

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

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2

3 Abstract

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

23

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

26 INTRODUCTION

27 It has often been assumed that plants do not experience whole-plant senescence, defined as a
28 decrease in individual fitness as an organism grows older (reviewed in (Dahlgren and Roach 2017)).
29 The lack of senescence has been attributed to plants' turnover of organs (e.g., leaves and flowers),
30 as well as varying degrees of clonality and indeterminate growth (Munné-Bosch 2015, Popov et al.
31 2022). From an evolutionary perspective, the potential lack of senescence has been attributed to the
32 absence of an early-life separation of somatic and germ cell lines (Kirkwood 1977, Popov et al.
33 2022), although a clear understanding of the timing of germ-soma separation in plants is lacking
34 (Lanfear 2018).

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

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

47 amongst closely related species (Webb et al. 2002); for example, the genus *Crepis* holds both
48 annuals and perennials, as well as mono- and polycarpic species (Mossberg and Stenberg 2014), so
49 diverse patterns of senescence may not be unexpected within taxa. Conversely, similarity in life-
50 history traits is also common, and it is possible that the degree to which degree species show
51 senescence corresponds to phylogeny (Pujol et al. 2014). Patterns suggesting similar increases in
52 mortality with age have been shown for a few mosses from the Polytrichaceae family (Watson
53 1979), as well as two species of *Lemna* (Barks and Laird 2015, Barks et al. 2018). Signs of
54 senescence have also been identified in several species of the orchid family (Orchidaceae). In
55 *Dactylorhiza lapponica*, mortality significantly increased with age indicating senescence (Dahlgren
56 et al. 2016). Also *Anacamptis morio* may senesce as older individuals made up more than half of
57 the deaths in harsh years in a study by Stroh (2019). However, actuarial senescence does not appear
58 to be a universal trait of the orchid family, as mortality has been documented to be age-independent
59 in *Ophrys sphegodes* (Hutchings 2010). Similarly, a study on twelve *Rhododendron* species, based
60 on botanical garden data, found different patterns across congeners: for some species mortality
61 increased with age, while for others it decreased or appeared unaffected by age (Baden 2020). In
62 summary, despite the evidence of senescence for multiple species within particular taxonomic
63 groups, to what extent general taxonomic patterns occur is unknown.

64 Rates of change in mortality with advancing age may also be affected by environmental conditions,
65 potentially leading to senescence being detected only under certain conditions (Quarles & Roach
66 2019). This has been observed in *Plantago lanceolata*, where the oldest individuals had the highest
67 mortality in years when ecological stress was high (Roach, Ridley & Dudycha 2009; Quarles &
68 Roach 2019; Baden et al. 2020). Similarly, a study on *Fumana procumbens* only detected actuarial
69 senescence in some closely situated populations, suggesting an effect of local environmental
70 conditions (Edelfeldt, Bengtsson & Dahlgren 2019). Moreover, the environment may influence the

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

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

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

90 MATERIALS AND METHODS

91 *Study species and sites*

92 The four species in this study were *Dactylorhiza incarnata*, *D. lapponica*, *D. maculata*, and
93 *Gymnadenia conopsea*. The taxonomy of these orchids is challenging, but in a wide sense they are
94 all found throughout Eurasia (and individually in other parts of the world) (Kühn, Pedersen & Cribb
95 2019). In the study areas the four species grow in rich fen vegetation (Moen, Lyngstad & Øien
96 2012). *D. incarnata* occur in wet (open carpet) vegetation, *D. lapponica* in lawn communities,
97 mainly in open sloping fens, and *D. maculata* and *Gymnadenia* in mire margin communities. All
98 four species are tuberous and are considered non-clonal in the study areas. They have purely
99 vegetative years during which they produce a rosette of several basal leaves; sometimes the rosette
100 is missing due to dormancy or herbivory. In reproductive years, they produce a single inflorescence
101 with multiple flowers that are nectar-producing only in *Gymnadenia*. Flowering occurs in mid-
102 summer (June-July) for *Dactylorhiza* and in mid-late summer (July-August) for *Gymnadenia*. The
103 latter species attracts butterflies and hawkmoths for pollination (Sletvold & Ågren 2010), while the
104 former mainly rely on deceiving bumblebees (Nilsson 1981; Sletvold, Grindeland & Ågren 2010).
105 For *D. lapponica*, actuarial senescence has been documented previously (Dahlgren et al. 2016), but
106 ageing has not been found to influence the probability of flowering or the size of individuals (Moen
107 and Øien 2002).

108 The species were studied within two nature reserves in central Norway: the coastal Nordmarka
109 (63°03'N, 9°05'E), and 145 km further inland, Sølendet (62°40'N, 11°50'E). Both are situated at
110 the transition between the middle boreal and the north boreal vegetation zones (Moen 1999), and
111 experience a short growing season from May to late August. Nordmarka has a more coastal local
112 climate (450 m a.s.l. and annual precipitation 1507 mm), while the inland population at Sølendet
113 experiences a more continental climate (770 m a.s.l. and annual precipitation 670 mm). Both sites
114 are dominated by sloping fen communities that share similar soil properties and management
115 histories (Moen, Lyngstad & Øien 2012). Historically, they have been used for haymaking until

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

118

119 *Data collection*

120 Monitoring began in 1981 in both study areas and demographic data has been collected annually in
 121 early July. Here we use data collected until 2015. Individuals were mapped in permanent plots
 122 (mainly 5 m × 2.5 m) in the year they were first observed flowering, after which they were
 123 monitored irrespective of reproductive status. Each year, presence, flowering status, and number of
 124 flowers were noted. If an individual was absent for three consecutive years, it was presumed that the
 125 individual had terminated in the first year of absence. At Sølendet/Nordmarka a total of 178/481 *D.*
 126 *incarnata*, 711/806 *D. lapponica*, 90/164 *D. maculata*, and 416/65 *G. conopsea* individuals were
 127 recorded over the years, totalling 1295/1516 individuals. The data for *D. lapponica* (up to 2012),
 128 have previously been used to compare mortality age trajectories across sites and in different
 129 mowing treatments (Dahlgren et al. 2016).

130

131 *Data analysis*

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

$$136 \mu(x | \boldsymbol{\beta}) = \lim_{\Delta x \rightarrow 0} \frac{\Pr(x < X < x + \Delta x | X > x, \boldsymbol{\beta})}{\Delta x}, \quad x \geq 0, \quad (1)$$

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

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

$$139 \quad H(x | \boldsymbol{\beta}) = \int_0^x \mu(t | \boldsymbol{\beta}) dt, \quad (2)$$

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

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

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

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

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

176 **RESULTS**

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

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

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

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

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

194 **DISCUSSION**

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

204 explored patterns of senescence in closely related species (Paiha & Laird 2022), nor in the same
205 species in different environments (Quarles & Roach 2019; Baden *et al.* 2020).

206 The fact that the same mortality model (the simple Weibull), with a similar pattern of increasing
207 mortality with age, had the best fit for all site-species combinations is indicative that actuarial
208 senescence and the way it manifests may be a general characteristic for *Dactylorhiza* and closely
209 related genera. Age-related increases in mortality have been found in various other plant species
210 (Silvertown, Franco & Perez-Ishiwara 2001; Barks & Laird 2015; Edelfeldt, Bengtsson & Dahlgren
211 2019), but is not a universal trait of the plant kingdom nor the orchid family (Chapman 1986; Rose,
212 Clarke & Chapman 1998; Hutchings 2010). Thus, our results highlight a possible phylogenetic
213 signal in ageing patterns of plants, and the need for additional studies allowing comparative
214 analyses. To our knowledge, only few studies on the same age-dependent vital rate of plants have
215 been carried out on two or more species within the same genera (e.g., *Lemna* (Barks & Laird 2015;
216 Barks *et al.* 2018; Paiha & Laird 2022), *Cistus* (Munné-Bosch & Lalueza 2007; Müller *et al.* 2014),
217 and *Silene* (Tuomi *et al.* 2013; Pujol, Marrot & Pannell 2014)), but in all these cases ageing patterns
218 were qualitatively similar. In addition, demographic senescence has been identified in closely
219 related species in studies quantifying different vital rates (e.g., *Silene latifolia* being studied in
220 regards to reproduction (Pujol, Marrot & Pannell 2014), while the focus was on mortality for *Silene*
221 *spaldingii* (Tuomi *et al.* 2013)). In contrast, a study on the *Rhododendron* genus found substantial
222 variation among species in mortality age-trajectories, including increasing versus decreasing
223 mortality with age, as well as age-independent mortality (Baden 2020). It should be noted though
224 that this study used data from botanical gardens, and it is unknown if similar patterns would exist in
225 natural populations. Finally, a comparative study on senescence in angiosperms deriving age-based
226 parameters from stage transition matrices documented a phylogenetic influence on ageing rates,
227 although senescence was only identified in phanerophytes, i.e. typically trees (Baudisch *et al.*

228 2013). Our study provides evidence that closely related plants can have very similar age trajectories
229 of mortality. In comparison, ageing patterns are found to be similar among mammals for which the
230 Gompertz-Makeham model invariably provides the best fit to adult age-specific mortality (Lemaître
231 *et al.* 2020; Colchero *et al.* 2021).

232 The whole-plant senescence now demonstrated for several orchid species points towards a need for
233 considering age-related declines in fitness in population viability analyses of the many threatened
234 species of this genus (Swarts & Dixon 2009; Wraith, Norman & Pickering 2020), because
235 accounting for age can affect predictions of extinction risk (Chu & Adler 2014; Edelfeldt *et al.*
236 2019). This would be particularly important for populations in similar contexts as the ones we
237 studied, where plants are at risk of being overgrown over succession after haymaking practices have
238 ceased (Moen & Øien 2002; Damgaard, Moeslund & Wind 2020). This is likely to first lead to
239 reduced recruitment while already established plants survive and experience the age-related
240 declines in fitness, potentially causing overly optimistic predictions by analyses that exclude age.

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

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

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

270

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438

439

440 **Table 1** The four mortality models that the BaSTA package can fit to data on presence/absence of
 441 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>

442

443

444 **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	$\mu_0(x \boldsymbol{\beta}, \boldsymbol{\alpha}, c) = \exp(\alpha_0 + \alpha_1 x) + c + \mu_0(x \boldsymbol{\beta}) \quad (6f) \quad \text{where } \alpha_0 \in \mathbb{R}, \alpha_1 > 0, c > 0.$ <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.

445

446

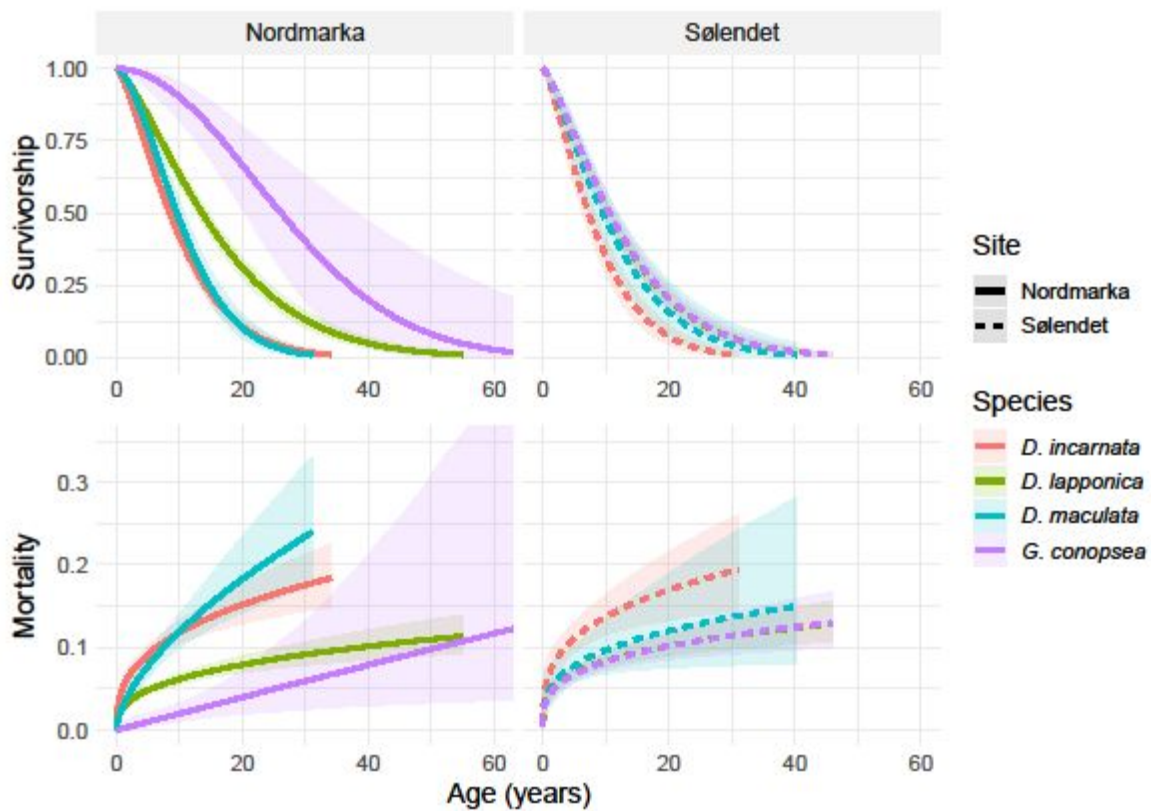
447 **Table 3** The three best-fitting mortality models for *Dactylorhiza incarnata*, *D. lapponica*, *D.*
 448 *maculata*, and *Gymnadenia conopsea* at the two sites Nordmarka (N) and Sølendet (S).

		<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		

449

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

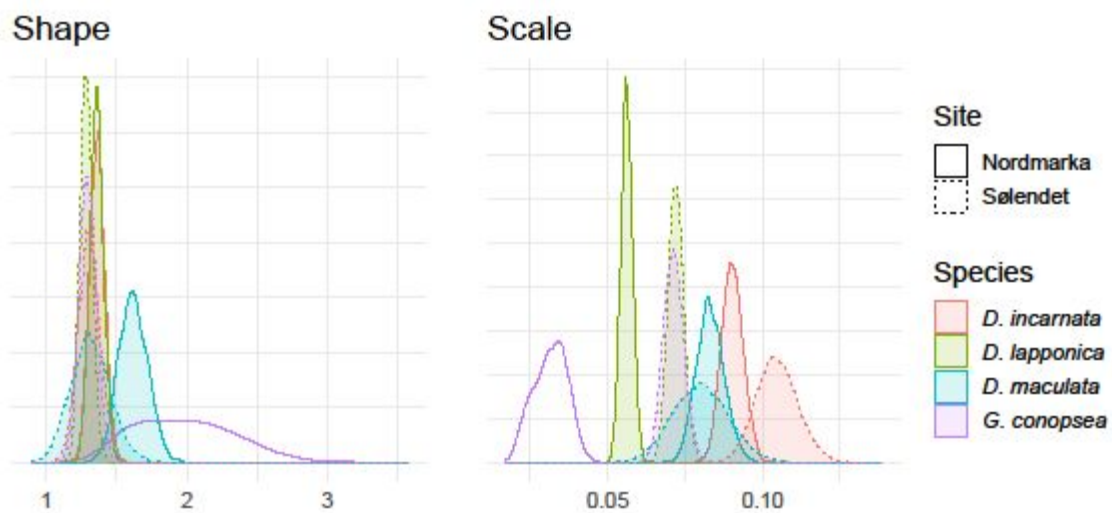
453



454

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

458



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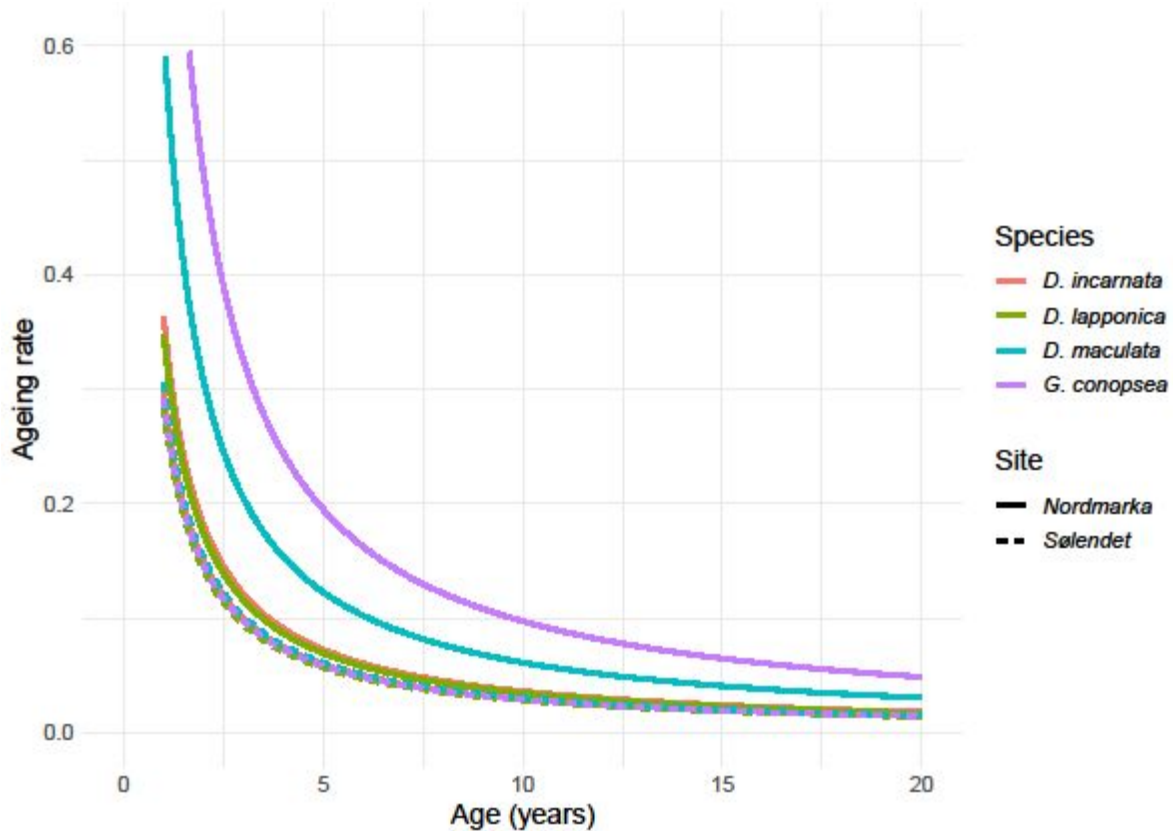
460 **Figure 2.** Parameter values from the simple Weibull models with species as a categorical variable.

461 Left) the shape parameter, Right) the scale parameter. The parameters for *G. conopsea* at

462 Nordmarka are uncertain (see Methods) but are included for comparison. See supplementary

463 information (Fig. S3) for each species separately.

464



465

466 **Figure 3.** Rates of senescence (ageing rates) for the first 20 years after first reproduction (age = 0-
 467 20 years) for all four species at Sølendet and Nordmarka. The age trajectory of *G. conopsea* at
 468 Nordmarka is highly uncertain. Notably, at Sølendet, all four species curves are on top of each other
 469 and the same is the case at Nordmarka for *D. incarnata* and *D. lapponica*.

470

Supporting information for ‘Actuarial senescence progresses similarly across sites and species in four boreal orchids’, submitted to Journal of Ecology 2023

Appendix S1 - BaSTA analysis

To understand age-specific mortality patterns of in the eight species – study area combinations, we used Bayesian survival trajectory analysis and the R package BaSTA (Colchero et al. 2012). BaSTA allows users to explore different functional forms of age-specific mortality when age information is incomplete (Colchero & Clark 2012). The package is based on survival analysis, requiring the definition of a random variable X for ages at death, where a given age is represented by x and the mortality or hazards rate is

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

1

where $\boldsymbol{\beta}$ is a vector of mortality parameters to be estimated. From (1) we calculate the cumulative hazards function as

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

2

From (1) and (2), demographic functions are derived, including the survival function

$$S(x|\boldsymbol{\beta}) = \Pr(X > x | \boldsymbol{\beta}) = e^{-H(x|\boldsymbol{\beta})},$$

3a

the cumulative distribution function of ages at death

$$F(x|\boldsymbol{\beta}) = \Pr(X < x | \boldsymbol{\beta}) = 1 - S(x|\boldsymbol{\beta}),$$

3b

and the probability density function of ages at death

$$f(x|\boldsymbol{\beta}) = \frac{d}{dx}F(x|\boldsymbol{\beta}) = \mu(x|\boldsymbol{\beta})S(x|\boldsymbol{\beta}). \quad 3c$$

Mortality models tested

We explored four different functional forms for the mortality function in (1). First a model with constant mortality

$$\mu_0(x|\boldsymbol{\beta}) = \beta_0, \quad 4a$$

where $\beta_0 > 0$, which assumes that mortality does not change with age. Second, the Gompertz mortality model (Gompertz 1825)

$$\mu_0(x|\boldsymbol{\beta}) = \exp(\beta_0 + \beta_1 x), \quad 4b$$

where $-\infty < \beta_0 < \infty$ is the baseline mortality (i.e. when $x = 0$) and mortality increases exponentially with age at a rate determined by parameter $\beta_1 \geq 0$. Third, the Weibull mortality model (Pinder et al. 1978)

$$\mu_0(x|\boldsymbol{\beta}) = \beta_0 \beta_1 (\beta_1 x)^{\beta_0 - 1}, \quad 4c$$

where $\beta_0 \geq 0$ is the shape parameter and $\beta_1 \geq 0$ is the scale parameter. This model assumes that mortality changes as a power function of age. Finally, the logistic mortality model

$$\mu_0(x|\boldsymbol{\beta}) = \frac{\exp(\beta_0 + \beta_1 x)}{1 + \frac{e^{\beta_0}}{\beta_1} \beta_2 (e^{\beta_1 x} - 1)}, \quad 4d$$

where $-\infty < \beta_0 < \infty$ and $\beta_1, \beta_2 \geq 0$, which is the solution to a Gamma-Gompertz model that incorporates the effect of individual differences in individual “frailty” on mortality, where parameter β_2 is the variance in

heterogeneity (Vaupel et al 1979). High variability in individual frailty results in a mortality plateau at older ages, and when $\beta_2 = 0$, then the model reduces to the Gompertz mortality model.

We extended the models to account for the effect of what is commonly described as age-independent mortality, with the addition of a “Makeham term” such that mortality becomes

$$\mu(x | \boldsymbol{\beta}, c) = c + \mu_0(x | \boldsymbol{\beta}), \quad 5$$

where $c \geq 0$, is commonly described as the “age independent” mortality. Finally, we tested “bathtub” or “U-shaped” models that allow declines in early mortality, given by

$$\mu(x | \boldsymbol{\beta}, \boldsymbol{\alpha}, c) = \exp(\alpha_0 - \alpha_1 x) + c + \mu_0(x | \boldsymbol{\beta}), \quad 6$$

where $-\infty < \alpha_0 < \infty$ and $\alpha_1 \geq 0$ are the parameters that account for the potential decline in early mortality with age, and parameter $c \geq 0$ is as described above.

The fit of the resulting models was compared based on their DIC (Deviance Information Criterion) (Spiegelhalter et al. 2002, Celeux et al. 2006), which is a Bayesian analogue to commonly used information criteria such as the AIC and the BIC. From the best-fitting model we calculated senescence rates (ageing rates) as the first derivative of the logarithm of the mortality function, given by $a_x = \frac{d}{dx} \ln[\mu(x | \dots)]$.

The package BaSTA performs sampling on the parameters and unknown times of birth and death by means of MCMC with Metropolis-Hastings sampling (Metropolis *et al.* 1953, Hastings 1970). For each population and model tested, we ran six parallel chains for 25000 iterations each, with a burn-in sequence of 5001 and thinning every 20 steps. We estimated convergence by means of the potential scale reduction factor (Gelman *et al.* 2013).

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Supporting tables

Table S1 Kullback–Leibler divergences between the ageing rates observed at each site for all species at four ages (1, 5, 10, and 20 years old). A value of 0.5 can be interpreted as no difference, while a value of 1 denotes no similarities between the two sites.

Age (years)	<i>D. incarnata</i>	<i>D. lapponica</i>	<i>D. maculata</i>	<i>G. conopsea</i>
1	0.541	0.534	0.698	0.757
5	0.509	0.507	0.559	0.579
10	0.504	0.503	0.531	0.542
20	0.502	0.502	0.516	0.522

Table S2 Kullback–Leibler divergences between the ageing rates observed for two species at either Nordmarka (N) or Sølendet (S) at four ages (1, 5, 10, and 20 years old). A value of 0.5 can be interpreted as no difference, while a value of 1 denotes no similarities between the two species.

Age (years)	<i>D. inc. vs D. mac. (S)</i>	<i>D. inc. vs D. mac. (N)</i>	<i>D. inc. vs D. lap. (N)</i>
1	0.510	0.642	0.508
5	0.502	0.535	0.502
10	0.501	0.518	0.501
20	0.501	0.509	0.500

Supporting figures

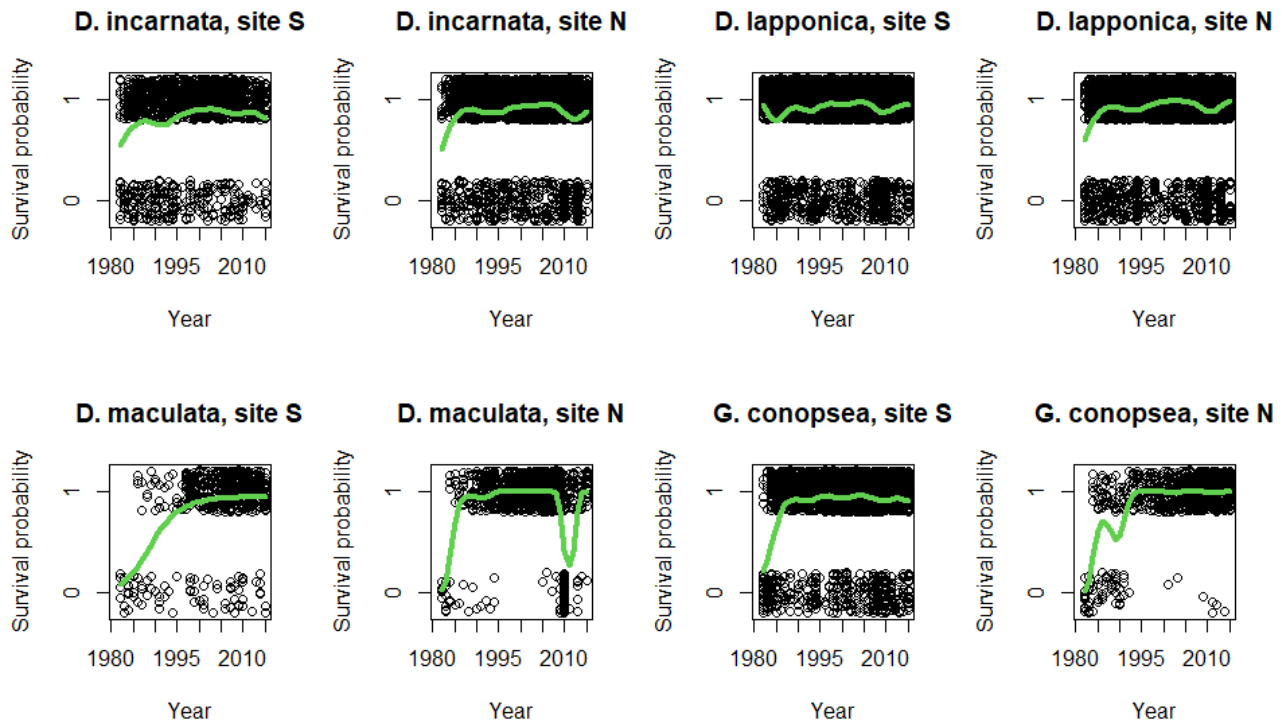


Fig. S1 Survival in the four orchid species at sites S and N over calendar year. The curves represent generalized additive model (gam) fits using the R package 'mgcv', with a logit link function and binomial error distribution (logistic regression). The overall trend was an increase in survival probability over years ($p < 0.0001$, for all data pooled). Number of knots (model complexity) was chosen using generalized cross-validation using default settings in the 'gam' function.

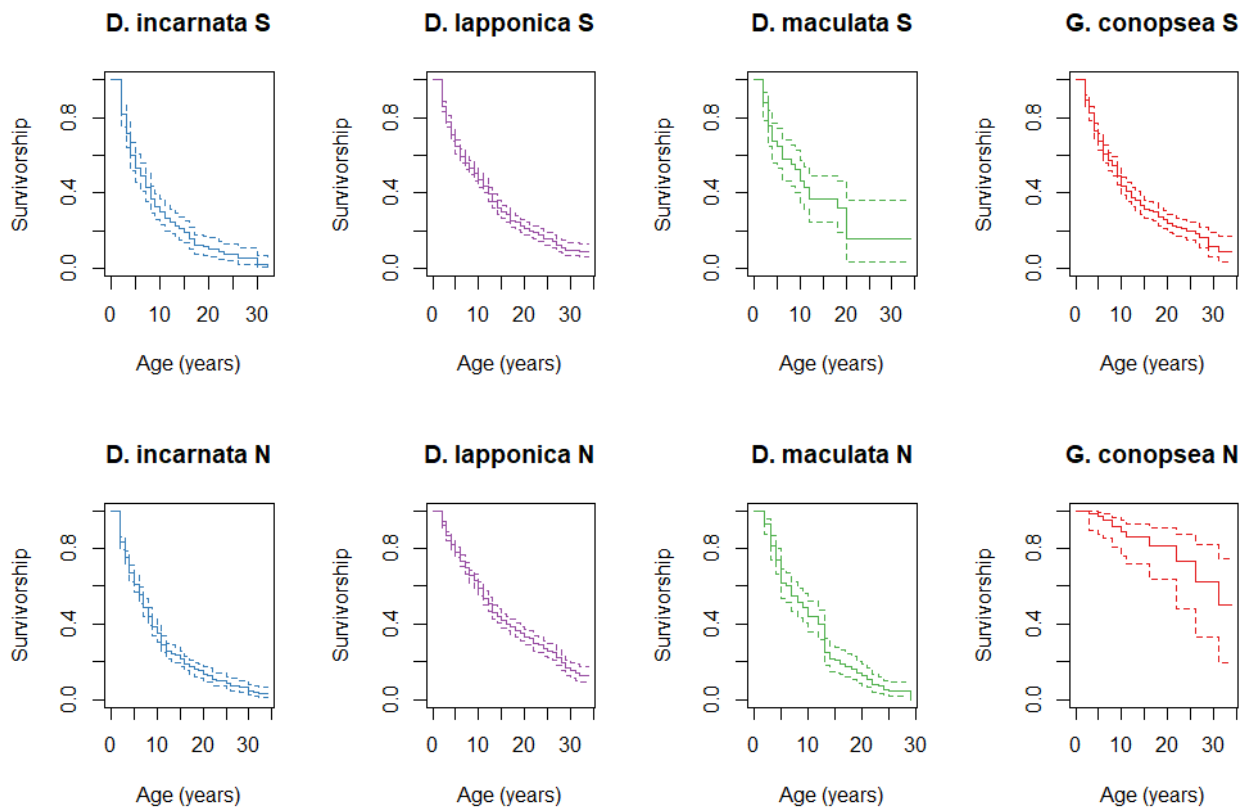


Fig. S2 Kaplan-Meier plots of survivorship (the cumulative proportion of individuals surviving) for the four orchid species at sites S and N, based on the raw data (assuming the first flowering event occurred when individuals were first observed), correspond qualitatively with the BaSTA predictions of differences among species and sites (see Fig. 1).

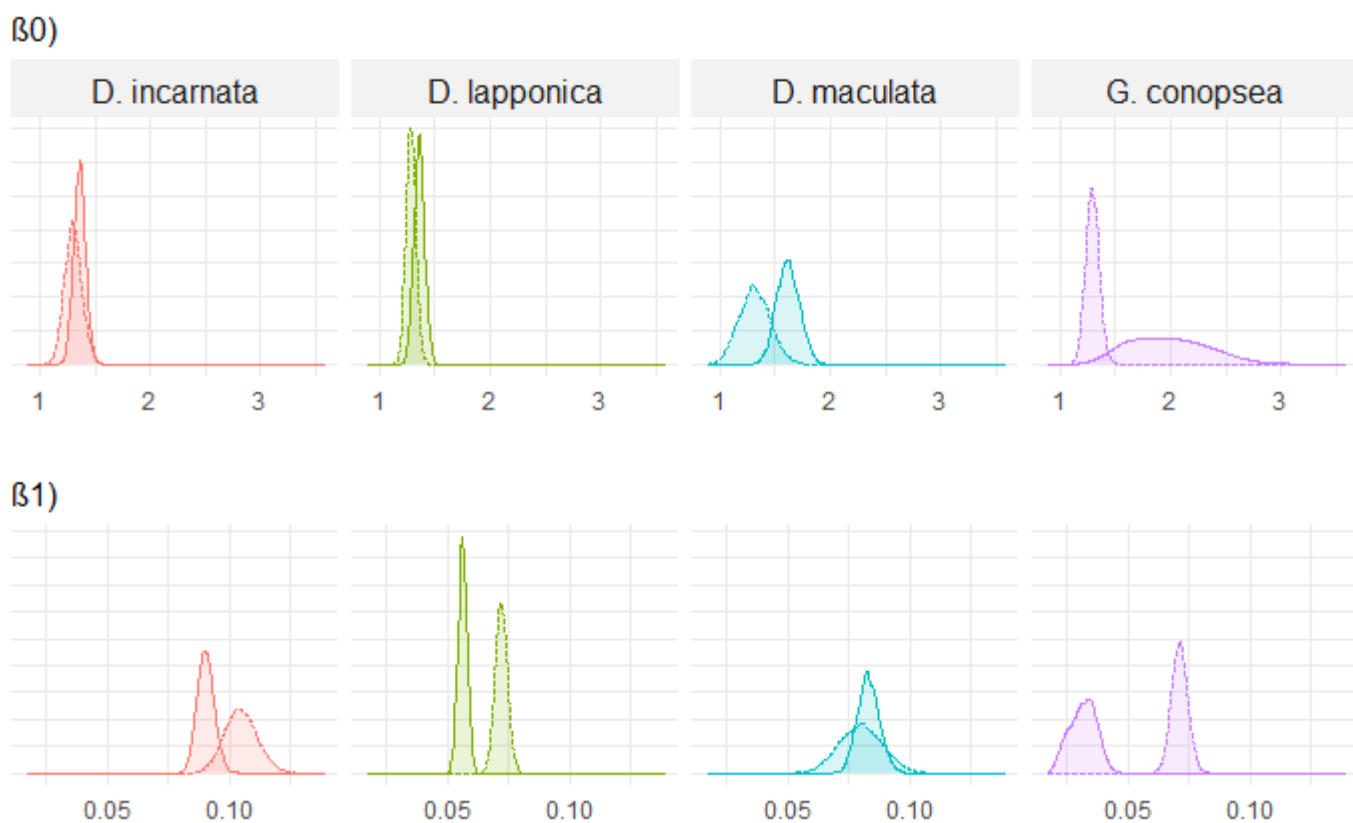


Fig. S3 Parameter values from the simple Weibull models with species as a categorical variable. Top) the shape parameter β_0 , Bottom) the scale parameter β_1 . The parameters for *G. conopsea* at Nordmarka are uncertain (see Methods) but are included for comparison.