogenetic covariance. The classic assumption of Brownian trait evolution is often not supported, with increasing recognition for the need to incorporate evolution towards trait optima and to identify and account for shifts in trait optima across taxa [61]. There is a strong potential to find patterning in life history strategies common across all species, but we should be ready to be 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 [47] 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, and particularly phylogenetically-controlled confirmatory FA methods. We also urge for 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.

CONCLUDING REMARKS: ARE ALL SPECIES FAST OR SLOW?

Hypothesis-driven research, rather than exploratory data analyses, should guide the study of multivariate life history traits and the eco-evolutionary drivers and limits that shape them. Prevailing evidence shows that the fast-slow continuum is the major structuring axis of life history variation in several taxa, but also that this continuum alone does not fully describe life history variation. We advocate for the development of further theory to test hypotheses regarding which axes, clusters, syndromes, and constraints shape said variation. Likely candidates include different reproductive or developmental tactics (see Outstanding Questions). As we make further progress in the era of "empirical sufficiency", we must also take more mechanistic approaches. These approaches must be coupled with higher-quality data and robust analytical methods. Ultimately, 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. Concurrently, the search for universal syndromes of life history across all currencies of measurement must continue, encompassing the whole Tree of Life.

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OUTSTANDING QUESTIONS

* Is there a universal characterisation of life histories across the tree of life?

* Does the fast-slow continuum explain the majority of life-history variation across all taxa? It does in Tetrapods (especially mammals and birds), which are relatively over-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 has not been studied in most invertebrates other than insects, where the fast-slow continuum was identified [6], but seems to be less structuring than in tetrapods [7].

* 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 analysed so far prevents us from concluding taxonomic universality.

* What, if any, are the implications of particular choices of data and analytical approaches? Certainly the choice of multivariate data to analyse, and the availability of particular measures by taxa, will vary. If the impact of these choices on research outcomes is significant, cognisance of such consequences is of paramount importance.

* 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 [62]. Intuitively, certain life history strategies should not exist if they defy physical or evolutionary laws. How will human actions and climate change alter these boundaries and shape rates of extinction/invasion?

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/references

Simple traits, based on expert natural historian knowledge and opinion.
Simple traits, derived from published measurements.
Life cycle models with age- or stage-based schedules of survival (l_x) and reproduction (m_x), e.g., life tables, projection matri
Life history traits derived from life cycle models using algebraic and computational methods.
Selection pressures on traits, describing the "importance" of vital rates to fitness using the derivative of the latter with resp
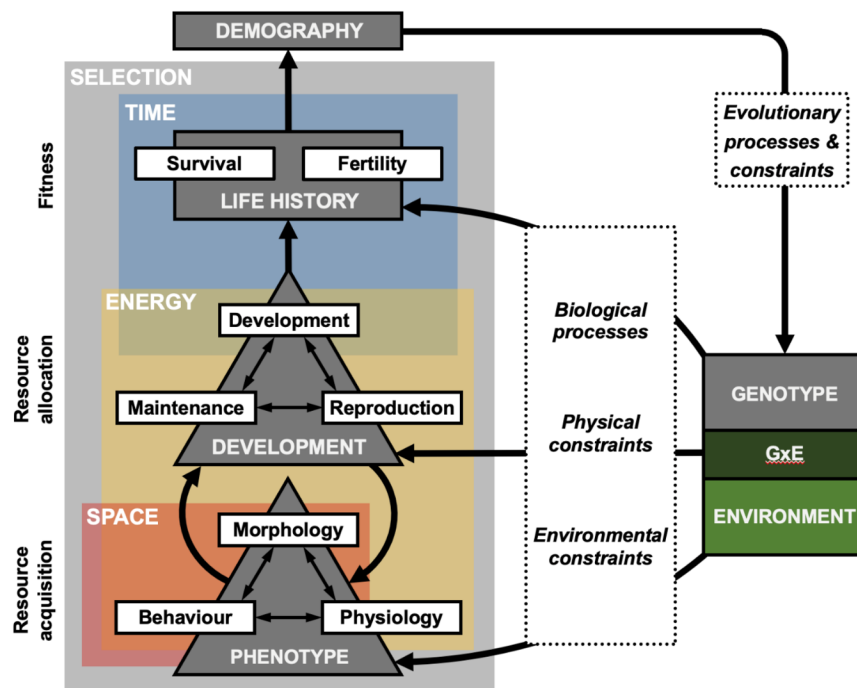
BOX 1. LIFE HISTORY STRATEGIES

Are carrots (*Daucus carota*) similar to blue ringed octopuses (*Hapalochlaena lunulata*)? They both start life small, grow fast but few survive to adulthood, produce many offspring in one breeding event at around 1 years old, and are **semelparous**. In contrast, humans (*Homo sapiens sapiens*) and blue whales (*Balaenoptera musculus*) grow slowly, 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 [64]. 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. *Xestospongia muta* and *F. religiosa* are also like humans and blue whales, however, as 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 2,300 years old is similar in age to the oldest known Caribbean giant barrel sponge [65].

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Whilst 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 [66], with dasyurid species showing different life history strategies, despite being closely related. Maturity occurs at ˜11 months but, while in some species all individuals die by 12 months old following a single synchronous mating, others reproduce many times annually and live for several years [67] . 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 [68], whereas bristlecone pine (*P. longaeva*) hold the record of non-clonal longevity, at 4,850 year old [69]. Selection for varying longevities in pines may be a result of the differing fire environments [70].

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.

BOX 2. A MODEL LIFE HISTORY: FROM RESOURCE ACQUISITION TO ALLOCATION AND FITNESS

An organism's life history strategy is shaped by traits that have a natural hierarchy. The organism's *phenotype* determines how the individual acquires resources [71] through morphological, physiological, and behavioural adaptations. *Development* describes the allocation of those resources to competing processes: supporting somatic maintenance *vs.* supporting the germline *vs.*development in either [72]. The consequences of these allocations are **life history traits** . These traits are characterised by probability distributions of survival and fertility. As survival and fertility govern the number of individuals in populations, life history traits govern not just an organism's *fitness* but also its*demography* - population size, structure, and dynamics [1]. Traits at all hierarchical levels covary with, and feed-back on one another, and are subject to constraints

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imposed by evolutionary history, physical laws, bauplan, and the environment [73]. Natural selection acts to favour life history strategies that maximise the organism's fitness in its environment, given those constraints [1].

Trait currencies and their units vary considerably among life history studies. Moreover, these units do not necessarily correspond with trait types or hierarchies. Physiological traits often measure *energy*expenditure (*e.g.,* metabolic rate). Behavioural traits typically quantify energetic expenditure (*e.g.,* foraging efficiency) or space usage (*e.g.*, home range size). However, space units are also common among morphological traits (*e.g.,* specific root length). Rates of energetic allocation are used to describe resources given to developmental processes (*e.g*., change in body size over time), thus combining energy and time currencies. Time is commonly used to measure life history traits, whether as durations (*e.g*., mean life expectancy), rates (*e.g*., number of offspring per year), or temporal probabilities linked to survival, development, and reproduction (*e.g.*, probability of reaching maturity at a given age). Life history traits are often converted to expectations of life history for populations or species, which is especially necessary where events occur only once. For example, an individual only dies once, but the aggregate deaths in a population yield the distribution of survival for the population's average phenotype, from which we can estimate *e.g.*mean life expectancy. *Selection* on phenotypic, developmental, or life history traits can quantify the trait's contribution to fitness (*e.g*., selection pressure). Shaded areas on the figure are indicative, but not exhaustive, of common currencies used at each level and their overlap.

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 [3–5,7,9,26,27,29,30,33,34,74,75]. Although some -largely arbitrary- guidance exists regarding how many dimensions explain meaningful amounts of variation [48], it is less clear how to compare dominant axes across independent analyses with data sets comprising different traits, taxa, and sampling methodologies.

It is also possible to explore relationships between two different multivariate data sets (*e.g*., climatic and life history data). Canonical Correlation Analysis (CCA) yields two sets of emergent uncorrelated variables by calculating axes with highest correlation between variable sets. This approach recognises that dominant axes of variation (*e.g.*, fast-slow) may not yield strong relationships with other ecological or evolutionary processes.

Unlike both PCA and CCA, Factor Analysis (FA) [47,76] treats measured variables as functions of latent variables, with associated measurement and/or residual error. As FA does not require latent variables to be uncorrelated, the approach offers solutions to some problems of PCA and CCA [47]. We suggest that FA is better suited to the testing of hypothetical, rather than data-driven, axes of variation.

Dimension-reduction analyses fit axes through data, rather than measure the multidimensional boundaries of life history variation. Cluster Analyses (CA) may help understand, after standardising for the species-specific ranking on the fast-slow continuum (by using*e.g.* generation time), which and why certain life history strategies do not exist, as much as the clustered patterning of those that do. Hierarchical CA has previously been used to identify substructure in life history variation [77] and could prove a useful tool to apply much more widely in comparative life history theory [78–82].

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 [83]. Comparative analyses must account for the non-independence from shared evolutionary history [9,47]. Phylogenetic methods exist for PCA [83], but not yet for FA or CA, forcing researchers to use phylogenetically independent contrasts. Correlates of life history traits, particularly organism size, cause further challenges: including these correlates

in analyses risks deriving life history axes defined by non-life-history traits. Moreover, using residuals in multivariate analyses drawn from regressions of life history against body size can introduce statistical biases [84].

GLOSSARY

- **Actuarial** (or **reproductive**) **senescence** : Decreases in survival (or reproduction) with age after maturity.

- **Altricial** *vs.* **precocial** : born helpless and requiring significant parental care *vs.* born in an advanced state and able to feed itself and move independently almost immediately.

- **Bauplan** : the generalised structural body plan that characterises a group of organisms and especially a major taxon.

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

- **Fast-slow continuum** : pattern of species' life history strategies structured along two extremes: "fast" species develop fast, reproduce much, and die young, whereas "slow" species develop slowly, reproduce little, and live a long life. In its original inception, Stearns referred to it as 'slow-fast' [36], but here we revert it as this is currently a more widely used term.

- **Life expectancy** : the average period that an organism may expect to live in a population.

- **Life history trait** : key moments along the life cycle of an organism related to its investment on survival, development, and/or reproduction. Examples include generation time, age at maturity, longevity, *etc* .

- **Life history strategy** : the age- and/or stage-specific patterns and timings of events that make up an organism's life cycle. Life history strategies are defined by the combination of life history traits (e.g., long-lived semelparous).

- **Lifetime reproductive output** : total number of offspring produced over the lifetime of an individual.

- **Retrogression** : the ability to regress to a smaller, younger, or less developed stage with time.

- **Semelparity** *vs.* **iteroparity** : reproductive schedule whereby a single (*vs.* multiple) reproductive event(s) occurs during the lifecycle of an organism. In fatal semelparity, death occurs right after reproduction.

- **Vital 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* .