

My, how you've grown:
A practical guide to modeling size transitions
for Integral Projection Model (IPM) applications

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Submitted to: *Ecology* (Statistical Report)

Keywords: demography; growth; integral projection model; kurtosis; skewness

Open Research Statement: Data are already published and publicly available, with those items properly cited in this submission. Three data sets are cited as data packages (Miller, 2020; Ochocki *et al.*, 2023; Winfield *et al.*, 2013b). Two other data sets, as well as all of our code, are available in Miller and Ellner (2025).

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1 Abstract

2 Integral Projection Models (IPMs) are widely used for studying continuously size-structured populations.

3 IPMs require a growth sub-model that describes the probability of future size conditional on current size and

4 any covariates. Most IPM studies assume that this distribution is Gaussian, despite calls for non-Gaussian

5 models that accommodate skewness and excess kurtosis. We provide a general workflow for accommodating

6 non-Gaussian growth patterns while retaining important covariates and random effects. Our approach

7 emphasizes visual diagnostics from pilot Gaussian models and quantile-based metrics of skewness and kurtosis

8 that guide selection of a non-Gaussian alternative, if necessary. Across five case studies, skewness and excess

9 kurtosis were common features of growth data and non-Gaussian models consistently generated simulated data

10 that were more consistent with real data than pilot Gaussian models. However, effects of “improved” growth

11 modeling on IPM results were moderate to weak, and differed in direction or magnitude between different

12 outputs from the same model. Using tools not available when IPMs were first developed, it is now possible to fit

13 non-Gaussian models to growth data without sacrificing ecological complexity. Doing so, as guided by careful

14 interrogation of the data, will result in models that better represent the populations for which they are intended.

15 **1 Introduction**

16 Structured demographic models – matrix and integral projection models (MPMs and IPMs) – are powerful
17 tools for data-driven modeling of population and community dynamics. In contrast to MPMs for populations
18 with discrete structure (life stage, age class, etc.), IPMs (Easterling *et al.*, 2000) accommodate populations
19 structured by continuous state variables, most commonly size. A related innovation of the IPM framework
20 is its emphasis on regression-based modeling for parameter estimation, which often carries important
21 advantages for making the most of hard-won data (Ellner *et al.*, 2022).

22 A standard workflow allows ecologists to assemble an IPM from data using familiar regression
23 tools to describe growth, survival, reproduction, and other demographic transitions as functions of size
24 (Coulson, 2012; Ellner *et al.*, 2016). The relative ease of regression analyses, accommodating covariates
25 (e.g., environmental factors, experimental treatments) and complex variance structures (e.g., random effects,
26 correlated errors), has facilitated a growing IPM literature that examines how biotic or abiotic factors affect
27 population dynamics (e.g., Louthan *et al.*, 2022; Ozgul *et al.*, 2010) and explores the consequences of
28 demographic heterogeneity associated with spatial, temporal, and individual variation (e.g., Compagnoni *et al.*,
29 2016; Crone, 2016; Plard *et al.*, 2018). The vital rate regressions (or “sub-models”) are the bridge between
30 the individual-level data and the population-level model and its predictions; it is important to get those right.

31 Compared to other vital rates, growth is special. The survival and reproduction sub-models only
32 need to provide a single predicted value as functions of size (we use “size” as the name for whatever
33 continuous variable defines the population structure). But the growth model must specify the full probability
34 distribution of subsequent size conditional on initial size, defining the growth ‘kernel’ $G(z', z)$ that gives the
35 probability density of future size z' at time $t+1$ conditional on current size z at time t . Whenever survival
36 and reproduction are size-dependent, the entire distribution of size transitions can strongly influence IPM
37 predictions because it governs how frequently size changes are much greater or much lower than average.

38 Easterling et al. 2000 provided the original template for modeling size transitions in IPMs. They
39 first tried simple linear regression, assuming Normally distributed size changes with constant variance.
40 Because the residuals from this regression exhibited non-constant variance, they used a two-step approach
41 to estimate the size-dependence in mean squared residuals (better options soon became available, such
42 as the `lme` function in R). However, even after accounting for non-constant variance, growth data may
43 still be non-Normal. Size transitions are often skewed such that large decreases are more common than
44 large increases (Peterson *et al.*, 2019; Salguero-Gómez & Casper, 2010), or vice versa (Stubberud *et al.*,
45 2019). Size transitions may also exhibit excess kurtosis (“fat tails”), where extreme growth or shrinkage
46 is more common than predicted by the tails of the Normal distribution (Hérault *et al.*, 2011).

47 The observation that the Normal (or Gaussian) distribution may poorly describe size transitions in real
48 organisms has been made before, and several studies have emphasized that alternative distributions should be
49 explored (Easterling *et al.*, 2000; Peterson *et al.*, 2019; Rees *et al.*, 2014; Williams *et al.*, 2012). For example,
50 Peterson et al. 2019 showed that skewness in size transitions could be modeled through beta regression
51 on transformed data (for reasons we describe below, this approach also has some drawbacks), or by fitting
52 a skewed Normal distribution. They showed that incorporating skew could have important consequences for
53 model-based inferences, and concluded that “testing of alternative distributions for growth... [should] become
54 standard in the construction of size-structured population models.” Nonetheless, default use of Gaussian
55 growth distributions (often with non-constant variance) remains the standard practice. The general state-of-
56 the-art in the literature appears to remain where it was 20 or so years ago, using the default Gaussian model
57 without examining critically whether or not it actually describes the data well. We are guilty of this, ourselves.

58 The persistence of Gaussian growth models is understandable. Popular packages such as `lme4` (Bates
59 *et al.*, 2015), `mgcv` (Wood, 2017), and `MCMCglmm` (Hadfield *et al.*, 2010) make it easy to fit growth
60 models with potentially complex fixed- and random-effect structures, but the possible distributions of
61 continuous responses are limited, and default to Gaussian. Abandoning these convenient tools for the

62 sake of more flexible growth modeling means, it may seem, sacrificing the flexibility to model diverse
63 sources of demographic variation, some of which may be the motivation driving the study in the first place.

64 Our goal here is to present and illustrate a practical “recipe” that moves growth modeling past the
65 standards set over 20 years ago. Using software tools that are now readily accessible, ecologists can escape
66 the apparent trade-off between realistically modeling non-Gaussian size transitions and flexibly including
67 multiple covariates and random effects.¹ As with any recipe, users may need to make substitutions or
68 add ingredients to suit their needs. We emphasize graphical diagnostics for developing and evaluating
69 growth models, rather than a process centered on statistical tests or model selection. Through empirical
70 case studies we demonstrate how tools that were nonexistent or not readily available when IPMs first came
71 into use now make it straightforward and relatively easy to identify when the default model is a poor fit
72 to the data, and to then choose and fit a better growth model that is no harder to use in practice. We illustrate
73 our approach by revisiting three published case studies (and three additional case studies in Appendix
74 S3), including examples from our own previous work. In each case, the Gaussian assumption does not
75 stand up to close scrutiny. We illustrate how we could have done better, and the consequences of “doing
76 better” for our ecological inferences. All analyses were carried out in R (R Core Team, 2022) version
77 4.0 or higher and may be reproduced from publicly available code and data (see *Data Availability Statement*).

78 **2 Flexible growth modeling**

79 The modeling process that we suggest runs as follows (Fig. 1):

80 **1. Fit a “pilot” model assuming a Gaussian distribution, but allowing for non-constant variance.** This
81 step is familiar to most IPM users, as it is the start and end of the standard approach. It may include model
82 selection to identify which treatment effects or environmental drivers affect the mean and/or variance of future
83 size. Non-constant variance is often fitted in a two-stage process, first fitting mean growth assuming constant

¹Our statements about software availability are based on what current software reliably delivers in our personal experience, not on what they promise.

84 variance, then doing a regression relating the squared residuals to initial size or the fitted mean of subsequent
85 size. Fitting mean and variance simultaneously as functions of initial size, as can be done with R packages
86 **mgev** and **nmle**, is advantageous when possible because incorrectly assuming constant variance can affect
87 model selection for the mean. We illustrate both one-step and two-step approaches in the case studies below.

88 Allowing non-constant variance removes the need for transforming the data to stabilize growth variance.
89 Transformation may still be useful if it does not create new problems such as making some state-fate
90 relationships highly nonlinear. In particular, log-transformation often reduces or eliminates heteroskedasticity
91 in growth data (Ellner *et al.*, 2016) and also helps avoid eviction at small sizes (Williams *et al.*, 2012).

92 The fitted mean and variance functions should be checked before going any further. If they are
93 perfectly correct, standardized residuals (residuals scaled by the standard deviation) will have zero mean
94 and unit variance overall, and will exhibit no trends in mean or variance with initial size or fitted mean
95 value. However, estimates of the mean and variance functions are somewhat smoothed because of the
96 inescapable bias-variance tradeoff, so scaled residuals will retain some variation in location and scale.
97 Given enough data, statistical tests will detect that variation. So instead, we take for granted the presence
98 of trends and assess their importance by fitting nonparametric spline regression models for residuals (trend
99 in mean) and absolute residuals (trend in variance) as a function of initial size or fitted value. The mean
100 and variance functions can be accepted if the regression curves for the scaled residuals are nearly flat.

101 **2. Use graphical diagnostics to identify if and how the standardized residuals deviate from Gaussian,**
102 **and to choose a more appropriate distribution.** If the Gaussian growth model is valid, the standardized
103 residuals should be Gaussian with zero skewness or excess kurtosis. Growth data may deviate from this in many
104 ways, and the nature of the deviations can guide the search for a better distribution. Tests such as the D'Agostino
105 test of skewness (D'Agostino, 1970) and the Anscombe-Glynn test of kurtosis (Anscombe & Glynn, 1983)
106 can be used to diagnose whether the standardized residuals, in aggregate, deviate from normality (Komsta &

¹⁰⁷ Novomestky, 2015). However, the aggregate distribution may be misleading if skewness or kurtosis vary with
¹⁰⁸ size or other covariates. Skewness changing from positive at small sizes to negative at large sizes might produce
¹⁰⁹ zero overall skewness, but really requires a distribution that can allow both positive and negative skew, such
¹¹⁰ as the skewed Normal or Johnson S_U distributions. Alternatively, growth data may exhibit leptokurtosis (in
¹¹¹ which case the t distribution may be a good choice) or may shift from platykurtosis to leptokurtosis depending
¹¹² on initial size (in which case the power exponential distribution may be a good choice). It is therefore essential
¹¹³ to visualize trends in distribution properties with respect to either initial size, or expected future size for models
¹¹⁴ with multiple covariates. Fig. 1 includes guidance on how the skew and kurtosis properties of the standardized
¹¹⁵ residuals suggest options for an appropriate growth distribution. In our case studies we exploit the many
¹¹⁶ distributions in the **gamlss** R package (Stasinopoulos *et al.*, 2007), but other distribution families can be used.

¹¹⁷ **3. Refit the growth model using the chosen distribution.** In models with multiple covariates and/or random
¹¹⁸ effects, each potentially affecting several distribution parameters, “refit the model” could entail a massive
¹¹⁹ model selection process to identify the “best” non-Gaussian model. With so many options, model uncertainty
¹²⁰ may be overwhelming and over-fitting becomes a significant risk even when precautions against it are taken.

¹²¹ We therefore argue for adopting a more modest goal: remedy the defects evident in the standardized
¹²² residuals of the Gaussian model. This recommendation is based on the finding that parameter estimation
¹²³ using Gaussian regression models is generally robust to deviations from normality of the residuals (Scheipl et al.,
¹²⁴ 2020). That is, the fitted mean of the Gaussian model (as a function of covariates) is probably a
¹²⁵ very good approximation for the fitted mean in the corresponding non-Gaussian model — and if it is
¹²⁶ not, the next step in the modeling process will catch that. The functional forms for skew and kurtosis
¹²⁷ of the non-Gaussian model can be guided by the qualitative features of the graphical diagnostics (e.g.,
¹²⁸ that skewness switches from positive to negative with increasing size). As we demonstrate below, the
¹²⁹ mean and standard deviation functions can often be carried over exactly from the pilot Gaussian model.

130 **4. Evaluate the final growth model through graphical diagnostics comparing simulated and real**
131 **growth data.** A good model will generate simulated data that look like the real data. Again, it is important
132 to inspect the properties of simulated data as a function of initial size, fitted mean, or other covariates
133 rather than examining the aggregate distribution. We again suggest below graphical diagnostics, based
134 mainly on quantiles, that can be used to compare simulated with real growth data. If the simulated data do
135 not correspond well with the real data, alternative or more flexible distribution families should be considered,
136 or more complex functions relating distribution parameters to size and other covariates.

137 **3 How should skewness and kurtosis be measured?**

138 Non-Gaussian growth modeling requires scrutinizing the skewness and kurtosis of standardized residuals,
139 so measurement of these properties warrants attention. The standard measures are based on the third and
140 fourth central moments, respectively, of the distribution: skewness = m_3/σ^3 , excess kurtosis = $m_4/\sigma^4 - 3$
141 where $m_k = \mathbb{E}(X - \bar{X})^k$ is the k^{th} central moment of a random variable X and σ^2 is the variance (second
142 central moment). A Gaussian distribution has zero skewness and zero excess kurtosis.

143 The standard measures are simple and easy to use, but they have poor sampling properties. Because
144 the measures involve high powers of data values, a few outliers can produce very inaccurate estimates. Figure
145 2 shows a simulated example, where the underlying data are samples of 200 values from a t distribution
146 with 8 degrees of freedom, repeated 5000 times; the true skew is 0, and the true excess kurtosis is 1.5.
147 The distance between the largest and smallest estimates (indicated by the dotted red vertical lines), relative
148 to the distance between the 5th and 95th percentiles, shows the broad extent of extreme values that can
149 occur even with a large sample, especially for kurtosis.

150 We therefore recommend nonparametric (NP) measures of skewness and kurtosis that are based on
151 quantiles and thus are less sensitive to a few extreme values. Let q_α denote the α quantile of a distribution
152 or sample (e.g., $q_{0.05}$ is the 5th percentile). For any $0 < \alpha < 0.5$, a quantile-based measure of skewness

153 is given by (McGillivray, 1986)

154

$$\text{NP Skewness} = \frac{q_\alpha + q_{1-\alpha} - 2q_{0.5}}{q_{1-\alpha} - q_\alpha}. \quad (1)$$

155 NP Skewness measures the asymmetry between the tails of the distribution above and below the median.

156 The size of the upper tail can be measured (for any $0 < \alpha < 0.5$) by $\tau_U = q_{1-\alpha} - q_{0.5}$; for $\alpha = 0.05$ this is the

157 difference between the 95th percentile and the median. The lower tail size is $\tau_L = q_{0.5} - q_\alpha$. The definition

158 above is equivalent to

159

$$\text{NP Skewness} = \frac{\tau_U - \tau_L}{(\tau_U + \tau_L)}. \quad (2)$$

160 An NP Skewness of ± 0.2 says that the difference in tail sizes is 20% of their total. The range of possible

161 values is -1 to 1. Both $\alpha = 0.25$ (sometimes called “Kelly’s skewness”) and $\alpha = 0.1$ (“Bowley’s skewness”)

162 are common choices. We used $\alpha = 0.1$.

163 An analogous quantile-based measure of kurtosis (?) is

164

$$\text{NP Kurtosis} = \frac{q_{1-\alpha} - q_\alpha}{q_{0.75} - q_{0.25}}. \quad (3)$$

165 For $\alpha = 0.05$, NP Kurtosis is the difference between the 95th and 5th percentiles, relative to the interquartile

166 range. To facilitate interpretation, we scale NP Kurtosis relative to its value for Gaussian distribution,

167 and subtract 1 so that the value for a Gaussian is zero. We call this “NP Excess Kurtosis”. A value of ± 0.2

168 means that the tails are on average 20% heavier than those of a Gaussian with the same interquartile range.

169 We calculate NP Kurtosis using $\alpha = 0.05$, to focus on the tail edges, but again this is somewhat arbitrary.

170 Figure 2C,D illustrate how, applied to the same simulated samples, the nonparametric measures

171 produce a smaller fraction of highly inaccurate estimates caused by a few extreme values. Also note that,

172 in contrast to the moment-based measures, numerically small values of the nonparametric measures (e.g., 0.1

173 or 0.2) should not be disregarded, because both measures are scaled so that a value of 1 indicates extremely

174 large departures from a Gaussian distribution.

175 Using quantile-based measures carries the added value that quantile regression can be used to estimate
176 how they vary with initial size or expected future size. In the examples below, we use the **qgam** package
177 (Fasiolo *et al.*, 2020) to fit spline quantile regression models, which accommodate nonlinear size-dependence
178 in skewness and kurtosis. One risk of spline regression is that fitted quantiles may be excessively “wiggly”
179 without constraints on their complexity; with realistic amounts of data, we can hope to estimate broad trends
180 in distribution shape, but not fine-scale variation. In the examples below, we limit complexity by fitting
181 splines with $k=4$ basis functions unless otherwise noted. Parametric quantile regression is also an option.

182 For consistency we also use quantile-based measures of mean and standard deviation when comparing
183 real and simulated data, and use quantile regression to visualize their trends. Specifically, following Wan
184 *et al.* (2014),

$$185 \text{NP Mean} = \frac{q_{0.25} + q_{0.5} + q_{0.75}}{3}, \quad \text{NP SD} = \frac{q_{0.75} - q_{0.25}}{1.35}. \quad (4)$$

186 4 Case study: lichen, *Vulpicida pinastri*

187 We begin with a simple example where current size is the only predictor of future size. Growth data for
188 the epiphytic lichen *Vulpicida pinastri* were analyzed first by Shriver et al. 2012 and again by Peterson
189 et al. 2019 in their study of skewed growth distributions. We therefore had an *a priori* expectation of
190 deviation from normality. The data set includes 1,542 inter-annual transitions in thallus area (cm^2) observed
191 from 2004 to 2009 in Kennicott Valley, AK. Shriver et al. 2012 used a mixture distribution that separated
192 “normal growth or shrinkage” from “extreme shrinkage”. We aimed to fit a single growth model that could
193 realistically accommodate both types of size transition without requiring *ad hoc* decisions about which
194 observations of shrinkage were “extreme” or not.

195 With initial size as the only predictor, a convenient way to fit a Gaussian model with non-constant
196 variance is the `gam` function in **mgev** library (Wood, 2017) using the `gaulss` family. Following a bit
197 of model selection, we fit the mean and standard deviation of future size as second-order polynomials

198 of current size², then calculated the scaled residuals from the fitted mean and standard deviation. Here,
199 the first argument to `gam()` is a two-element list that defines the linear predictors for mean and sd:

```
200 # d is the data frame; t0,t1 are initial & final thallus area, respectively  
201 fitGAU <- gam(list(t1~t0 + I(t0^2), ~t0 + I(t0^2)), data=d, family=gaulss())  
202 d$fitted_mean = predict(fitGAU, type="response")[,1]  
203 d$fitted_sd <- 1/predict(fitGAU, type="response")[,2]  
204 d$scaledResids=residuals(fitGAU, type="response")/d$fitted_sd
```

205 The data and fitted mean and standard deviation are shown in Fig. 3A, and the corresponding diagnostic
206 plots are in Fig. 4A,B. Our diagnostic plots are similar to plots made by R's `plot.lm` function, except
207 that we use spline regression to allow data-driven choice of curve smoothness, and use absolute residuals
208 (rather than their square roots) so that the standard deviation of the regression curve is on the same scale
209 as the residuals. The spline curves are not exactly flat – their standard deviations, given above each panel,
210 are positive – but the trends are much too small to be worth fixing.

211 Quantile regression on the scaled residuals generates the skewness and kurtosis diagnostics shown
212 in Fig. 3B. As expected based on previous analyses, the graphical analysis of the standardized residuals
213 indicates negative skew, especially at larger sizes (Fig. 3B). We also find positive excess kurtosis for all sizes.

214 We turned to the Johnson's *S-U* (JSU) distribution for improvement. The JSU is a four-parameter
215 leptokurtic distribution allowing positive or negative skew, with the convenient property that its location
216 and scale parameters `mu` and `sigma` are the mean and standard deviation, respectively, which greatly
217 facilitates the transition from a pilot Gaussian model. JSU is not available in any standard linear or additive
218 modeling packages, to our knowledge. But that is not a barrier because we can write a likelihood function
219 using the `dJSU()` function in the **gamlss.dist** package. Following the best-fit Gaussian model, we defined
220 `mu` and `sigma` of the JSU as quadratic polynomials of initial size and, based on Fig. 3B) we define

²`gam()` is most commonly used to fit smooth splines (`s()`) for predictor variables, but it can also fit parametric regressions.

221 the skewness parameter `nu` as a linear function of size and kurtosis parameter `tau` as a positive constant.
 222 The likelihood function therefore has nine parameters to estimate. We fit the model using the **maxLik**
 223 package³ with starting coefficient values for `mu` and `sigma` based on the pilot Gaussian model:

```

224 ## define function that returns the JSU negative log-likelihood
225 LogLikJSU=function(pars){
226   dJSU(t1, mu=pars[1]+pars[2]*t0+pars[3]*t0^2,
227   sigma=exp(pars[4]+pars[5]*t0+pars[6]*t0^2),
228   nu = pars[7]+pars[8]*t0, tau = exp(pars[9]), log=TRUE)
229 }
230 ## starting parameter values
231 p0<-c(coef(fitGAU)[1:6],0,0,0)
232 ## fit with maxlik, adding some noise to starting values
233 outJSU=maxLik(logLik=LogLikJSU,start=p0*exp(0.2*rnorm(length(p0))),
234 method="BHHH",control=list(iterlim=5000,printLevel=2),finalHessian=FALSE);
  
```

235 Simulating data from the fitted JSU model indicates a compelling improvement over the best Gaussian
 236 model, not only in skewness and kurtosis (Fig. 5C-D) but also the nonparametric standard deviation (5B).
 237 Note, in these data simulation figures Gaussian and non-Gaussian data are offset by an arbitrary amount
 238 to more easily visualize their correspondence to the real data (black lines in Fig. 5).

239 To understand the practical consequences of improved growth modeling, we assembled the remainder
 240 of the lichen IPM following Shriver et al. 2012. The asymptotic population growth rate λ based on Gaussian
 241 growth differs from the JSU growth model by about 1% annual population growth (Table 1), in line with
 242 results of Peterson et al. 2019. However, even this modest difference can lead to biased estimates of extinction

³We chose **maxLik** because it offers the BHHH optimization method, which works well for non-Gaussian likelihoods in our experience.

243 risk from the Gaussian model, particularly over longer time horizons (Fig. 6). We also explored differences in
244 other life history metrics (Table 1) using functions from Hernández *et al.* (2024). For example, the JSU growth
245 model predicts values for mean lifespan, mean lifetime reproductive success, and generation time that are 15–
246 25% lower than the Gaussian growth model. In this case study, properly modeling non-normal size transitions
247 – which was easy to do with a few extra lines of code – can influence ecological inferences, at least based on
248 point estimates. However, Table 1 also provides bias-corrected, bootstrapped confidence intervals (Diciccio &
249 Efron, 1996), and these are heavily overlapping between the Gaussian and JSU models for all life history traits,
250 suggesting that effects of “improved” growth modeling are small relative to our uncertainty in model parameters.

251 One could argue that this example was a convenient “straw man” to disqualify Gaussian growth,
252 because it was recognized by the original and subsequent analysts that size transitions are strongly skewed
253 (Peterson *et al.*, 2019; Shriver *et al.*, 2012). In all remaining case studies, including those in Appendix
254 S3, we re-examine growth data that were modeled as Gaussian in the original published analysis.

255 **5 Case study: tree cholla cactus, *Cylindriopuntia imbricata***

256 The next case study, focused on the tree cholla cactus *Cylindriopuntia imbricata* at the Sevilleta Long-Term
257 Ecological Research site in central New Mexico, adds a new feature to the simple size-dependent regressions
258 in the previous study: random effects associated with temporal (year) and spatial (plot) environmental
259 heterogeneity. This long-term study was initiated in 2004 and different subsets of the data have been analyzed
260 in various IPM studies, all using Gaussian growth kernels (Compagnoni *et al.*, 2016; Czachura & Miller, 2020;
261 Elderd & Miller, 2016; Miller *et al.*, 2009; Ohm & Miller, 2014). In fact, Elderd and Miller 2016 presented
262 a Gaussian growth model as an example of a well fit growth function, based on an overall distribution of
263 residuals that appeared Gaussian and posterior predictive checks (PPCs) of a Bayesian model that suggested
264 consistency between the real data and data simulated from the fitted model (Fig. 4 in (Elderd & Miller,
265 2016)). While PPCs and the associated “Bayesian P-value” are popular diagnostic tools, they are often too

266 conservative (Conn *et al.*, 2018; Zhang, 2014), failing to reject marginally bad models even though they are
267 very effective in rejecting terrible models. The choice of discrepancy function (the statistic used to compare
268 real and simulated data) can also be limiting: in our previous work, we used a discrepancy function focused
269 on variance (the sum of squared residuals), creating a blind spot for poor modeling of higher moments.

270 The data includes 4844 size transition observations from 929 individuals spanning 13 transition years
271 (2004–2018) and 11 spatial replicates (three spatial blocks in years 2004–2008 and eight 30m-by-30m plots
272 in years 2009–2018). The data are provided in Miller (2020). Following previous studies, we quantified
273 size as the natural logarithm of plant volume (cm^3), derived from height and width measurements.

274 We begin growth modeling, as above, with a generalized additive model with the mean and standard
275 deviation of size in year $t+1$ modeled as smooth function of size in year t , with random intercepts for
276 year and plot and assuming normally-distributed residuals:

```
277 # t0 and t1 are initial and final log(volume), respectively  
278 fitGAU <- gam(list(t1 ~ s(t0,k=4) + s(plot,bs="re") + s(year,bs="re"),  
279 ~ s(t0,k=6)), data=caactus, family=gaulss())
```

280 Note that here we fitted the standard deviation function with $k = 6$ basis functions rather than our default
281 of $k = 4$ because, in a preliminary analysis, we found a moderate variance trend in the standardized residuals
282 using $k = 4$, suggesting a need for greater flexibility. With $k = 6$, spline regression detected essentially
283 no trend in the mean of the resulting standardized residuals (Fig. 4C,D).

284 The growth variance is estimated to peak at small to medium sizes (Fig. 3C). The standardized
285 residuals show clear signals of negative skew and positive excess kurtosis across most of the size distribution,
286 but strongest in the middle (Fig. 3D). We therefore need a distribution family allowing negative skew
287 and positive excess kurtosis, both of which may be negligible at some sizes. We first tried Johnson's S_U and
288 then the skewed t distributions, which provided some improvements but there were still visible discrepancies

289 between simulated and real data. We next turned to the SHASH distribution, which allows a greater range
290 of kurtosis for a given amount of skew, and vice versa (?; Appendix S1). This flexibility proved necessary
291 to generate simulated data that compared favorably to the real data, so we proceeded with the SHASH.
292 Conveniently, SHASH is available as an **mgcv** family, allowing for flexible size-dependence in skewness
293 and kurtosis without having to select specific size-dependent functions.

294 Here, the first argument to `gam()` is now a four-element list specifying the linear predictors for
295 the four parameters of the SHASH distribution.

```
296 fit_shash <- gam(list(t1 ~ s(t0,k=4) +  
297   s(plot,bs="re") + s(year_t,bs="re"), # location  
298   ~ s(t0,k=4), # log-scale  
299   ~ s(t0,k=4), # skewness  
300   ~ s(t0,k=4)), # log-kurtosis  
301   data = cactus, family = shash,optimizer = "efs")
```

302 Data simulated from the SHASH model compared favorably to the real data (Appendix S4, Fig. S-1).
303 Similar to the lichen case study, we see that correctly modeling skewness and kurtosis improved estimation
304 of the nonparametric mean and standard deviation (Appendix S4, Fig. S-1A,B), yielding a growth model
305 that is truer to the data.

306 We next explored how improved growth modeling influenced IPM results. The λ values predicted
307 by Gaussian and SHASH growth functions, corresponding to the average plot and year, were nearly
308 identical (Table 1) but we could also leverage structure of the study design to quantify demographic
309 variance associated with temporal and spatial heterogeneity. We used the fitted random effects from
310 the vital rate models to estimate the asymptotic growth rate for each year (λ_t), centered on the average
311 plot, and for each plot (λ_p), centered on the average year. Estimates of λ_t from the Gaussian growth

model were often greater than estimates from the SHASH growth model, particularly in some of the
harshest years (Fig. 7A), and therefore the Gaussian model predicted lower temporal variance in fitness
($SD(\lambda_{t(Gaussian)}) = 0.04$, $SD(\lambda_{t(SHASH)}) = 0.048$). Plot-to-plot variation was more similar between the
two models ($SD(\lambda_{p(Gaussian)}) = 0.0026$, $SD(\lambda_{p(SHASH)}) = 0.0028$), although spatial variation in fitness
was much lower than temporal variation (Fig. 7B). The difference in temporal variance would suggest that
Gaussian growth modeling would predict a higher stochastic growth rate λ_S , because temporal variance has a
negative effect on λ_S . However, the stochastic growth rate from the Gaussian growth model ($\lambda_S = 0.992$) was
nearly identical to that of the SHASH growth model ($\lambda_S = 0.991$). This is likely because temporal fluctuations
in vital rates, which is where the SHASH growth model would make a difference, have a weaker influence
on λ_S than the temporal fluctuations in size structure that they generate (Compagnoni *et al.*, 2016; Ellis
& Crone, 2013). The SHASH and Gaussian growth models predicted small differences in other life history
traits but, as in the lichen case study, these differences were small relative to the uncertainty captured by
bootstrapped confidence intervals (Table 1). Interestingly, the SHASH model had wider uncertainty intervals,
particularly for lifespan and lifetime reproductive output, presumably because the additional parameters
it requires introduce additional sources of uncertainty in these estimates. Thus, in this case study, modeling
non-Gaussian size transitions with a Gaussian growth model may or may not influence IPM results depending
on the target of the analysis, and whether the emphasis is on point estimates or uncertainty intervals.

6 Case study: lady orchid, *Orchis purpurea*

Our final case study examines selection on life history strategies in the lady orchid *Orchis purpurea*. In
a prior study, Miller et al. 2012 analyzed how costs of reproduction (flowering or not in year t) affected
growth from year t to $t+1$. The two growth kernels for flowering and non-flowering were then used in
an IPM to quantify the optimal flowering size that balances the benefits of waiting to flower at larger sizes
against the greater risk of death before flowering. The original study assumed Gaussian size transitions

335 with non-constant variance depending on initial size. Here we re-visit that analysis to derive improved
336 growth kernels. We use this case study to illustrate several new elements and challenges, including modeling
337 skewness and kurtosis as functions of expected future size.

338 The data, originated by Dr. Hans Jacquemyn, come from 368 plants in a Belgian population censused
339 annually from 2003 through 2011. Here we use data only from the “light” habitat in the original study.

340 We used the natural logarithm of total leaf area as the size variable in the IPM.

341 As a variation on software, we fitted the pilot Gaussian model using the `lmer` function in the **lme4**
342 package, as in the original study. We fit three candidate linear models that included fixed effects of size
343 in year t (model 1), additive effects of size and flowering status in year t (model 2), or an interaction between
344 size and flowering (model 3), all including random intercepts for year. The interaction model was strongly
345 favored ($\Delta AIC = 10.5$). Unlike our previous case studies, here we have multiple fixed effects (initial size
346 and flowering status) that may influence the variance of future size. In cases such as this it is convenient
347 to model variance as a function of expected future size, rather than initial size as we did with the lichens
348 and cacti. The expected (or “fitted”) values reflect the combined influence of all fixed and random effects,
349 and therefore implicitly account for multiple sources of variation in the variance.

350 Models where error variance is a function of fitted values cannot be fitted directly with `lme4` (nor in
351 the **mgcv** functions for generalized additive models). But it can still be done with `lmer` through an iterative
352 re-weighting approach, as follows. In `lmer`, weights w_i can be used to indicate that the observations y_i
353 have error variance proportional to $1/w_i^2$. The iterative steps are as follows, and code that executes these
354 steps is in `orchid_growth_modeling.R`.

- 355 1. Fit the expected value assuming Gaussian-distributed residuals with constant variance.
- 356 2. Fit the standard deviation of the residuals as a function of the corresponding fitted value.
- 357 3. Re-fit the model, with weights equal to the inverse of the standard deviation estimated in step 2.

358 We iterated steps 2 and 3 until the root mean square change in weights was below 10^{-6} . This is not elegant,
359 but it works and converges quickly. In step 2, we modeled the log of the standard deviation (because standard
360 deviations cannot be negative) as a quadratic polynomial in the fitted mean. In exploratory analyses we found
361 that the quadratic term was necessary to fit the standard deviation. We did this for all candidate models and,
362 for a fair AIC comparison, we then re-fit all candidate models with the weights estimated from the top model.

363 The updated model selection continued to favor the size \times flowering interaction model (3), but now
364 with a weaker improvement over the next-best model ($\Delta AIC = 6.7$). The fitted mean (a function of initial
365 size and flowering status) and fitted standard deviation (a function of the fitted mean) are shown in Fig.
366 3E. Spline regression found no trend in the mean of the resulting standardized residuals, and only small
367 variation in the variance (Fig. 4E,F).

368 The best Gaussian model indicated a growth cost associated with flowering at the start of the census
369 interval and a decline in growth variance with increasing expected values (Fig. 3E). The standardized
370 residuals indicated negative skewness (10–20% difference in tail weight) and excess kurtosis (10–40% fatter
371 than Gaussian) across much of the size distribution but both negligible at large expected sizes (Fig. 3F).

372 As possible improvements, we explored the skewed *t* and JSU distributions, both leptokurtic
373 distributions with flexible skewness. Based on comparisons between real and simulated data we were
374 happier with the skewed *t*, which we fit with a custom likelihood function similar to the JSU growth model
375 for the lichen data. However, rather than re-fitting all parameters of the skewed *t* model, as we did with
376 the lichen JSU, we built a “hybrid” likelihood function that uses the fitted mean and standard deviation from
377 the best Gaussian model, and estimates parameters that control skewness and kurtosis as linear functions
378 of expected future size. This is easy because the **gamlss.dist** package provides a parameterization of the
379 skewed *t* in which the location parameter μ is the mean and scale parameter σ is the standard deviation
380 (Rigby *et al.*, 2019). The hybrid likelihood looks like this:

```

381 ## GAU_fitted and GAU_sd are mean & standard deviation from the best Gaussian.
382 SSTLogLik=function(pars){
383   dSST(log_area_t1,
384   mu=GAU_fitted, sigma=GAU_sd,
385   nu = exp(pars[1] + pars[2]*GAU_fitted),
386   tau = exp(pars[3] + pars[4]*GAU_fitted)+2, log=TRUE)
387 }
388 p0<-c(0,0,0,0) ## default starting parameters
389 SSTout=maxLik(logLik=SSTLogLik,start=p0) ## fit with maxLik

```

390 Based on diagnostics of the standardized residuals, parameters that control skewness and kurtosis are defined as
391 linear functions of the mean (note that the `tau` parameter uses a $\log(x-2)$ link function). This approach relies
392 on the robustness of fitted Gaussian models to deviations from normality, which implies that the fitted mean
393 and variance from a Gaussian model are good approximations for the mean and variance of the corresponding
394 non-Gaussian model. If one is skeptical of this approach, it is possible to simultaneously re-fit all parameters of
395 the skewed t . However, recall that unlike the lichen case study, the pilot Gaussian model here includes random
396 year effects, and the expected values getting passed into `dSST` account for this source of variation. Estimating
397 random effects “from scratch” with a custom likelihood model is possible (we provide guidance on doing this
398 with a “shrinkage” approach, in Appendix S2), but generally should not be necessary. Instead, a key advantage
399 of the hybrid approach is retention of the fitted random effects and associated variance components, which get
400 shuttled from the Gaussian model into the non-Gaussian model without any fuss (though it was critical to use
401 a parameterization of the skewed t for which `mu` is the mean and `sigma` is the standard deviation). And, if this
402 approach does not “work” (i.e., deviations from normality biased the fitted values of the Gaussian model) one
403 would quickly find out when comparing simulated with real data. In this case, size transition data simulated

404 from this model corresponded favorably to the real data, much better than the pilot Gaussian model, including
405 improvements in the standard deviation, skewness, and kurtosis of future size (Appendix S4, Fig. S-2).

406 Finally, we used the improved growth model to revisit key results of the original study. Miller et
407 al. (2012) used the orchid IPM to estimate the evolutionarily stable strategy (ESS) as the mean size at
408 flowering that maximizes lifetime reproductive success (R_0), given the constraint that flowering when
409 small reduces growth and thus elevates mortality risk. Repeating that analysis here, we found that improved
410 growth modeling has virtually no influence on predictions for optimal life history strategies (Fig. 8). ESS
411 flowering sizes were nearly identical between IPMs with Gaussian vs skewed t growth models, and both
412 aligned well with the observed mean flowering size (dashed vertical line in Fig. 8). Similarly, there were
413 very small differences between growth functions in other metrics of orchid life history and, again, these
414 differences were overwhelmed by uncertainty associated with parameter estimation (Table 1).

415 7 Discussion

416 Much of the appeal of IPMs has stemmed from their embrace of continuous size structure through regression-
417 based approaches, and the potentially complex fixed- and random-effect structures that those approaches allow.
418 Using familiar statistical tools and with relatively few parameters to estimate, IPM users can incorporate
419 important sources of variation in demography and interrogate their influence on ecological and evolutionary
420 dynamics. With this opportunity comes the burden of getting it right: an IPM is only as good as the statistical
421 sub-models for the underlying data. The growth sub-model is the trickiest part because it defines a distribution
422 of future size conditional on current size. Distributions have many properties – “moments” – and a good
423 growth model should recapitulate the properties of real size transitions. The default assumption of Normally
424 distributed size transitions, employed overwhelmingly across 20+ years of IPM studies, is an arbitrary historical
425 precedent. In our case studies and, we suspect, more broadly, skewness and excess kurtosis were common

426 features of size transitions. Our most important message is that the assumption of normally-distributed size
427 transitions can easily be abandoned, and a more inquisitive process of growth modeling should take its place.

428 We have attempted to lay out what that process should look like, emphasizing visual diagnostics
429 to characterize how data deviate from Gaussian. One implication of relying on visual diagnostics is that
430 goodness of fit is in the eye of the beholder. This empowers IPM users to make informed choices, but it is not
431 very prescriptive; we have not suggested any hard rules for choosing among distributions, only that a good
432 growth model should generate data that look like the real thing. Alternatively, model selection could be used
433 to identify best-fitting growth distributions and best-fitting functions for higher moments. However, model
434 selection among growth distributions with 3-5 parameters, each of which may be functions of multiple state
435 variables or fitted values, can quickly explode in complexity, and we are not convinced it is worth the trouble.

436 Our work follows the important contribution of Peterson et al. 2019, who were similarly motivated
437 by inadequacy of the Gaussian model but arrived at different recommendations. These authors developed
438 a creative approach in which size data are transformed onto a [0,1] scale and size transitions on that scale
439 are modeled using beta regression. The beta distribution can accommodate positive, negative, or zero skew,
440 potentially varying with size, so the Peterson et al. approach is a flexible option for skewed growth data.
441 However, beta regression also has some limitations: common beta regression packages do not fit random
442 effects (e.g., **betareg** (Cribari-Neto & Zeileis, 2010)) or do not do so reliably (in our experience **gamlss**
443 regressions with random effects are numerically unstable); and the two-parameter beta distribution does not
444 allow skewness and kurtosis to be fitted independently. Additionally, the initial transformation onto [0,1] scale
445 requires estimating extreme quantiles of the growth distribution (e.g., 0.01 and 0.99) as a function of initial size.
446 In our experience those quantile estimates can be very sensitive to how size-dependence is modeled, and model
447 selection is challenging for extreme quantiles where data are (by definition) very sparse. Rather than picking
448 one distribution as a new default, users can leverage the vast arsenal of continuous probability distributions
449 – all at one's fingertips with a few lines of code – so that the data and their particular deviations from

450 normality can guide the choice of a better distribution. It is also possible to use mixtures of multiple growth
451 distributions, as done by Shriver et al. 2012 to model “normal” and “extreme” types of lichen shrinkage. In
452 re-analyzing that data set, we found that a single, flexible distribution (Johnson’s *S-U*) could recapitulate the
453 observed size transitions, but there may be other cases where mixture distributions are preferable or necessary.

454 In all of our case studies, non-Gaussian growth models always yielded more satisfying fits to size
455 transition data than the Gaussian models published in those papers. However, to our relief, none of these
456 re-analyses yielded a “gotcha” result that overturned results of the original study. In fact, in this small
457 sampling of case studies, improved growth modeling had weak to modest effects on IPM results, similar in
458 magnitude to the results of Peterson *et al.* (2019), and for most species and life history metrics these effects
459 were overwhelmed by the uncertainty associated with parameter estimation (Table 1). For some case studies,
460 one might argue that non-Gaussian modeling was not worth the trouble – only it was almost no trouble
461 at all, and we could not have known whether or not a non-Gaussian model would have made a difference
462 before fitting it. Even where Gaussian and improved growth models differed in IPM results, we do not know
463 “true” values to compare them against, only that one describes the data better than another, and a closer
464 match to the data does not necessarily translate to better predictive ability due to the bias-variance trade-off.

465 We caution against taking too much comfort in weak effects of “improved” growth modeling; in
466 other scenarios the choice of growth distribution could be more consequential. We focused on life history
467 metrics such as mean lifespan and mean lifetime reproductive success (Table 1). It is possible that higher
468 moments of those traits (e.g., variance or skewness of lifespan and lifetime reproduction) are more sensitive
469 to the tails of the growth distribution. It is also worth noting that most of our case studies focused on
470 perennial life histories (perennial plants and lichens) characterized by relatively slow growth, heavy losses
471 during recruitment, and high survival once established, and these species all had mean lifespans between
472 one and six years and generation times on the order of decades. Life histories such as these may be relatively
473 robust to subtle features of the growth kernel. In Appendix S3 we present three additional case studies

474 that broaden our life history coverage, including pike (*Esox lucius*), a fish with a generation time of four
475 to five years and creosotebush (*Larrea tridentata*), a desert shrub that is virtually immortal once established.
476 Life history metrics from these “fast” and “slow” populations were no more sensitive to improved growth
477 modeling than those of the perennial plants and lichens (Table 1). More systematic comparative analyses
478 may provide insight into which types of species and life histories are more likely to exhibit strong skewness
479 and kurtosis, and which demographic quantities are more or less sensitive to these features of size transition.

480 Our case studies illustrate a diversity of software packages and computational approaches, to reflect the
481 diversity of preferences and habits that the community of IPM analysts bring to their own problems. We like
482 spline generalized additive models (gams) for their flexibility and for **mgcv**’s numerous options for distribution
483 families and overall speed and reliability. However, there are some applications for which classical parametric
484 regression would be preferable because the coefficients carry biological meaning. For example, regression
485 coefficients may be targets of natural selection (Rees & Ellner, 2016) and may combine to influence traits
486 of interest such as the expected size at flowering (e.g. in Fig. 8A), a function of the intercept and slope of the
487 size-dependent flowering function (Metcalf *et al.*, 2003). Some potentially useful distributions are not available
488 in linear modeling software packages, but that should not be a barrier to their use: as in several of our case
489 studies, custom likelihood functions allow non-Gaussian models without sacrificing the complex, multi-level
490 features that one might be accustomed to fitting in **lme4**, for example. Bayesian analysis may further broaden
491 the options for non-Gaussian candidate distributions and may help estimate hard-to-fit parameters through the
492 brute force of sampling algorithms. Bayesian analysis also provides a natural way to propagate uncertainty from
493 vital rate sub-models to full model predictions (Elderd & Miller, 2016), as an alternative to our bootstrapping
494 approach. However, as of this writing, most of the non-Gaussian distributions that we have discussed are
495 not available in popular Bayesian software packages such as Stan or JAGS. While user-defined distributions
496 can always be coded from scratch, this may be a significant technical barrier for many IPM analysts.

497 From the outset there have been concerns about “how well these methods [IPM growth kernels]
498 can deal with different patterns of growth, stasis, and shrinkage” (Morris & Doak, 2002, p. 200), compared
499 to “binning” methods that use observed transition frequencies between user-defined size classes as the
500 transition probabilities in a (possibly large) matrix model (Doak *et al.*, 2021). The non-Gaussian models that
501 we have considered here are not a panacea. For example, none of them allow bimodal growth, such as might
502 occur if herbivore- or pathogen-attached individuals experience rapid tissue loss. When the shape of the
503 growth distribution is nearly the same for all initial sizes, a nonparametric IPM growth kernel can be defined
504 from a kernel density estimate for scaled residuals (Ellner *et al.*, 2016, p. 288). Outside that special situation,
505 nonparametric approaches require choosing multiple smoothing parameters, which is very challenging.
506 We are currently exploring whether “targeted learning” approaches developed for causal inference (van der
507 Laan & Rose, 2011) can be used to circumvent smoothing parameter selection. Targeted learning starts
508 with a pilot model and updates it iteratively to achieve unbiased estimates and valid confidence intervals for
509 a particular “target” quantity, such as λ or mean lifespan. Preliminary results suggest that targeted learning
510 with a deliberately under-smoothed pilot model works well for complex growth patterns (Zhou & Hooker,
511 2024). But nonparametric methods are data-hungry, so when departures from Gaussian are quantitative
512 rather than qualitative, parametric modeling as developed here will make more efficient use of limited data.

513 Conclusion

514 Gaussian-distributed size transitions are probably the exception in nature, not the rule, yet two decades
515 of IPM studies have relied overwhelmingly on Gaussian growth models. Using tools not available when
516 IPMs were first developed, it should often be possible now to make major improvements over a Gaussian
517 model, without worrying about finding the “best” alternative. By generating predicted size transitions
518 that are truer to the data, IPM analysts can narrow the gap between model and nature.

519 **Acknowledgements:** This research was supported by US NSF grants DEB-1933497 to SPE and
520 DEB-1754468, 2208857, and 2225027 to TEXM. The Sevilleta LTER (source of the cactus and creosote
521 case studies) is supported by DEB-1655499 and DEB-1748133. Giles Hooker gave us the very good
522 idea to use quantile regression instead of binning to estimate trends in skewness and kurtosis. Ali Campbell
523 and Jacob Moutouama provided helpful discussion and comments on the manuscript.

524 **Authorship statement:** All authors discussed all aspects of the research and contributed to developing
525 methods, analyzing data, and writing and revising the paper.

526 **Conflict of interest statement:** The authors have none to declare.

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644 Table 1. Life history attributes derived from IPM kernels that included Gaussian or “improved” growth
 645 sub-models for six case studies. The improved distributions were JSU (lichen, creosote), SHASH (cactus,
 646 pike, coral), and skewed t (orchid). Pike, creosote and coral case studies are presented in Appendix S3. The
 647 original coral case study assumed an open population with constant recruitment from a large source region,
 648 so some life history attributes cannot be computed from the published model. Values in parenthesis are 95%
 649 bootstrap confidence intervals, specifically the bias-corrected (BC) bootstrap confidence intervals Diciccio
 650 & Efron (1996). Table can be reproduced from scripts `cross spp.growth.R`, `Vulpicida.boot.R`,
 651 `Akumal.corals.boot.R`.

Table 1

Species	Growth model	λ	Lifespan	Lifetime reproductive output	Age at reproduction	Generation time
Lichen (<i>V. pinastri</i>)	Gaussian	1.01 (0.99, 1.04)	6.4 (3.6, 11.1)	1.4 (0.5, 3.1)	6.5 (5.7, 7.3)	40.8 (30.5, 57.4)
	Improved	1.00 (0.98, 1.03)	5.4 (3.1, 9.7)	1 (0.4, 2.4)	6.4 (5.4, 7.3)	36.6 (27.5, 48.6)
Cactus (<i>C. imbricata</i>)	Gaussian	0.994 (0.99, 0.996)	6.11 (3.66, 8.63)	21.8 (8.27, 49.4)	17.6 (1.75, 22.7)	189 (131, 266)
	Improved	0.993 (0.991, 0.998)	5.38 (3.34, 16.3)	13.4 (5.72, 251)	20.3 (1.21, 22.2)	179 (133, 298)
Orchid (<i>O. purpurea</i>)	Gaussian	1.09 (1.08, 1.1)	1.08 (1.06, 1.11)	20.0 (12.6, 31.0)	5.07 (4.78, 5.31)	104 (73.1, 150)
	Improved	1.09 (1.08, 1.1)	1.08 (1.06, 1.1)	19.3 (12.0, 29.9)	5.03 (4.75, 5.3)	100.7 (71.0, 145.0)
Pike (<i>E. Lucius</i>)	Gaussian	1.62 (1.35, 1.89)	1.2 (1.09, 1.35)	5.75 (2.9, 9.7)	1.09 (1.03, 1.18)	4.96 (4.26, 5.84)
	Improved	1.62 (1.35, 1.88)	1.2 (1.09, 1.35)	5.76 (2.91, 9.73)	1.09 (1.03, 1.18)	4.94 (4.30, 5.84)
Creosote (<i>L. tridentata</i>)	Gaussian	1.033 (1.029, 1.04)	4.52×10^6 (2.14×10^5 , 1.82×10^8)	3.19×10^5 (1.27 × 10^4 , 1.24×10^7)	32.7 (29.2, 36.0)	5.27×10^6 (2.50 × 10^5 , 1.95×10^8)
	Improved	1.034 (1.03, 1.04)	3.26×10^5 (1.98×10^3 , 1.66×10^7)	2.31×10^4 (5.83 × 10^2 , 1.27×10^6)	32.8 (29.3, 36.0)	3.7×10^5 (2.63 × 10^3 , 1.93×10^7)
Coral (<i>G. ventalina</i>)	Gaussian	—	17.3 (11.9, 24.3)	—	10.5 (9.3, 11.8)	31.6 (28.3, 36.7)
	Improved	—	17.5 (12.1, 24.3)	—	10.7 (9.4, 12.2)	30.9 (27.4, 35.3)

652 8 Figure Legends

653 **Figure 1** Recommended steps in growth modeling (left) and guide to common non-Gaussian distributions
654 of size x for $x \in \mathbb{R}$ that can accommodate different combinations of skewness and kurtosis (right). All
655 of these distributions (often including multiple versions or parameterizations of each) are available in the R
656 package **gamlss.dist**, except for the skewed generalized t , which is available in the package **sgt** (Davis, 2015).

657 **Figure 2** Histograms of skewness and kurtosis estimates using moment-based definitions (top two panels),
658 compared with the nonparametric measures based on quantiles (bottom two panels). Note the very large
659 differences in scale. Histograms are based on 5000 replicate draws of a sample of 200 independent values,
660 from a t distribution with 8 degrees of freedom. Dotted red vertical lines mark the minimum and maximum
661 of sample estimates, and dashed blue lines show the 5th and 95th percentiles. The true value is indicated
662 by a black dot on the x -axis. Figure drawn by script `NPmoments.R`

663 **Figure 3** Best Gaussian models and diagnostics of standardized residuals for lichen (*Vulpicida pinastri*)
664 **A,B**, cactus *Cylindriopuntia imbricata* **C,D**, and orchid *Orchis purpurea* **E,F** case studies. **A,C**, fitted
665 mean (red) and standard deviation (blue) of size at time $t+1$ conditional on initial size at time t . **E**, fitted
666 means for plants that were vegetative (solid line) or flowering (dashed line) at the start of the census interval
667 and standard deviation as a function of the fitted mean (inset). **B,D,F** Quantile regressions of scaled residuals
668 (lines show 5%, 10%, 25%, 50%, 75%, 90%, and 95% quantiles) and non-parametric measures of skewness
669 (blue) and excess kurtosis (red) derived from them. In **B,D** scaled residuals are shown with respect to initial
670 size and in **F** they are shown with respect to fitted values. Figure made by script `crosspp.growth.R`.

671 **Figure 4** Diagnostic plot for trends in the mean (left column) or variance (right column) of scaled residuals
672 from a pilot Gaussian model, for the lichen (*Vulpicida pinastri*) **A,B**, cactus *Cylindriopuntia imbricata* **C,D**,
673 and orchid *Orchis purpurea* **E,F** case studies. In **A,C,E** the standardized residuals are plotted, and in **B,D,F**
674 the absolute values of standardized residuals, as functions of fitted mean subsequent size values. The solid

675 curves are cubic splines (R function `smooth.spline`) fitted by generalized cross-validation with a modest
676 over-penalization of model degrees of freedom to prevent overfitting (`penalty=1.4` as recommended by
677 Gu (2013)). The numbers appearing above each panel are the standard deviation of the values on the spline
678 regression curve, evaluated at all of the fitted values. Figure made by script `cross spp diagnose pilot.R`.

679 **Figure 5** Comparisons among real lichen data and data simulated from Gaussian and JSU growth models
680 for NP mean, NP standard deviation, NP skewness, and NP excess kurtosis of future size conditional on
681 current size. Colored lines show 100 simulated data sets from the fitted Gaussian (red) or JSU (blue) growth
682 models. Thick black line shows the real data. Gaussian and JSU data are offset by one unit and the real data
683 line is duplicated with a one-unit offset for ease of visualization. Figure made by script `Vuplicida_IPMs.R`.

684 **Figure 6** Extinction risk estimated from individual-based simulation of IPMs based on Gaussian and
685 Johnson's S-U (JSU) growth distributions. Figure made by script `Vuplicida_IPMs.R`.

686 **Figure 7** Temporal (A) and spatial (B) heterogeneity in fitness for the tree cholla cactus (*Cylindropuntia*
687 *imbricata*) predicted by IPMs using Gaussian or SHASH growth models. Figure made by script
688 `cactus_growth_modeling_qgam.R`.

689 **Figure 8** Orchid life history results from IPMs using Gaussian or skewed t growth models. Lifetime
690 reproductive success (R_0) is shown as a function of mean size of flowering. Dashed vertical line shows
691 the observed mean flowering size.

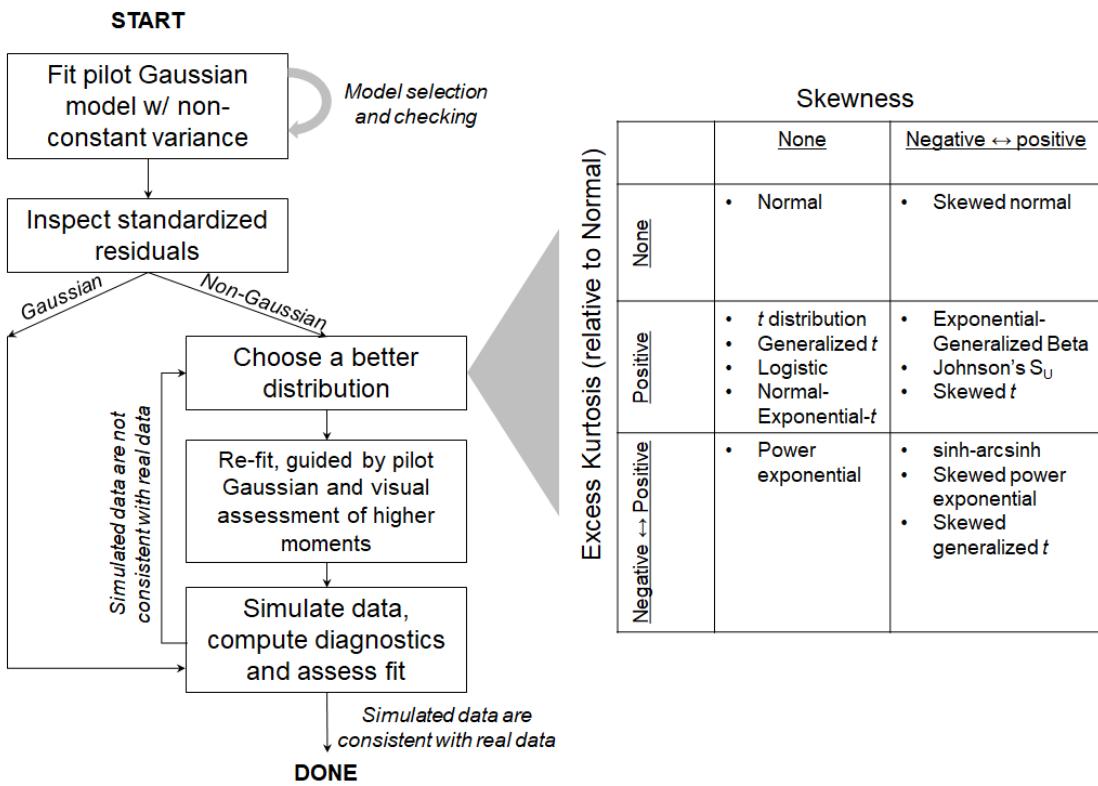


Figure 1: Recommended steps in growth modeling (left) and guide to common non-Gaussian distributions of size x for $x \in \mathbb{R}$ that can accommodate different combinations of skewness and kurtosis (right). All of these distributions (often including multiple versions or parameterizations of each) are available in the R package **gamlss.dist**, except for the skewed generalized *t*, which is available in the package **sgt** (Davis, 2015).

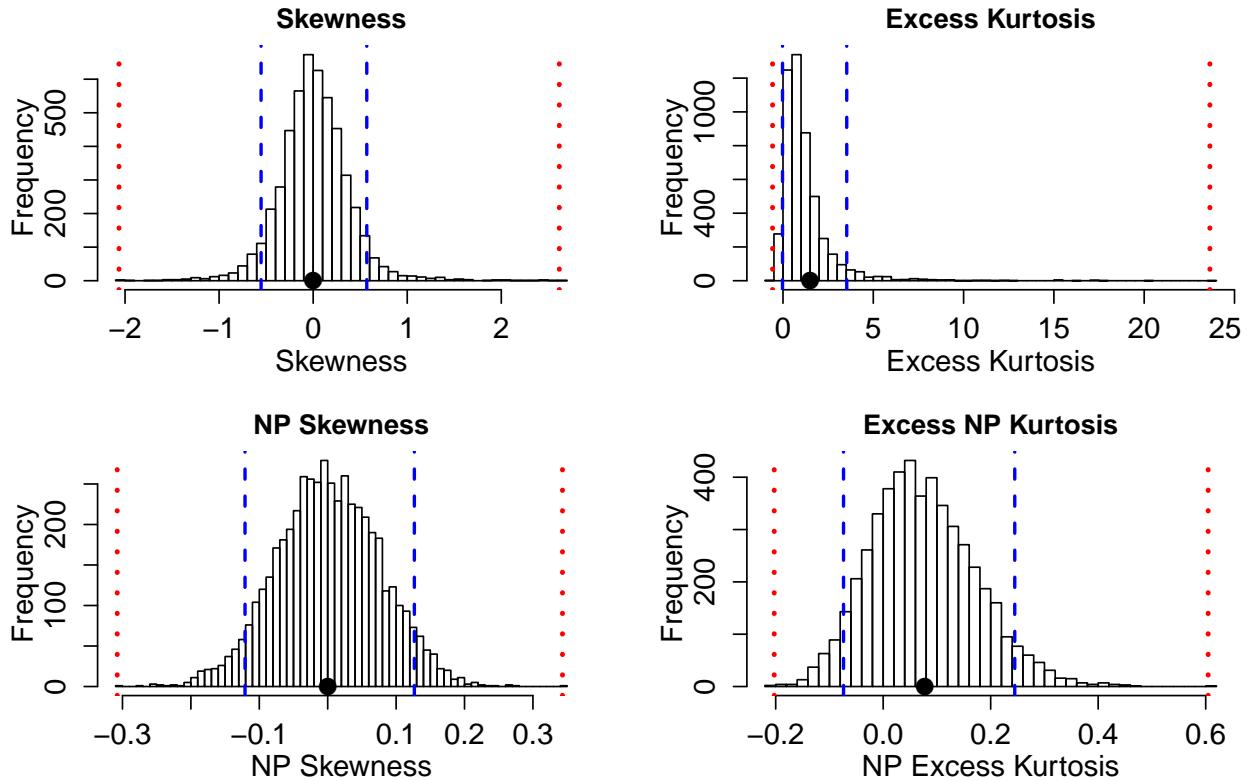


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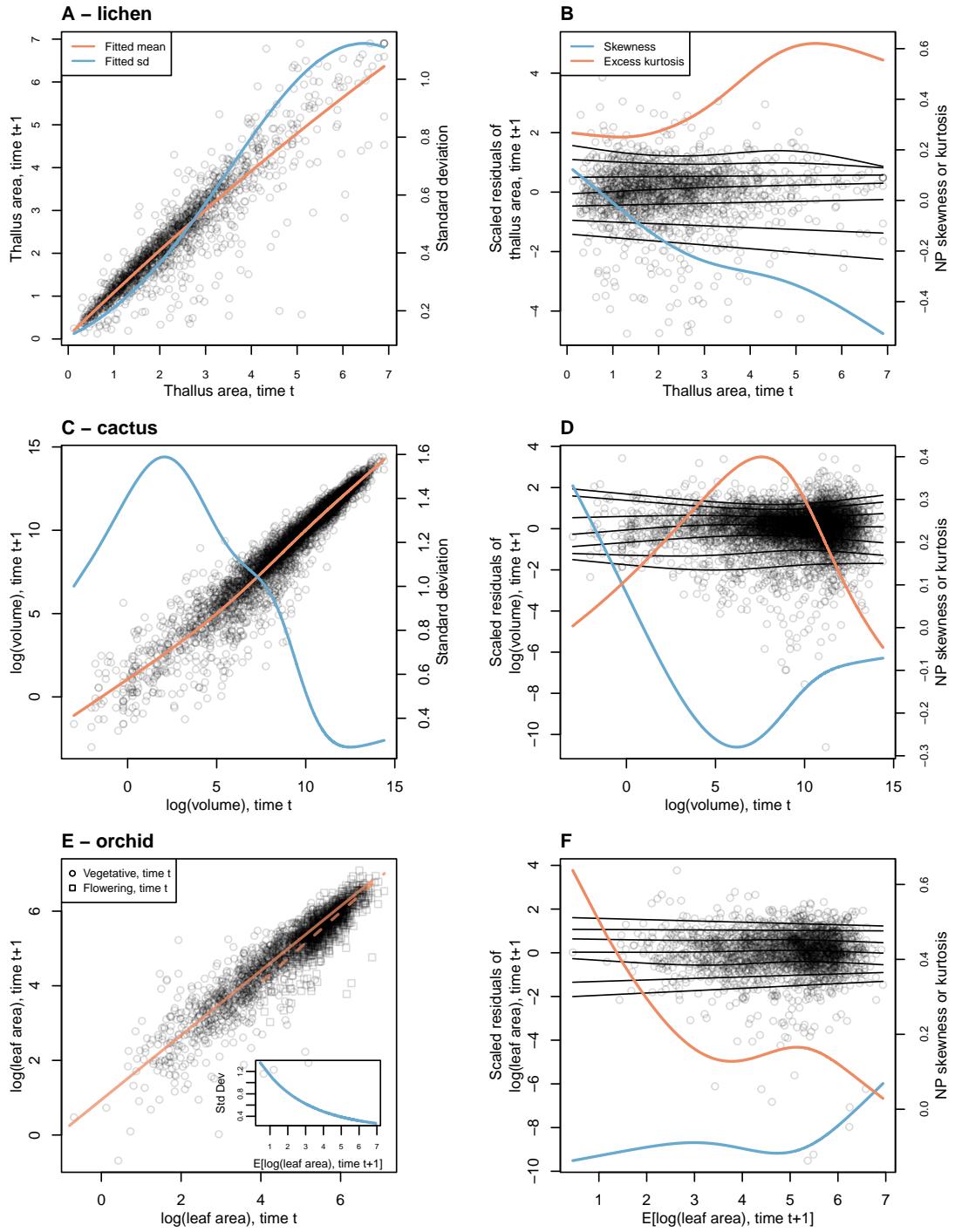


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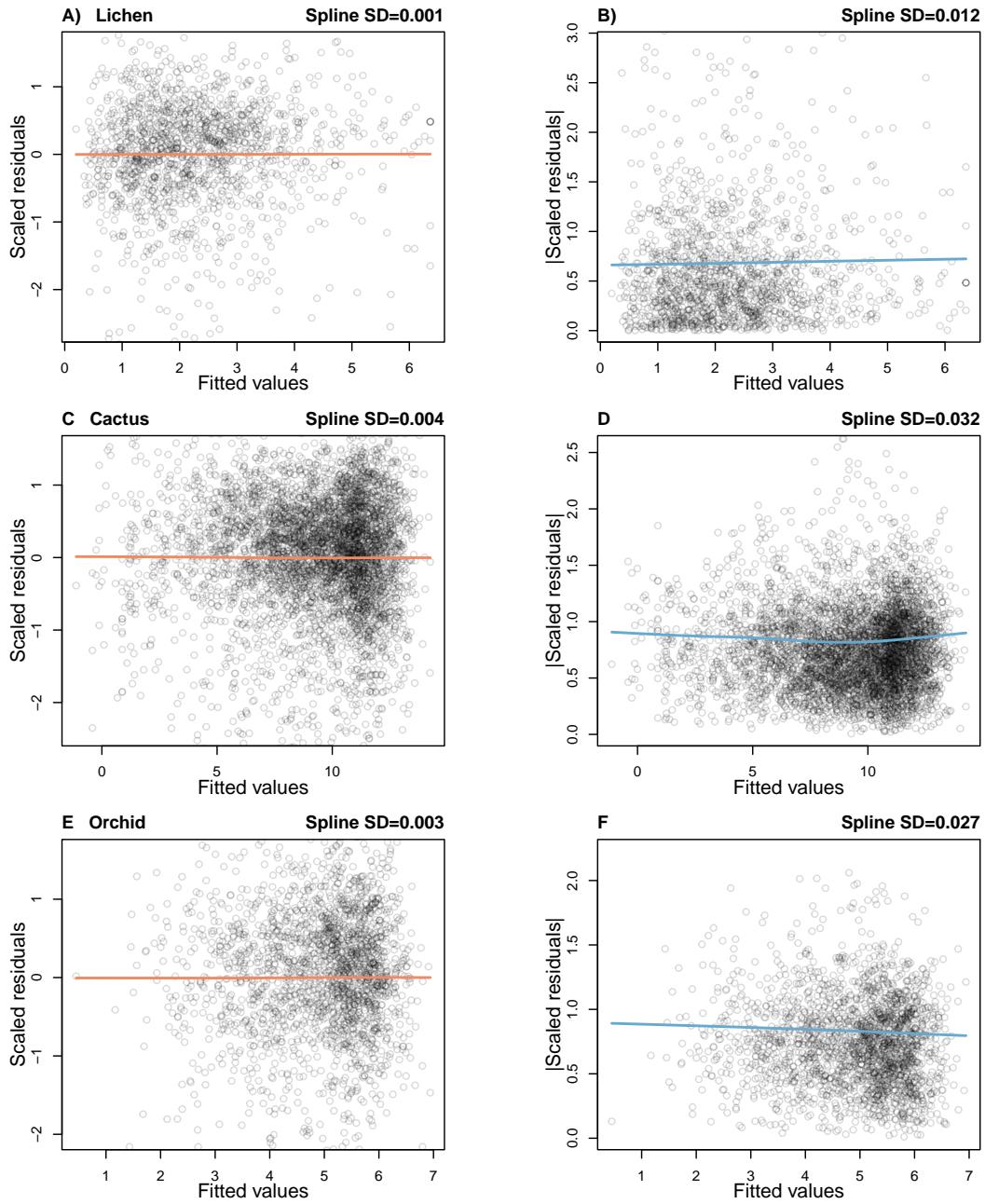


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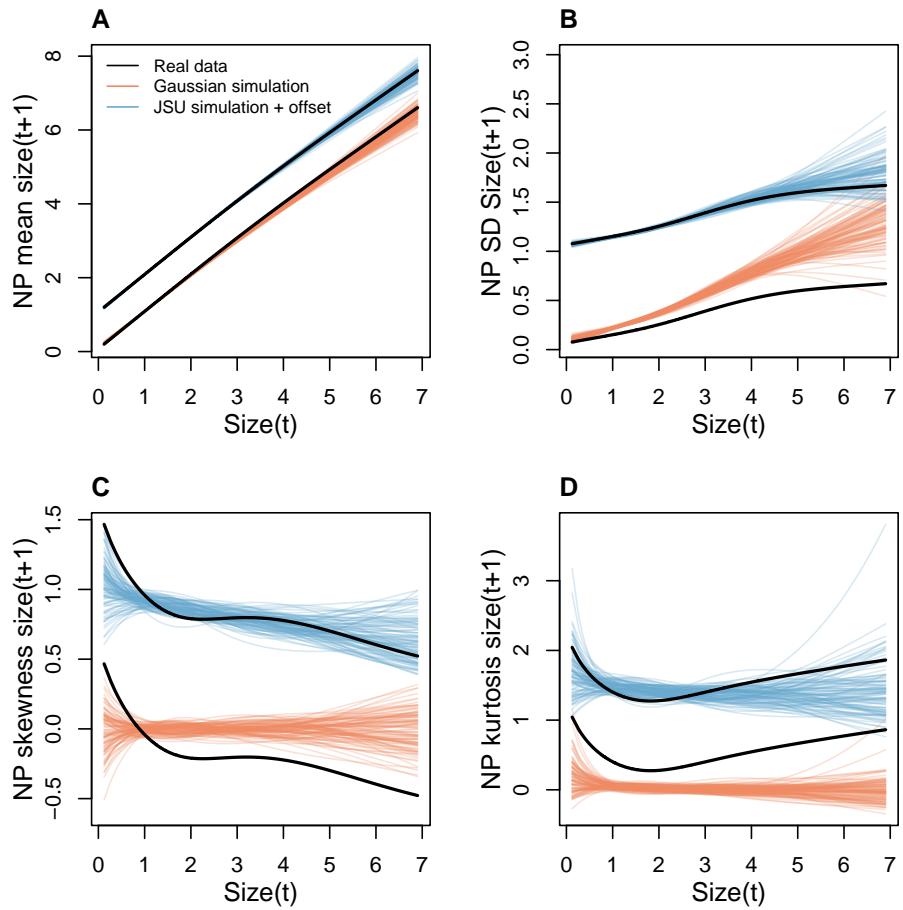


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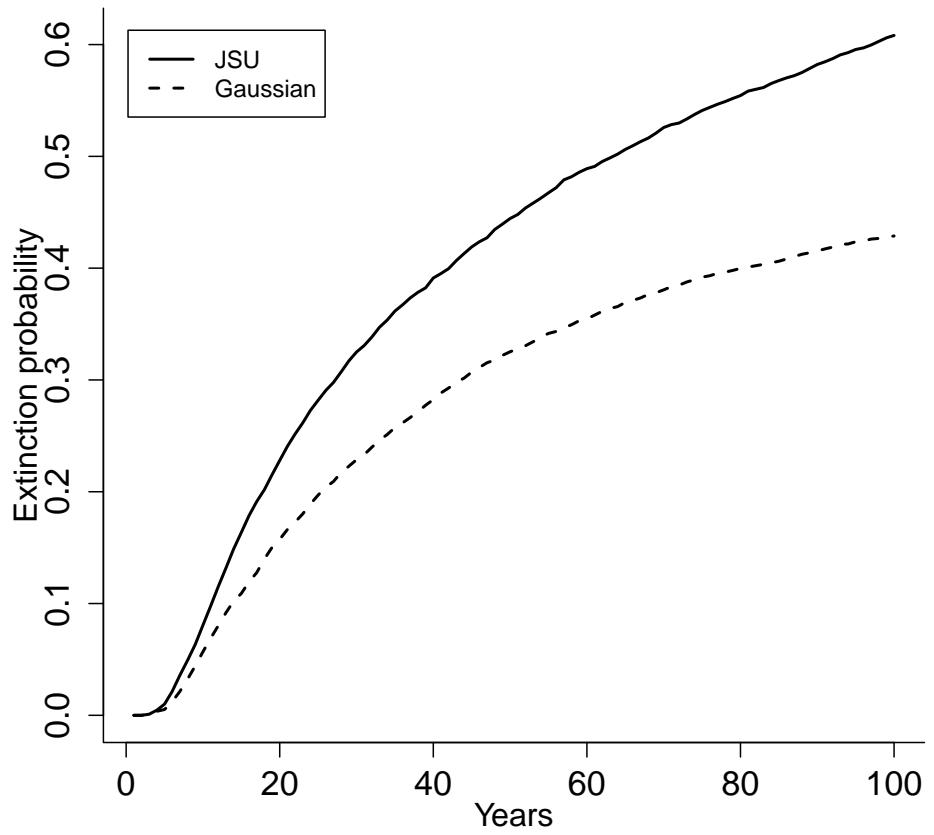


Figure 6: Extinction risk estimated from individual-based simulation of IPMs based on Gaussian and Johnson's S-U (JSU) growth distributions. Figure made by script `Vuplicida_IPMs.R`.

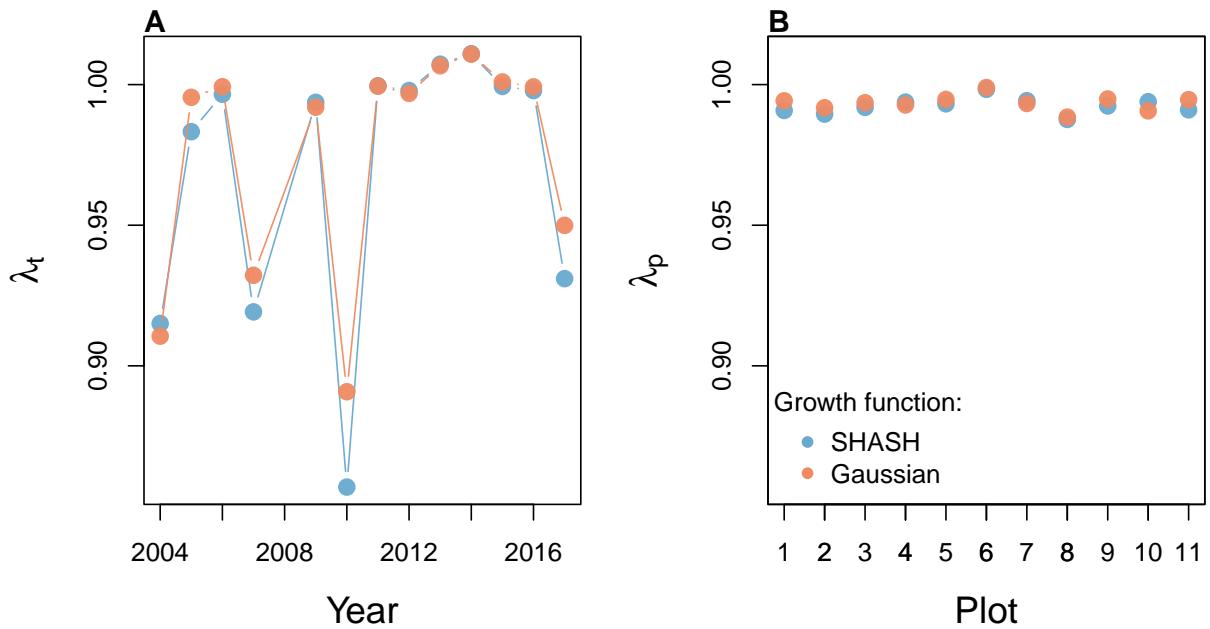


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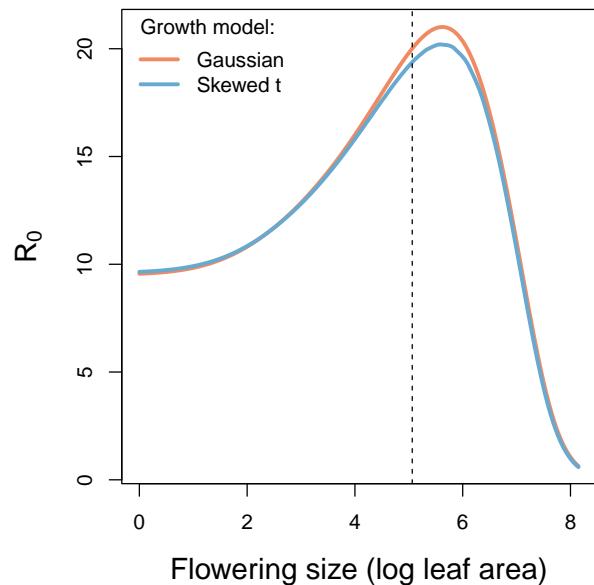


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