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RESEARCH ARTICLE

Discretising Keyfitz' entropy for studies of actuarial senescence and comparative demography

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Abstract

1. Keyfitz' entropy is a widely used metric to quantify the shape of the survivorship curve of populations, from plants to animals and microbes. Keyfitz' entropy values <1 correspond to life histories with an increasing mortality rate with age (i.e. actuarial senescence), whereas values >1 correspond to species with a decreasing mortality rate with age (negative senescence), and a Keyfitz entropy of exactly 1 corresponds to a constant mortality rate with age. Keyfitz' entropy was originally defined using a continuous-time model, and has since been discretised to facilitate its calculation from discrete-time demographic data.

2. Here, we show that the previously used discretisation of the continuous-time metric does not preserve the relationship with increasing, decreasing or constant mortality rates. To resolve this discrepancy, we propose a new discrete-time formula for Keyfitz' entropy for age-classified life histories.

3. We show that this new method of discretisation preserves the relationship with increasing, decreasing, or constant mortality rates. We analyse the relationship between the original and the new discretisation, and we find that the existing metric tends to underestimate Keyfitz' entropy for both short-lived species and long-lived species, thereby introducing a consistent bias.

4. To conclude, to avoid biases when classifying life histories as (non-)senescent, we suggest researchers use either the new metric proposed here, or one of the many previously suggested survivorship shape metrics applicable to discrete-time demographic data such as Gini coefficient or Hayley's median.

KEYWORDS
demography, Keyfitz entropy, mortality, senescence, shape of life measures

1 | INTRODUCTION

Actuarial senescence is defined as the increased risk of dying as an individual gets older (Hamilton, 1966; Medawar, 1952). Getting older cannot be avoided in that it is a natural consequence of surviving, but some species seem to be able to avoid senescing (Jones et al., 2014; Roper et al., 2021; Vaupel et al., 2004). It is tempting to assume that long-lived organisms suffer from actuarial senescence less than short-lived organisms, but of course it is possible for an organism to have a constant but high mortality rate over its entire lifespan (see

Box 1 for a definition of lifespan, and other demographic terms used throughout this text), and thus be (relatively) short-lived and negligibly senescent (Péron et al., 2019). For example, Baudisch (2011) compared 10 animal species and found that robins *Erithacus rubecula* rank as having the shortest life expectancy while at the same time having the least senescent survivorship curve (out of this admittedly small sample of 10 animal species). Likewise, an organism can have an increasing but relatively low mortality rate over its entire lifespan, and thus be long-lived and senescent. For example, bamboo (*Phyllostachys*) stands rapidly die following a period of relatively low mortality lasting 60–100 years (Finch & Rose, 1995; Janzen, 1976). Similarly, long-lived semelparous plants such as long-lived *Puya raimondii* (living up to 150 years; Finch (1998)) and *Agave americana* (which often live decades; Harper and White (1974)) show delayed, but rapid declines in vitality with age.

To disentangle these two dimensions of ageing, namely life expectancy and the shape of the survivorship curve, demographers typically distinguish the two using the pace of ageing and the shape of ageing, respectively (Baudisch, 2011; Keyfitz, 1968, 1977). The *pace* of life is often quantified through demographic metrics such as mean life expectancy, reproductive window, or generation time, which tend to be highly correlated. The pace of life behaves intuitively: it is high for short-lived organisms and low for long-lived organisms. The *shape* of ageing, on the other hand, is determined by the time-standardized shape of the mortality or survival curve. The goal of shape metrics is to classify survival curves by whether the mortality rate mostly increases or decreases with (standardized) time (respectively, senescent versus negative senescent curves), see Figure 1 for some examples of different survivorship curve shapes.

Keyfitz' entropy is one of the metrics that has been proposed to quantify the shape of ageing (Keyfitz, 1977; Wrycza et al., 2015). Keyfitz' entropy was originally identified as a dimensionless measure of the elasticity of lifespan to a uniform change in age-specific mortality (Leser, 1955). Population entropy was later re-derived and popularized by Keyfitz (1977). A similar measure was introduced through

independent proofs by Demetrius, which helped attract interest to the measure (Demetrius, 1974, 1978). Demetrius (1978) noted the potential use of Keyfitz' entropy for the classification of survivorship curves, pointing out that it has the useful property that $H = 1$ corresponds to a constant mortality rate (type II curve), $H < 1$ corresponds to mortality increasing with age (type I curve), and $H > 1$ corresponds to mortality decreasing with age (type III curve, see Figure 1 for an example of all three types of curves).

Salguero-Gómez et al. (2016) introduced a discretized version of Keyfitz entropy that interchanges the integral for summation which has been subsequently used in a number of publications (Beckman et al., 2018; Bernard et al., 2020; Capdevila et al., 2020; Salguero-Gómez, 2017). In this short note, we show that this approach to discretise Keyfitz entropy does not fully capture the expected relationship with increasing, decreasing and constant mortality rates of the continuous-time metric. To resolve this discrepancy, we introduce a different discrete-time version of Keyfitz' entropy based on previous work on matrix formulas for life disparity (Caswell, 2013; Caswell et al., 2018; Keyfitz & Caswell, 2005; Vaupel & Canudas-Romo, 2003).

We then show that our alternative discretisation does preserve the expected relationship between Keyfitz' entropy, and increasing, decreasing, or constant mortality curves in age-structured matrix population models. We analyse the relationship between the two Keyfitz' metrics to test if any consistent biases might exist. We evaluate this relationship empirically using animal and plant matrix population models. We find that the two metrics classify survivorship with a similar profile across values, with a consistent, strong trend toward underestimating entropy values (suggesting stronger senescence) using the original discrete entropy metric. That is, curves classified as (weakly) negatively senescent by the new discrete entropy metric are likely to be incorrectly classified as senescent by the original discrete entropy metric, and

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BOX 1   Definitions of common demographic terms.

Life expectancy: the average number of additional years that an individual of age x can expect to live, given a set of age-specific mortality rates. Life expectancy at birth is therefore the mean number of years a newborn individual can expect to live.

Life span: the amount of time (e.g. days, weeks, years) that an individual lives.

Survivorship ($l(x)$): the probability that an individual survives from age 0 to age x.

Longevity: generally used as a synonym for life expectancy.
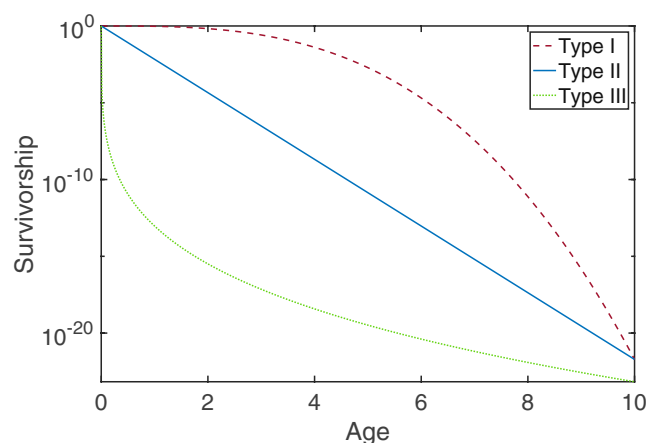
FIGURE 1 Three example survivorship functions of the three different types (type I: senescence; type II: constant mortality; type III, negative senescence). The two Keyfitz entropy measures given by Equations (5) and (10)) are calculated for these three curves using two different widths of the age classes, Δt, given below in Table 1. That is, we discretized the survivorship curves shown in the Figure using two different sizes of discrete intervals, $\Delta t = 0.01$ and $\Delta t = 1$.

TABLE 1 Comparison of the two Keyfitz entropy discretisations for the curves in Figure 1 for a discrete time interval of $\Delta t = 0.01$ and a discrete time interval of $\Delta t = 1$. Original discrete entropy is given by Equation (5), and new discrete entropy is given by Equation (10).

	Original discrete entropy		New discrete entropy	
	$\Delta t = 0.01$	$\Delta t = 1$	$\Delta t = 0.01$	$\Delta t = 1$
Survivorship curve type I	0.33	0.30	0.33	0.44
Survivorship curve type II	0.96	0.75	1.00	1.00
Survivorship curve type III	1.85	0.76	1.94	1.18

constant mortality curves are regularly incorrectly classified as senescent curves by the original discrete-time entropy metric. In addition, life expectancy strongly correlates with deviation between the two entropy metrics, with long-lived species showing little bias and short-lived species showing a stronger bias in the original discrete-time Keyfitz metric.

2 | METHODS: KEYFITZ ENTROPY

2.1 | Continuous-time formulas for Keyfitz entropy

Keyfitz (1977) (or the recent edition, Keyfitz and Caswell (2005)) define the measure H as

$$H = - \frac{\int_0^\omega \left[\log l(a)\right] l(a)\,da}{\int_0^\omega l(a)\,da}, \tag{1}$$

where $l(a)$ is survivorship at age a (see Box 1). Keyfitz and Caswell (2005) note that H has been called entropy of information in other contexts (section 4.3 of Keyfitz & Caswell, 2005). H as defined above, since then generally known as Keyfitz' entropy, is a weighted average of the logarithm of survival, where the weights reflect normalized survivorship. The use of entropies and information theory has a long history in ecology and evolution (e.g. Shannon biodiversity indices, Kullback–Leibler and Jenzen-Shannon divergence, and Maximum Entropy distribution modelling). Note, however, that Keyfitz' entropy does not integrate to one and is therefore not an entropy in the strictest sense (Shannon & Weaver, 1949).

Keyfitz and Caswell (2005) derived the formula by calculating the effect of a proportional change in age-specific mortality on the life expectancy at birth, and the measure therefore relates to the similarity of mortality across age-classes. As a result, Keyfitz' entropy is also a measure of the concavity of the survivorship curve. Goldman and Lord (1986), Vaupel (1986), and recently Vaupel and Canudas-Romo (2003) showed that Keyfitz entropy can be decomposed into two constituent measures that demographers use: Life disparity, $e^\dagger$, which is defined as the average remaining life expectancy at the ages when death occurs, and measures the number of life years lost due to death. Average lifespan of an individual at the time of birth, e^0, which is calculated by integrating the survival density function. The ratio of the aforementioned indices represents an equivalent formulation of Keyfitz' entropy:

$$H = \frac{e^\dagger}{e^0}, \tag{2}$$

whereby

$$e^\dagger = - \int_0^\omega \left[\log l(a)\right] l(a)\,da, \tag{3}$$

$$e^0 = \int_0^\omega l(a)\,da. \tag{4}$$

2.2 | Discretisation of Keyfitz entropy

Salguero-Gómez et al. (2016) introduced a discretised version of Keyfitz entropy,

$$H_{lx} = - \frac{\sum_{x=0}^\infty \log(l_x) l_x}{\sum_{x=0}^\infty l_x}, \tag{5}$$

see Table S2 from the Supplementary Materials of Salguero-Gómez et al. (2016). A few lines of algebra will show that the continuous-time version of Keyfitz' entropy, Equation (1) is equal to 1 when the mortality rate, μ, is constant such that $l(x) = \exp(-\mu x)$. The discretization in Equation 5 (which we refer to as the Original Discrete-time Entropy measure) no longer sums to one for constant mortality curves as can be seen from the Keyfitz entropies in Table 1. The Keyfitz entropies in Table 1 are calculated for the three example survivorship curves in Figure 1. In Supplementary Materials 1, we calculate the value of H_{lx} when mortality is constant and show that it approximates one as mortality gets close to zero but is lower than one otherwise.

2.3 | An alternative discretisation of Keyfitz entropy

We propose an alternative discrete-time formula for Keyfitz' entropy, derived from the definition of Keyfitz' entropy as the ratio of life disparity to life expectancy at birth (which we refer to as the New Discrete-time Entropy measure). Starting from the fundamental matrix **N** (Caswell (2001), p. 112), life expectancy at birth is defined as

$$e_0 = \mathbf{1}^T \mathbf{N} \mathbf{e}_1, \tag{6}$$

$$= \boldsymbol{\eta}_1^T \mathbf{e}_1, \tag{7}$$

where $\boldsymbol{\eta}_1$ is the vector of life expectancies at each age, $\mathbf{1}^T$ is a vector of ones and $\mathbf{e}_1$ is a vector with zeros in all entries except the first entry which is one (see for example Caswell (2013) or Caswell

et al. (2018)). Similarly, life disparity at birth can be calculated from the fundamental matrix $\mathbf{N}$ and the mortality matrix $\mathbf{M}$ as

$$e^\dagger = \mathbf{1}^\mathrm{T}\mathbf{NMNe}_1, \tag{8}$$

$$= \boldsymbol{\eta}_1^\mathrm{T}\mathbf{Be}_1, \tag{9}$$

where the matrix $\mathbf{B}$ contains the distribution of age at death for an individual of each age, and the vector $\mathbf{Be}_1$ selects the distribution of age at death for a newborn individual, see also equation (57) in Caswell et al. (2018) or section 3 in Caswell (2013). Keyfitz' entropy is then given by

$$H_N = \frac{\mathbf{1}^\mathrm{T}\mathbf{NMNe}_1}{\mathbf{1}^\mathrm{T}\mathbf{Ne}_1}, \tag{10}$$

or equivalently by

$$H_N = \frac{\boldsymbol{\eta}_1^\mathrm{T}\mathbf{Be}_1}{\boldsymbol{\eta}_1^\mathrm{T}\mathbf{e}_1}. \tag{11}$$

In Supporting Information 2, we show that Equation (11) yields a value greater than 1 when mortality rate μ is a decreasing function of age, a value less than 1 when mortality is an increasing function of age, and exactly 1 when mortality is constant.

Note that Keyfitz derived his continuous-time measure by considering a proportional change in mortality at all ages (section 4.3 in Keyfitz and Caswell (2005)). We did not derive our formula from this starting point, and instead used existing discrete-time expressions for the numerator and denominator in the continous-time expression derived by Keyfitz. Therefore it remains to be shown whether our new expression for H, H_N in Equation (10), can also be derived by following Keyfitz' proof and considering a proportional change in mortality at all ages in a discrete-time model.

2.4 | Comparing the metrics in real species using the COM(P)ADRE databases

To compare how the two discrete-time entropy measures perform in the context of biologically realistic models, we calculated entropies for age-structured matrix population models. We evaluated both animal and plant population models from the COMADRE (version 4.21.8.0) and COMPADRE (version 6.22.5.0) matrix population databases (both available from https://www.compadre-db.org). The empirical comparison included 401 species animal matrix population models and 34 species plant matrix population models.

We initially screened the matrix population models in COMPADRE and COMADRE based on their inclusion in previous publications that used Keyfitz' entropy (Bernard et al., 2020). These models were selected based on duration of study, and whether the population monitored was subject to experimental manipulation, among other criteria. Within the abovementioned subset, we selected unique records where duplicates existed based on maximizing study duration. We evaluated whether models were age or stage classified and removed any records that included NA values in

reproductive elements or stage-specific survival values greater than unity (three matrices were removed from COMADRE, none from COMPADRE).

For models from previous analyses that were stage-based (80 of 400 in COMADRE; 148 of 150 in COMPADRE), we converted them to age-based matrices. The stage-to-age transformation was based on life table projections of the stage matrix using the mpm to table function from the package RAGE (Cochran & Ellner, 1992; Jones et al., 2022). We constructed Leslie matrices by putting survival vectors (px) on the subdiagonal and fertility vectors (mx) in the top row for ages within 90% of the starting population size based on the survivorship curve (lx). We compared higher and lower thresholds of the cohort size cut-off and found little variation in the number of viable age-specific analogues to stage matrices. The difference in the number of matrices using 90%, 95%, and 98% thresholds was three and five matrices for COMADRE and COMPADRE, respectively.

Age-specific models converted from stage-specific models were validated to see if the intrinsic population growth rate, reproductive rate, and generation time were consistent with those of the stage matrix that generate the life table from which the age-models were calculated. Differences arise between demographic metrics from the stage matrix and from the age-from-stage matrix because some information is inevitably lost in the conversion (for more information, see section 5.3 in Caswell (2001)). We only retained stage-based models where differences between stage and their age-equivalent matrices were within 5% of one another along the above demographic metrics. Nineteen matrices were dropped from COMADRE; 117 matrices were dropped from COMPADRE. The 5% cut-off was an arbitrary threshold that allowed us to retain only those models that in the age-from-stage conversion remain similar to the original models. In most cases for the matrices satisfying the 5% threshold, the difference in demographic metrics from the corresponding stage matrix were $< 1\%$.

3 | RESULTS: BIAS OF THE EXISTING METRIC CORRELATES WITH LONGEVITY

To compare the original and new discrete-time entropy measures, in Table 1 we calculate the entropy using both measures for a few example survivorship curves shown in Figure 1. Both metrics change as the step size is changed, as is generally the case for demographic outcomes in matrix models (Enright et al., 1995; Picard et al., 2010; Torres et al., 2008). However, the value given by the New Discrete-time Entropy metric does not cross the classification threshold of one, and therefore its classification of the survivorship curve as senescent, non-senescent, or negative senescent (sensu Vaupel et al. (2004)) does not change. The Original Discrete-time Entropy metric, on the other hand, changes from above one to below one for the type III curve.

Figure 2a,c show how the Original and the New Discrete Entropy metrics are correlated for matrix models from COMADRE and COMPADRE, respectively. The sparseness of data in the bottom
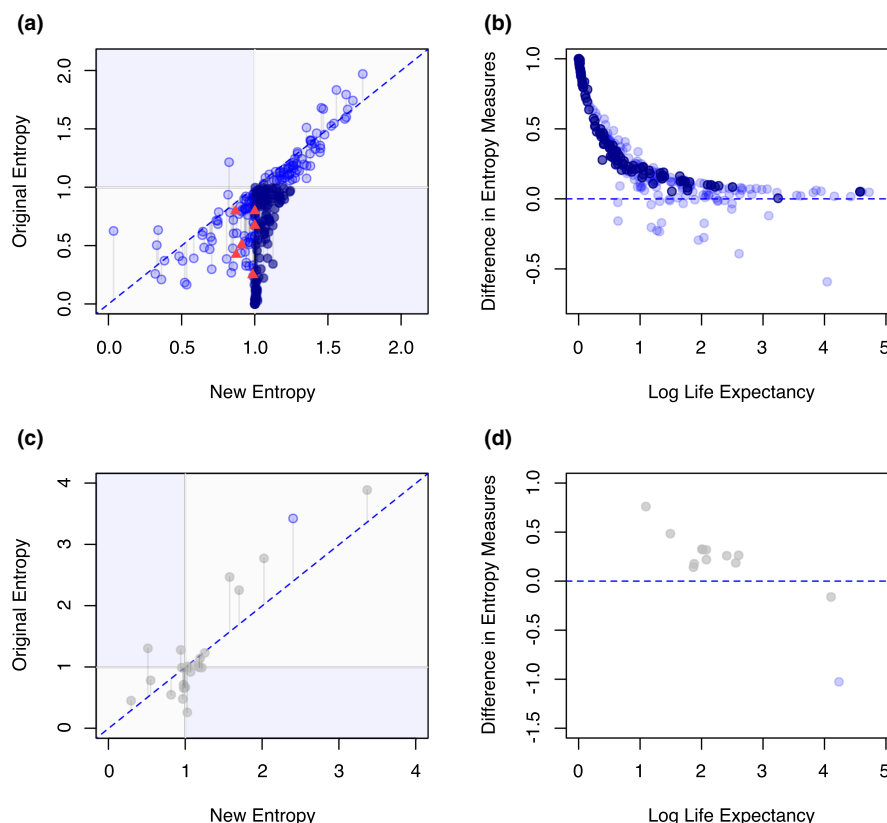
FIGURE 2   Variation between the Original Discrete Entropy (H_{lx}) and New Discrete Entropy (H_N) measures from matrix population models of animals in the COMADRE database (panels a and b), and of plants in the COMPADRE database (panels c and d). The blue shaded areas in (a and c) represent regions where the two entropy metrics have given a different classification to a survivorship curve (top blue square: New Discrete metric classified the curve as senescent whereas the Original Discrete metric classified the curve as negatively senescent; bottom blue square: vice versa). (a) Comparing Keyfitz' entropy of animal matrix models from the COMADRE database using the Original Discrete and the New Discrete metric. Points in dark blue are matrices where entropy shifted from negative values (positive senescence) to positive values (negative senescence); points in light blue do not have that shift. Matrices converted from stage to age are shown in orange. (b) Plot of the difference between the new and the existing metric $\left(H_N - H_{lx}\right)$ as a function of the life expectancy of animal species from COMADRE. (c) Comparing Keyfitz' entropy of plant matrix models from the COMPADRE database using the Original Discrete and New Discrete Entropy metric. Points in grey are converted stage-to-age matrix models that were not included in the analyses in Bernard et al. (2020). (d) Plot of the difference between the new and the existing metric $\left(H_N - H_{lx}\right)$ as a function of the life expectancy of plant from COMPADRE.

panels C and D for plants (COMPADRE) are a consequence of the fact that COMPADRE contains largely stage-structured matrices which required a stage-to-age conversion as described in the methods. We excluded models if the demographic quantities such as population growth rate of the converted stage-to-age model differed from the original stage-structured models by more than 5%, which led to many exclusions and therefore a sparser plot for COMPADRE than for COMADRE (117 exclusions versus 19 exclusions, respectively; bottom two panels versus top two panels in Figure 2). As a consequence of these exclusions, virtually no models from the original datasets analysed in Bernard et al. (2020) were left (one of 143 matrices converted). Therefore we included stage-to-age converted models from COMPADRE outside of the set analysed by Bernard et al. (2020), shown in grey in panels C and D (19 matrices).

Entropy estimates were correlated between the Original Discrete-time Entropy measure and the New Discrete-time Entropy formulation, but expressed high variability. The Original Discrete Entropy measure introduced a consistent bias of over-estimating

senescence (78.6% of models (264/336) had a greater New Discrete Entropy value than Original Discrete Entropy value). Bias was weaker at the extremes (colinearly high and low values of entropy) with the strongest overestimation of senescence occurring under the Original Discrete Entropy centered at the threshold value where New Discrete Entropy = 1 (Figure 2a).

In COMADRE, senescence was strongly underestimated when using the Original Discrete-time Entropy metric (Figure 2a), and also changed sign in a substantial number of cases (126 of 334 models; two blue surfaces in Figure 2a). Sign changed between the two shape measures in COMADRE almost exclusively in the direction of weak negative senescence (small survivorship increase with age) interpreted as positive senescence by the Original Discrete Entropy metric (decreasing survivorship with age; bottom right quadrant of Figure 2a). Nearly 40% of models in COMADRE (126 of 334) inverted sign between the two entropy measures. Around 34% of the models were more than 0.25 units entropy in absolute error (i.e. residual difference from the 1:1 equivalency line), and

18% of models were more than 0.50 units entropy in error from the true value.

In COMPADRE, senescence was also underestimated when using the Original Discrete-time Entropy metric (Figure 2c), changing sign in a modest number of cases (8 of 33 models). Sign changed between the two shape measures in COMPADRE in both directions (2 overestimated; 6 underestimated; blue surface in Figure 2a). Around 25% of models (8 of 33) inverted sign between the two measures. The mean entropy difference between the metrics was 0.35 units in COMPADRE. Deviations from the 1:1 line occurred in both directions in COMPADRE with 16 models overestimating entropy and 10 models underestimating entropy with the Original Discrete-time metric.

The distance between the two discrete entropy metrics was correlated with life expectancy (Figure 2b,d). For data from COMADRE (panel B), the mean error for models with life expectancy <2 was −0.63, the mean error with life expectancy between 3–5 years was −0.15, and for 5–10 years it was −0.06.

These findings have important implications for the recent and future waves of comparative demographic research evaluating the number of species escaping or undergoing actuarial senescence (e.g. Beckman et al., 2018; Bernard et al., 2020; Capdevila et al., 2020; Salguero-Gómez, 2017) because Figure 2a implies that these studies have likely underestimated the number of species with negligible actuarial senescence using this Original Discrete Keyfitz metric, and Figure 2b implies that this underestimation was especially strong for short-lived species, therefore introducing a spurious correlation between shape and pace.

In Supporting Information 1 we show why the original discretisation, H_{lx}, classifies constant mortality curves as negatively senescent curves, and why it does so more strongly for species with shorter lifespans. We find that for constant mortality μ, $H_{lx} = \frac{\mu exp(-\mu)}{1-exp(-\mu)}$. This function is smaller than one whenever the mortality rate is nonzero, that is, when μ is larger than 0. Furthermore, $\frac{\mu exp(-\mu)}{1-exp(-\mu)}$ is a decreasing function of μ such that the Original Discrete Keyfitz metric gets closer to zero as the constant mortality gets larger and life expectancy gets shorter, leading to the correlation seen in Figure 2b. In the limit of infinitesimally small time steps, survival approaches one (or μ approaches zero), and the sum approximates the continuous time formula well in this limit.

4 | DISCUSSION AND CONCLUSION

We have shown that the commonly used time-discretized formula for Keyfitz' entropy (referred to here as the Original Discrete Entropy measure) does not preserve the relationship between Keyfitz' entropy and the shape of the survivorship curve that exists for a continuous-time definition of survivorship entropy. That is, constant mortality curves do not yield a Keyfitz' entropy of one, and life histories with decreasing mortality will not always yield values above one (e.g. see Table 1). Specifically, nearly 40% of classified survivorship curves (126 of 336) changed classification when using

the new discrete metric from senescent to negatively senescent, or vice versa. Furthermore, the distance between the original and the new discrete Keyfitz' entropy metric correlates with life expectancy (Figure 2b). As a consequence, any correlations obtained between pace and shape of life in previous publications using the existing Keyfitz metric may need to be reevaluated.

We propose a different formula for the discretisation of Keyfitz' entropy (referred to here as the new entropy measure), based on life disparity and life expectancy in Equation 10. We show in Supporting Information 2 that this new formula does preserve the relationship between the shape of the survivorship curve and Keyfitz entropy (that is, $H_N > 1$ when mortality is a decreasing function of age, $H_N < 1$ when mortality is an increasing function of age, and $H_N = 1$ when mortality is constant). However, a major downside of the formula we have proposed is that it is only a measure of the shape of ageing for age-structured survival matrices (Leslie matrices). If the survival and population matrix are stage-structured, then the New Discrete Entropy measure quantifies whether mortality rate increases or decreases with stage. Stage-to-age conversion methods can offer one way around this limitation to the method (for more information on stage-to-age conversion methods see section 5.3 in Caswell, 2001, and for an implementation of the methods in R see Jones et al., 2022).

Besides the new shape metric proposed here, there are many other shape metrics that have been proposed and can be used to classify survivorship curves. For example, other life table statistics that have been used to quantify the age-specific decline in survival include Hayley's median (Hailey, 1874); the age-dependent mortality parameter of mortality distributions (e.g. Gompertz, Weibull, Siler, Logistic, etc.; Ricklefs & Scheuerlein, 2002); the age at the onset of senescence (Jones et al., 2008) and the integration of the remaining lifespan and survival function (Wrycza et al., 2015). Wrycza et al. (2015) highlight a number of other potential candidates, such as a modified Gini coefficient (reviewing 7 possible metrics), and highlight the value of the entropy as a measure of the shape of life (see also Aburto et al. (2022) for a recent discussion of measures of lifespan inequality).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/2041-210X.14083.

DATA AVAILABILITY STATEMENT

Code used in this paper can be found at Zenodo with https://zenodo.org/badge/latestdoi/532871458, and at https://github.com/Lotte-biology/Keyfitz.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Supporting Information S1. Properties of the Original Discrete-time Entropy metric.

Supporting Information S2. Properties of New Discrete Keyfitz Entropy metric.

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