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Actuarial senescence progresses similarly across sites and species in four boreal orchids

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Author contributions

Nina Sletvold and Johan Dahlgren conceived the general study questions, Ditte Wiig Tholstrup and Johan Dahlgren conceived the specific study questions. Asbjørn Moen and Dag-Inge Øien collected the data, Ditte Wiig Tholstrup analysed the data with support from Fernando Colchero, and Ditte Wiig Tholstrup led the writing of the manuscript. All authors contributed critically to the revisions and gave final approval for publication.

Conflict of interest statement

The authors declare no conflict of interest.

Data availability statement

The data is published on Dryad: <https://doi.org/10.5061/dryad.q2bvq83s2> (Dahlgren 2023).

Actuarial senescence progresses similarly across sites and species in four boreal orchids

Abstract

1. Whole-plant senescence, defined as a decrease in individual fitness as an organism grows older, has often been assumed to not occur in plants; however, it has now been detected in a range of plant taxa. Still, reported senescence patterns vary substantially, and it remains unknown how consistent patterns are within phylogenetic groups and how they may be affected by environmental factors. Plants show a high diversity in life-history traits within phylogenetic groups and environments, but shared traits amongst related species are also common, making both diverse and similar patterns probable.
2. Here, we explore how mortality changes with advancing age in four closely related species (*Dactylorhiza incarnata*, *D. lapponica*, *D. maculata*, and *Gymnadenia conopsea*) across two sites in Norway: the coastal Nordmarka and inland Sølendet. Using data collected over 34 years, following more than 2500 individual plants, we conduct Bayesian survival trajectory analysis to assess mortality age-trajectories.
3. A simple Weibull model, illustrating increasing mortality at a decelerating rate with age, was the best fit for all species at both sites. From these models, we calculate rates of senescence and compare them using Kullback-Leibler divergences, finding no notable differences in rates between species or sites.
4. *Synthesis.* Our findings suggest that actuarial senescence, an increase in mortality with advancing age, may be common in orchids and show that demographic ageing can proceed similarly in closely related taxa across different environments.

Keywords: ageing, demographic senescence, demography, life-history theory, mortality, rate of aging

INTRODUCTION

It has often been assumed that plants do not experience whole-plant senescence, defined as a decrease in individual fitness as an organism grows older (reviewed in (Dahlgren and Roach 2017)). The lack of senescence has been attributed to plants' turnover of organs (e.g., leaves and flowers), as well as varying degrees of clonality and indeterminate growth (Munné-Bosch 2015, Popov et al. 2022). From an evolutionary perspective, the potential lack of senescence has been attributed to the absence of an early-life separation of somatic and germ cell lines (Kirkwood 1977, Popov et al. 2022), although a clear understanding of the timing of germ-soma separation in plants is lacking (Lanfear 2018).

Current empirical evidence, however, suggests that many different ageing patterns exist in plants. Actuarial senescence, defined as increasing mortality with age (Hamilton 1966, Kirkwood 1977, Kirkwood & Holliday 1979), hereafter *senescence*, has been identified in a range of species (Silvertown et al. 2001, Roach and Smith 2020), including both short- (Picó and Retana 2008, Roach et al. 2009) and long-lived perennial herbs (Silvertown et al. 2001, Edelfeldt et al. 2019), as well as some tree species (Baudisch et al. 2013) and a moss (Tholstrup et al. 2021). In contrast, several other species have been documented to display mortality patterns suggesting negligible (i.e., mortality being almost or fully unaffected by age) (Harper 1980) or even negative senescence (i.e., mortality decreasing with age) (Lauenroth and Adler 2008, Garcia et al. 2011).

Although detected in many different families and genera, it remains unknown whether changes in vital rates such as mortality over life spans are consistent within taxonomic groups (Roach and Smith 2020). Plants are known to show a great deal of variation in life-history traits, often even

amongst closely related species (Webb et al. 2002); for example, the genus *Crepis* holds both annuals and perennials, as well as mono- and polycarpic species (Mossberg and Stenberg 2014), so diverse patterns of senescence may not be unexpected within taxa. Conversely, similarity in life-history traits is also common, and it is possible that the degree to which degree species show senescence corresponds to phylogeny (Pujol et al. 2014). Patterns suggesting similar increases in mortality with age have been shown for a few mosses from the Polytrichaceae family (Watson 1979), as well as two species of *Lemna* (Barks and Laird 2015, Barks et al. 2018). Signs of senescence have also been identified in several species of the orchid family (Orchidaceae). In *Dactylorhiza lapponica*, mortality significantly increased with age indicating senescence (Dahlgren et al. 2016). Also *Anacamptis morio* may senesce as older individuals made up more than half of the deaths in harsh years in a study by Stroh (2019). However, actuarial senescence does not appear to be a universal trait of the orchid family, as mortality has been documented to be age-independent in *Ophrys sphegodes* (Hutchings 2010). Similarly, a study on twelve *Rhododendron* species, based on botanical garden data, found different patterns across congeners: for some species mortality increased with age, while for others it decreased or appeared unaffected by age (Baden 2020). In summary, despite the evidence of senescence for multiple species within particular taxonomic groups, to what extent general taxonomic patterns occur is unknown.

Rates of change in mortality with advancing age may also be affected by environmental conditions, potentially leading to senescence being detected only under certain conditions (Quarles & Roach 2019). This has been observed in *Plantago lanceolata*, where the oldest individuals had the highest mortality in years when ecological stress was high (Roach, Ridley & Dudycha 2009; Quarles & Roach 2019; Baden et al. 2020). Similarly, a study on *Fumana procumbens* only detected actuarial senescence in some closely situated populations, suggesting an effect of local environmental conditions (Edelfeldt, Bengtsson & Dahlgren 2019). Moreover, the environment may influence the

rate of senescence in the orchid *D. lapponica*, with higher rates at a site with more benign environmental conditions, perhaps because of a life history strategy prioritising reproduction (Dahlgren *et al.* 2016). Thus, environmental effects on senescence may cause species that show similar patterns in one environment to have differing patterns in another.

Here, we investigated the age-trajectories of mortality of four closely related orchids (*Dactylorhiza incarnata*, *D. lapponica*, *D. maculata*, and *Gymnadenia conopsea*) across two sites, one inland and one coastal, using data on almost 3000 individuals collected over 34 years. We used Bayesian survival trajectory analysis (Colchero & Clark 2012; Colchero, Jones & Rebke 2012) to estimate how mortality changed with age and quantified rates of actuarial senescence. We then evaluated how average mortality and actuarial senescence varied across species and environmental conditions. We hypothesized that all four orchids

1. show actuarial senescence and have a similar increasing but decelerating age-specific mortality (corresponding to previous results with *D. lapponica*, in Dahlgren *et al.* (2016)),
2. have a higher rate of senescence at the coastal site (Nordmarka) due to the milder climate, assuming that senescence rates may be higher if more resources are devoted to reproduction in more benign environments, and
3. senesce at different rates, corresponding to their life history. Specifically, we expect generally higher rates of ageing in more frail, short-lived species (i.e., *D. maculata* and *D. incarnata*).

MATERIALS AND METHODS

Study species and sites

The four species in this study were *Dactylorhiza incarnata*, *D. lapponica*, *D. maculata*, and *Gymnadenia conopsea*. The taxonomy of these orchids is challenging, but in a wide sense they are all found throughout Eurasia (and individually in other parts of the world) (Kühn, Pedersen & Cribb 2019). In the study areas the four species grow in rich fen vegetation (Moen, Lyngstad & Øien 2012). *D. incarnata* occur in wet (open carpet) vegetation, *D. lapponica* in lawn communities, mainly in open sloping fens, and *D. maculata* and *Gymnadenia* in mire margin communities. All four species are tuberous and are considered non-clonal in the study areas. They have purely vegetative years during which they produce a rosette of several basal leaves; sometimes the rosette is missing due to dormancy or herbivory. In reproductive years, they produce a single inflorescence with multiple flowers that are nectar-producing only in *Gymnadenia*. Flowering occurs in mid-summer (June-July) for *Dactylorhiza* and in mid-late summer (July-August) for *Gymnadenia*. The latter species attracts butterflies and hawkmoths for pollination (Sletvold & Ågren 2010), while the former mainly rely on deceiving bumblebees (Nilsson 1981; Sletvold, Grindeland & Ågren 2010). For *D. lapponica*, actuarial senescence has been documented previously (Dahlgren et al. 2016), but ageing has not been found to influence the probability of flowering or the size of individuals (Moen and Øien 2002).

The species were studied within two nature reserves in central Norway: the coastal Nordmarka (63°03'N, 9°05'E), and 145 km further inland, Sølendet (62°40'N, 11°50'E). Both are situated at the transition between the middle boreal and the north boreal vegetation zones (Moen 1999), and experience a short growing season from May to late August. Nordmarka has a more coastal local climate (450 m a.s.l. and annual precipitation 1507 mm), while the inland population at Sølendet experiences a more continental climate (770 m a.s.l. and annual precipitation 670 mm). Both sites are dominated by sloping fen communities that share similar soil properties and management histories (Moen, Lyngstad & Øien 2012). Historically, they have been used for haymaking until

around 1950, which was then reintroduced in the 1970s as a management tool in select areas. The plant populations included in this study have not been subjected to this management.

Data collection

Monitoring began in 1981 in both study areas and demographic data has been collected annually in early July. Here we use data collected until 2015. Individuals were mapped in permanent plots (mainly 5 m × 2.5 m) in the year they were first observed flowering, after which they were monitored irrespective of reproductive status. Each year, presence, flowering status, and number of flowers were noted. If an individual was absent for three consecutive years, it was presumed that the individual had terminated in the first year of absence. At Sølendet/Nordmarka a total of 178/481 *D. incarnata*, 711/806 *D. lapponica*, 90/164 *D. maculata*, and 416/65 *G. conopsea* individuals were recorded over the years, totalling 1295/1516 individuals. The data for *D. lapponica* (up to 2012), have previously been used to compare mortality age trajectories across sites and in different mowing treatments (Dahlgren et al. 2016). The fieldwork did not require a permit.

Data analysis

We used Bayesian survival trajectory analysis (BaSTA (Colchero & Clark 2012)) for inference on age-specific mortality and survival of the four species at the two sites, using the R package BaSTA (Colchero, Jones & Rebke 2012). Building on the principles of survival analysis, which require defining a random variable X for ages at death, this package defines the mortality or hazards rate as

$$\mu(x|\boldsymbol{\beta}) = \lim_{\Delta x \rightarrow 0} \frac{\Pr(x < X < x + \Delta x | X > x, \boldsymbol{\beta})}{\Delta x}, \quad x \geq 0, \quad (1)$$

where x represents any given age and $\boldsymbol{\beta}$ are the mortality parameters that will be estimated. From

equation (1), the cumulative hazards function is then calculated as

$$H(x|\boldsymbol{\beta}) = \int_0^x \mu(t|\boldsymbol{\beta})dt, \quad (2)$$

with survivorship function given by $S(x|\boldsymbol{\beta}) = \exp[-H(x|\boldsymbol{\beta})]$ and probability density function of ages at death $f(x|\boldsymbol{\beta}) = \mu(x|\boldsymbol{\beta})S(x|\boldsymbol{\beta})$. We explored four different basic mortality models based on the function in equation (2) (Table 1); exponential (i.e., constant mortality with age), Gompertz (Gompertz 1825), Weibull (Pinder III, Wiener & Smith 1978), and logistic (Pletcher 1999) models, with the addition of a ‘Makeham term’ (Makeham (1867), commonly described as age-independent mortality) and a ‘bathtub’ (allowing declines in early mortality, e.g., Siler (1979)) term (Table 2). Thus, we tested ten different models: all combinations of mortality models and shape terms excluding the exponential model, which can only be ‘simple’. Due to the way the data were collected, we modelled lifespan as age since first reproduction. The package also calculates the models’ deviance information criterion (DIC) (Spiegelhalter *et al.* 2002; Celeux *et al.* 2006), which can be considered a Bayesian analogue to commonly used model selection criteria based on theoretic information approaches such as the AIC (Akaike information criterion, Akaike (1974)) and BIC (Bayesian information criterion, Schwarz (1978)), allowing for easy comparison of model fits. See Appendix S1 for a more detailed explanation of the BaSTA analysis.

The four types of mortality models describe different types of ageing patterns. If the exponential model fits best, then actuarial (or negative) senescence is not present. A Gompertz model indicates actuarial senescence due to increased vulnerability to death by causes shared among all ages (Ricklefs & Scheuerlein 2002). A logistic model allows mortality to plateau after an initial increase, which occurs in populations where there is substantial heterogeneity in mortality among individuals. Meanwhile, a Weibull model, where the rate of change in mortality decelerates with age may capture a slowing down in ageing that is less extreme than in the logistic model, and may

have a better fit than a Gompertz model if causes of death for old individuals differ from those of young (Ricklefs & Scheuerlein 2002).

From the best fitting mortality models, the rate of senescence (ageing rate) was calculated as the first derivative of the logarithm of the mortality function. To compare rates, we calculated the Kullback–Leibler divergences (Kullback & Leibler 1951), D_{KL} , of the ageing rate posterior densities between sites for all four species. The D_{KL} provides a measure of the amount of information lost if we were to use the posterior density of the ageing rate from site i to predict the ageing rate from site j . We used a standardisation proposed by McCulloch (1989) that bounds the range of D_{KL} in the interval [0.5, 1], where a value of 0.5 implies no loss (i.e., full correspondence between the posterior densities), and a value of 1 means full loss (no overlap between the posterior densities).

To investigate whether there was a general increase in annual mortality that might potentially confound the effect of ageing, we also conducted generalized additive model analyses of the effect of year (Fig. S1). However, we detected no indication of an overall decline in habitat suitability over the study period, with annual mortality fluctuating over years and generally decreasing over the study period.

RESULTS

A simple Weibull mortality model was the best fit for all species at both Sølendet and Nordmarka (Table 3). Mortality increased, but the ageing rate decreased with advancing age (Fig. 1, Fig. S2).

Mortality increased with age since first reproduction for all four species at both sites (Fig. 1), however for *G. conopsea* at Nordmarka the results are highly uncertain due to a low number of individuals. All species but *D. maculata* experienced lower mortality, and thus greater predicted

lifespans, at Nordmarka when compared to Sølendet – the reverse was true for *D. maculata*. At both sites, *D. lapponica* and *G. conopsea* were the two most long-lived species (Table 3).

The differences in mortality trajectories for *D. incarnata* and *D. lapponica* between the two sites were mainly caused by differences in the scale parameter of the Weibull mortality model (Fig. 2), which was generally smaller at Nordmarka, causing average mortality to be higher at the inland Sølendet (cf. Table 3). For *D. maculata* the difference across sites was primarily caused by the shape parameter being higher at Nordmarka (Fig. 2), causing mortality to increase faster at this site (Fig. 1).

All four species experienced higher ageing rates at Nordmarka than at Sølendet (Fig. 3), however the Kullback-Leibler divergences (all < 0.76) indicated that these differences are too small to conclude that the rates varied between sites for any species (Table S1). Similarly, differences between species at either site were too small (all < 0.64) to be supported statistically (Table S2).

DISCUSSION

In this long-term study of closely related, long-lived orchids at two sites in Norway we found evidence of actuarial senescence in all four study species: *Dactylorhiza incarnata*, *D. lapponica*, *D. maculata*, and *Gymnadenia conopsea*, with increases in mortality following a similar decelerating age-trajectory across species. Although rates of senescence were higher for all species at the coastal site with a more oceanic climate, the differences between their distributions were not sufficiently large to conclude that rates of senescence varied between sites. Rather, differences in mortality trajectories were mainly caused by differences in average mortality and not ageing rates. This result indicates that the degree to which plants experience actuarial senescence can be similar across closely related species. These findings are particularly interesting because few studies have

explored patterns of senescence in closely related species (Paiha & Laird 2022), or for the same species in different environments (Quarles & Roach 2019; Baden *et al.* 2020).

The fact that the same mortality model (the simple Weibull), with a similar pattern of increasing mortality with age, had the best fit for all site-species combinations is indicative of that actuarial senescence and the way it manifests may be a general characteristic for *Dactylorhiza* and closely related genera. Age-related increases in mortality have been found in various other plant species (Silvertown, Franco & Perez-Ishiwara 2001; Barks & Laird 2015; Edelfeldt, Bengtsson & Dahlgren 2019), but is not a universal trait of the plant kingdom nor the orchid family (Chapman 1986; Rose, Clarke & Chapman 1998; Hutchings 2010). Thus, our results highlight a possible phylogenetic signal in ageing patterns of plants, and the need for additional studies allowing comparative analyses. To our knowledge, only few studies on the same age-dependent vital rate of plants have been carried out on two or more species within the same genera (e.g., *Lemna* (Barks & Laird 2015; Barks *et al.* 2018; Paiha & Laird 2022), *Cistus* (Munné-Bosch & Lalueza 2007; Müller *et al.* 2014), and *Silene* (Tuomi *et al.* 2013; Pujol, Marrot & Pannell 2014)), but in all these cases ageing patterns were qualitatively similar. In addition, demographic senescence has been identified in closely related species in studies quantifying different vital rates (e.g., *Silene latifolia* being studied in regards to reproduction (Pujol, Marrot & Pannell 2014), while the focus was on mortality for *Silene spaldingii* (Tuomi *et al.* 2013)). In contrast, a study on the *Rhododendron* genus found substantial variation among species in mortality age-trajectories, including increasing versus decreasing mortality with age, as well as age-independent mortality (Baden 2020). It should be noted though that this study used data from botanical gardens, and it is unknown if similar patterns would exist in natural populations. Finally, a comparative study on senescence in angiosperms deriving age-based parameters from stage transition matrices documented a phylogenetic influence on ageing rates, although senescence was only identified in phanerophytes, i.e. typically trees (Baudisch *et al.*

2013). Our study provides evidence that closely related plants can have very similar age trajectories of mortality. In comparison, ageing patterns are found to be similar among mammals for which the Gompertz-Makeham model invariably provides the best fit to adult age-specific mortality (Lemaître *et al.* 2020; Colchero *et al.* 2021).

The whole-plant senescence now demonstrated for several orchid species points towards a need for considering age-related declines in fitness in population viability analyses of the many threatened species of this genus (Swarts & Dixon 2009; Wraith, Norman & Pickering 2020), because accounting for age can affect predictions of extinction risk (Chu & Adler 2014; Edelfeldt *et al.* 2019). This would be particularly important for populations in similar contexts as the ones we studied, where plants are at risk of being overgrown over succession after haymaking practices have ceased (Moen & Øien 2002; Damgaard, Moeslund & Wind 2020). This is likely to first lead to reduced recruitment while already established plants survive and experience the age-related declines in fitness, potentially causing overly optimistic predictions by analyses that exclude age.

Although ageing rates varied slightly between the two sites, relatively low Kullback-Leibler divergences indicated that all four species have similar senescence patterns at both sites. Similarly lacking effects of environmental conditions on ageing rates has been documented for other organism groups; for example, Ricklefs (2000) found that ageing rates were similar in wild and captive bird populations and Colchero *et al.* (2021) documented little variation in ageing rates among wild and captive primates. Despite similar ageing rates, the differences we detected in overall (age-independent) mortality rates across sites still illustrate that environmental factors affect mortality trajectories. In addition, the most notable difference in ageing rates across sites was observed for *D. maculata*, where mortality increased at a higher rate in the presumably more benign coastal climate at the Nordmarka site, as we hypothesized. A study by Tye *et al.* (2018) on the same populations documented that mortality tended to decrease with or be unrelated to summer

temperature at both sites, except for in *D. maculata*, which experienced higher mortality in the year following a warm summer. This divergent response to climatic factors by *D. maculata* may be part of the explanation of why this species stood out also in terms of senescence patterns. This difference between sites could also potentially be affected by that at the Sølendet site, *D. maculata* occurs in stands with the genetically close *D. fuchsii* (Kühn, Pedersen & Cribb 2019), with which it is known to hybridize (Mossberg & Stenberg 2003). These hybrids are highly likely to exist in the Sølendet population. Nonetheless and despite the weak statistical support of effects of site on rates of senescence in our study, we suggest that the tendencies we observe warrant further studies evaluating potential environmental effects on actuarial senescence.

In conclusion, we found that mortality increased with age in all four closely related orchids at both sites, with qualitatively similar age trajectories. Taken together with previous studies, these results may reflect that actuarial senescence is common in orchids and that demographic ageing proceeds similarly in closely related plant taxa. In addition, despite that differences in age trajectories of mortality across our sites did not seem to be driven by differences in rates of senescence, we argue that future studies on age-based demography of plants should ideally be made in multiple populations across multiple sites, and that larger-scale studies assessing relationships between phylogenetic distances and senescence patterns will likely be important to understand the evolutionary background of the existence of actuarial senescence in some plants.

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Table 1 The four mortality models that the BaSTA package can fit to data on presence/absence of individuals.

Mortality model	Equation
Exponential	$\mu_0(x \boldsymbol{\beta}) = \beta_0 \quad (6a) \quad \text{where } \beta_0 > 0.$ <p>β_0 is the mortality and it does not change with age (x).</p>
Gompertz	$\mu_0(x \boldsymbol{\beta}) = \exp(\beta_0 + \beta_1 x) \quad (6b) \quad \text{where } \beta_0 \in \mathbb{R}, \beta_1 > 0.$ <p>β_0 is the baseline mortality (i.e., when $x = 0$). Mortality increases exponentially with age (x), the rate of which is determined by parameter β_1.</p>
Weibull	$\mu_0(x \boldsymbol{\beta}) = \beta_0 \beta_1 (\beta_1 x)^{\beta_0 - 1} \quad (6c) \quad \text{where } \beta_0, \beta_1 > 0.$ <p>β_0 is the shape parameter and β_1 is the scale parameter, while x is age. Mortality increases (or decreases) as a power function.</p>
Logistic	$\mu_0(x \boldsymbol{\beta}) = \frac{\exp(\beta_0 + \beta_1 x)}{1 + (e^{\beta_0}/\beta_1)\beta_2(e^{\beta_1 x} - 1)} \quad (6d) \quad \text{where } \beta_0 \in \mathbb{R}, \beta_1, \beta_2 > 0.$ <p>β_0 is the baseline mortality (i.e., when $x = 0$). Mortality increases exponentially with age (x), the rate of which is determined by parameter β_1, and plateaus in older ages as the variability of individual frailty (β_2) increases.</p>

Table 2 The different mortality shape-terms that the BaSTA package can fit.

Shape	Equation
Makeham	$\mu(x \boldsymbol{\beta}, c) = c + \mu_0(x \boldsymbol{\beta}) \quad (6e) \quad \text{where } c > 0.$ <p>c is ‘age-independent’ mortality.</p>
bathtub	$\mu_0(x \boldsymbol{\beta}, \boldsymbol{\alpha}, c) = \exp(\alpha_0 + \alpha_1 x) + c \quad (6f) \quad \text{where } \alpha_0 \in \mathbb{R}, \alpha_1 > 0, c > 0.$ $+ \mu_0(x \boldsymbol{\beta})$ <p>α_0 and α_1 are the parameters that account for the potential decline in early mortality with age, while c is as described above.</p>
simple	No shape was added to the mortality model.

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Table 3 The three best-fitting mortality models for *Dactylorhiza incarnata*, *D. lapponica*, *D. maculata*, and *Gymnadenia conopsea* at the two sites Nordmarka (N) and Sølendet (S).

		<i>D. incarnata</i>			<i>D. lapponica</i>			<i>D. maculata</i>			<i>G. conopsea</i>		
		<i>model</i>	<i>DIC</i>	<i>LE</i>	<i>model</i>	<i>DIC</i>	<i>LE</i>	<i>model</i>	<i>DIC</i>	<i>LE</i>	<i>model</i>	<i>DIC</i>	<i>LE</i>
N	WE.si	5839	34	WE.si	11,958	55	WE.si	1928	31	WE.si	854	68	
	WE.Ma	5844		GO.si	11,971		WE.Ma	1931		LO.ba	1028		
	LO.Ma	5849		WE.Ma	11,995		WE.ba	1936		LO.Ma	1051		
S	WE.si	2121	31	WE.si	10,003	46	WE.si	1189	40	WE.si	5822	46	
	LO.si	2123		WE.Ma	10,016		WE.Ma	1207		WE.Ma	5830		
	WE.Ma	2127		WE.ba	10,040		GO.si	1210		WE.ba	5856		

Notes. Abbreviations for the models are GO (Gompertz), LO (logistic), and WE (Weibull), with shape terms ba (bathtub), Ma (Makeham), or si (simple). DIC = deviance information criterion. LE = life expectancy (years) after first reproduction predicted from the best-fitting model.

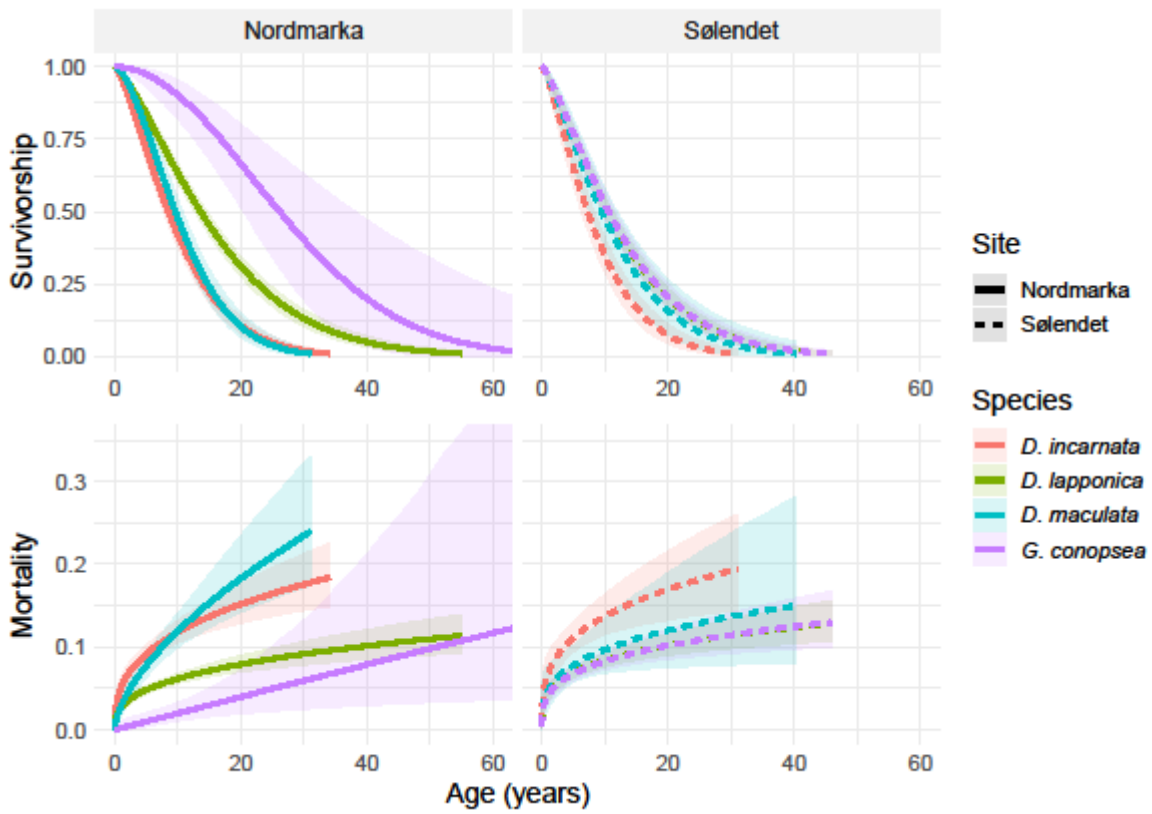


Figure 1. Survivorship and mortality as a function of years after first reproduction (age = 0) for all four species at each site. Shaded polygons are 95 % credible intervals. Non-parametric Kaplan-Meier plots are presented in Fig. S2.

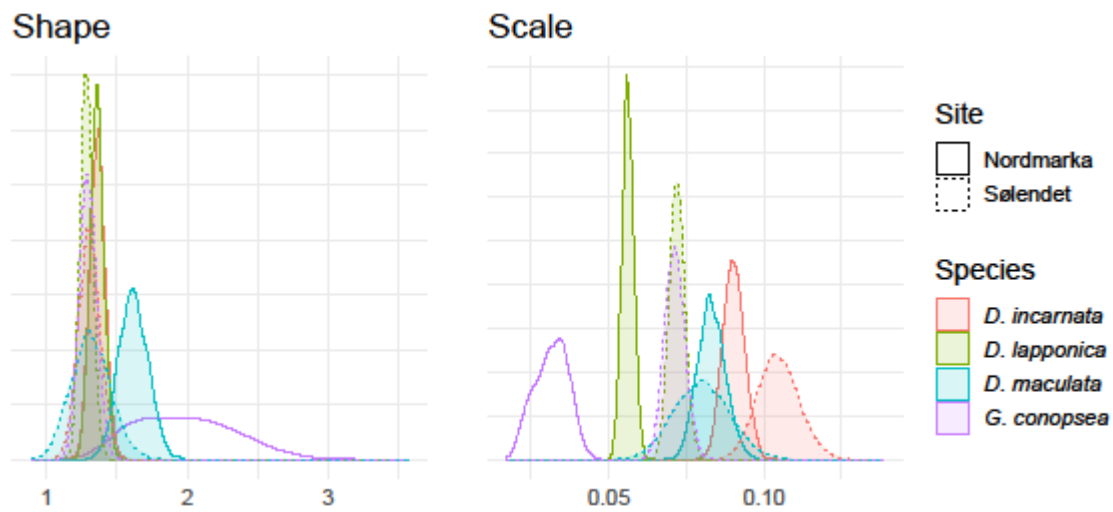


Figure 2. Parameter values from the simple Weibull models with species as a categorical variable.

Left) the shape parameter, Right) the scale parameter. The parameters for *G. conopsea* at Nordmarka are uncertain (see Methods) but are included for comparison. See supplementary information (Fig. S3) for each species separately.

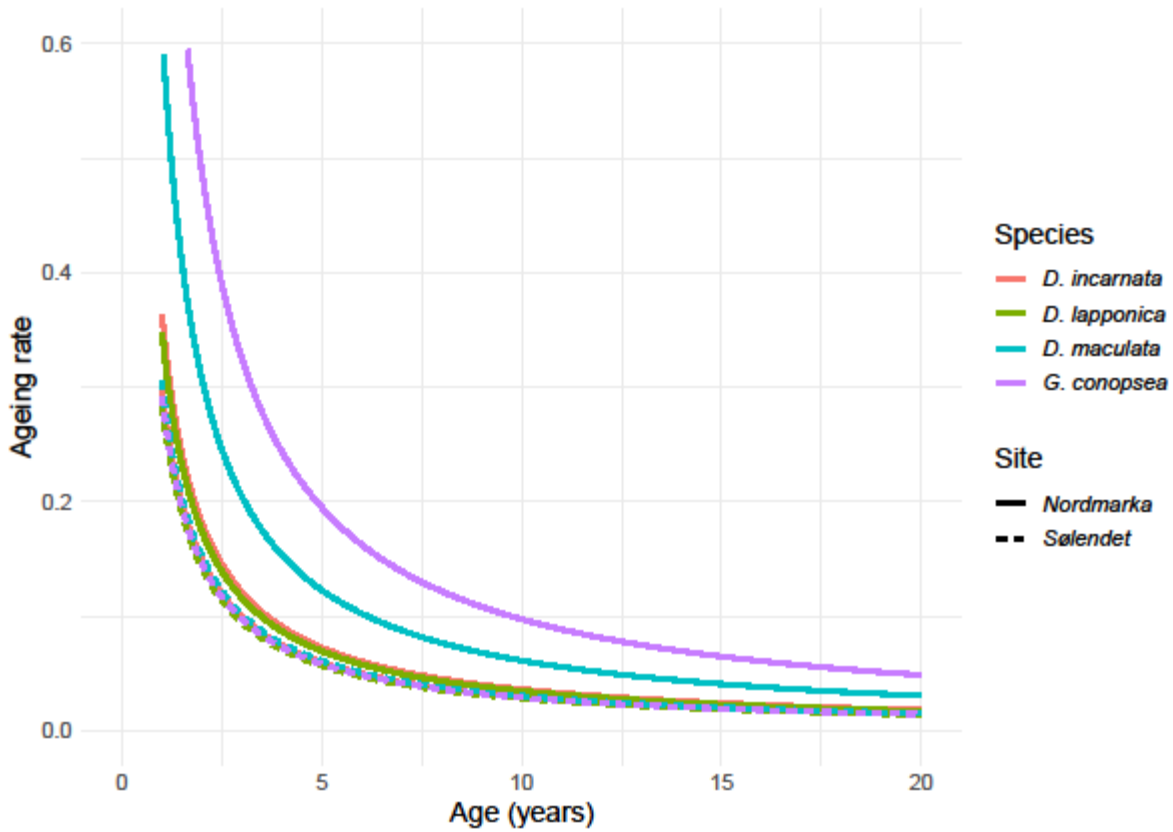


Figure 3. Rates of senescence (ageing rates) for the first 20 years after first reproduction (age = 0-20 years) for all four species at Sølendet and Nordmarka. The age trajectory of *G. conopsea* at Nordmarka is highly uncertain. Notably, at Sølendet, all four species curves are on top of each other and the same is the case at Nordmarka for *D. incarnata* and *D. lapponica*.