

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

Tom E.X. Miller^{*a} and Stephen P. Ellner^b

^aDepartment of BioSciences, Rice University, Houston, TX

^bDepartment of Ecology and Evolutionary Biology, Cornell University,
Ithaca, New York

Running header: Better growth modeling for IPMs

*Corresponding author. Department of BioSciences, Rice University, Houston, TX 77005-1827. Email:
tom.miller@rice.edu Phone: 713-348-4218

¹ **Abstract**

- ² 1. Integral Projection Models (IPMs) are widely used for studying the dynamics of
³ continuously size-structure populations. IPMs require a growth sub-model that
⁴ describes the probability of future size conditional on current size. Over the past
⁵ two decades, most IPM studies have assumed that this probability is normally-
⁶ distributed, despite repeated calls for non-Gaussian approaches that accommodate
⁷ skewness and kurtosis known to occur in size transition data.
- ⁸ 2. We provide a general workflow for modeling size transitions that accommodates
⁹ non-Gaussian growth patterns while retaining the desirable features (ecologically
¹⁰ important covariates and random effects) that Gaussian approaches typically pro-
¹¹ vide. Our approach emphasizes visual diagnostics of residuals from pilot Gaussian
¹² models and quantile-based metrics of skewness and kurtosis that vet the fit of the
¹³ Gaussian distribution and guide the selection of an alternative, if necessary. We
¹⁴ illustrate our methods by reanalyzing size transition data from our published IPM
¹⁵ studies, targeting a diversity of demographic quantities including population growth
¹⁶ rate, invasion wave velocity, and evolutionarily stable life history strategies.
- ¹⁷ 3. Across one coral and three plant case studies, skewness and excess kurtosis were
¹⁸ common features of size transition data and non-Gaussian growth models consis-
¹⁹ tently generated simulated data that were more consistent with the real data than
²⁰ pilot Gaussian models. However, in these case studies, the effects of “improved”
²¹ growth modeling on IPM results were generally modest, and differed in direction or
²² magnitude between different outputs from the same model.
- ²³ 4. Using tools that were not available when IPMs were first developed, it is now possi-
²⁴ ble to fit non-Gaussian models to size transition data without sacrificing ecological
²⁵ complexity; our worked examples demonstrate how, including open-access data and
²⁶ computing scripts. Doing so, as guided by careful interrogation of the data, will re-
²⁷ sult in a model that better represents the population for which it is intended.

²⁸ **Keywords**

29 Introduction

30 Structured demographic models – matrix and integral projection models (MPMs and
31 IPMs) – are powerful tools for data-driven modeling of population dynamics and via-
32 bility that are widely used in basic and applied settings. In contrast to MPMs for pop-
33 ulations with discrete structure (life stage, age class, etc.), IPMs (Easterling et al., 2000)
34 readily accommodate populations structured by continuous state variables, most com-
35 monly size. A related innovation of the IPM framework is its emphasis on regression-
36 based modeling for parameter estimation, which often carries important advantages for
37 making the most of hard-won data (Ellner et al., 2022).

38 A standard workflow allows ecologists to assemble an IPM from data using famili-
39 iar statistical tools to describe growth, survival, reproduction, and other demographic
40 transitions as functions of size (Coulson, 2012; Ellner et al., 2016). The relative ease of
41 the regression-based approach, accommodating multiple covariates (e.g., environmental
42 factors, experimental treatments) and complex variance structures (e.g., random effects,
43 correlated errors), has facilitated a growing body of IPM literature that examines how
44 biotic or abiotic factors affect population dynamics (e.g., Louthan et al., 2022; Ozgul
45 et al., 2010; Schultz et al., 2017) and explores the consequences of demographic hetero-
46 geneity associated with spatial, temporal, and individual variation (e.g., Compagnoni
47 et al., 2016; Crone, 2016; Plard et al., 2018). The vital rate regressions (or “sub-models”)
48 are the bridge between the individual-level data and the population-level model and its
49 predictions; it is important to get them right.

50 Compared to other vital rates, growth is special. The regression sub-models for
51 survival and reproduction only need to provide a single mean value as functions of
52 size (we use “size” as the name for whatever continuous variable defines the population
53 structure, which could instead be immune competence, mother’s weight, etc.). But for
54 modeling growth, the full probability distribution of subsequent size, conditioned on
55 initial size, must be defined. This distribution defines the growth ‘kernel’ $G(z', z)$ that
56 gives the probability density of any future size z' at time $t + 1$ conditional on current size
57 z at time t . Whenever survival and reproduction are size-dependent, the entire distribu-
58 tion of size transitions can strongly influence IPM predictions because this distribution
59 governs how frequently size changes are much greater or much lower than average.

60 The original template for modeling size transitions in IPMs was provided by East-
61 erling et al. 2000. They first tried simple linear regression, assuming normally dis-
62 tributed size changes with constant variance. Because the residuals from this regression
63 exhibited non-constant variance, they used a two-step approach that estimated the size-

64 dependence in the residual variance (better options soon became available, such as the
65 `lme` function in R). However, even after accounting for non-constant variance, growth
66 data may still deviate from the assumption that size transitions are normally distributed.
67 Size transitions are often skewed such that large decreases are more common than large
68 increases (Peterson et al., 2019; Salguero-Gómez and Casper, 2010), or vice versa (Stub-
69 berud et al., 2019). Size transitions may also exhibit excess kurtosis ('fat tails'), where
70 extreme growth or shrinkage is more common than predicted by the tails of the normal
71 distribution (Hérault et al., 2011).

72 The observation that the normal distribution may poorly describe size transitions
73 in real organisms has been made before, and several studies have emphasized that al-
74 ternative distributions should be explored (Easterling et al., 2000; Peterson et al., 2019;
75 Rees et al., 2014; Williams et al., 2012). Nonetheless, default use of Gaussian growth
76 distributions (often with non-constant variance) remains the standard practice. The gen-
77 eral state-of-the-art in the literature appears to remain where it was 20 or so years ago,
78 using the default model without pausing to examine critically whether or not it actually
79 provides a good description of the data. We are guilty of this, ourselves.

80 The persistence of Gaussian growth modeling is understandable. There is a long
81 tradition of statistical modeling built on the assumption of normally distributed resid-
82 uals with constant variance. Popular packages such as `lme4` (Bates et al., 2007), `mgcv`
83 (Wood, 2017), and `MCMCglmm` (Hadfield et al., 2010) make it easy to fit growth models
84 with potentially complex fixed- and random-effect structures, but the possible distribu-
85 tions of continuous responses are limited, and default to Gaussian. Abandoning these
86 convenient tools for the sake of more flexible growth modeling means, it may seem,
87 sacrificing the flexibility to rigorously model diverse and potentially complex sources of
88 variation in growth, some of which may be the motivation driving the study in the first
89 place.

90 The question we address here is: how can ecologists escape the apparent trade-off
91 between realistically capturing the variance, skew, and kurtosis of size transition data
92 on the one hand, and flexibly including the multiple covariates and random effects that
93 often have substantial impacts on demographic rates? In this article, we offer an answer.

94 Our goal here is to present and illustrate a general and practical "recipe" that moves
95 growth modeling past the standards set over 20 years ago, using software tools available
96 now.¹ Like any recipe, users may need to make substitutions or add ingredients to
97 suit their situation. Our approach emphasizes graphical diagnostics for developing and

¹Our statements about what is available now are based on what tools reliably deliver in our experience, not on what they promise.

98 evaluating growth models, rather than a process centered on statistical model selection.
99 Through a set of empirical case studies we demonstrate how a simple workflow, using
100 tools that were nonexistent or not readily available when IPMs first came into use, makes
101 it straightforward and relatively easy to identify when the default model is a poor fit to
102 the data, and to then choose and fit a substantially better growth model that is no harder
103 to use in practice. We illustrate our approach by revisiting four of our own, mostly
104 published IPM analyses that assumed Gaussian growth. In each case, the Gaussian
105 assumption does not stand up to close scrutiny. We illustrate how we could have done
106 better, and the consequences of “doing better” for our ecological inferences. All of our
107 analyses may be reproduced from code and data that are publicly available (see Data
108 accessibility statement).

109 A workflow for growth modeling

110 The modeling workflow that we suggest runs as follows (Fig. 1):

- 111 1. *Fit a “pilot” model or models assuming a Gaussian distribution, but allowing for non-*
112 *constant variance.*

113 This step is familiar to most IPM users, as it is the start and end of the traditional
114 workflow. A well-fitted Gaussian model accurately describes the mean and variance
115 of future size conditional on current size and possibly on other measured covari-
116 ates or random effects. This step may include model selection to identify which
117 treatment effects or environmental drivers affect the mean and/or variance of future
118 size. Non-constant variance is often fitted in a two-stage process, first fitting mean
119 growth assuming constant variance, then doing a regression relating the squared
120 residuals to initial size or the fitted mean of subsequent size. Fitting mean and
121 variance simultaneously, as can be done with R packages **mrgcv** and **nmle**, is ad-
122 vantageous when it is possible because incorrectly assuming constant variance can
123 affect model selection for the mean. But two-step fitting may be convenient when
124 there are multiple fixed and random effects that can affect growth variance, because
125 the fitted mean value implicitly accounts for all of them. We illustrate both one-step
126 and two-step approaches in the case studies below.

127 Allowing non-constant variance means removes the need for transforming the
128 data to stabilize the growth variance. Transformation remains an option when it
129 does not create new problems (see Discussion), and it may have advantages besides

130 variance stabilization. In particular log-transformation is often appropriate for size
131 data (Ellner et al., 2016), and it helps to avoid eviction at small sizes.

- 132 2. *Use statistical and graphical diagnostics to identify if and how the standardized residuals*
133 *deviate from Gaussian, and to identify a more appropriate distribution.*

134 If the Gaussian pilot model is valid, the set of standardized residuals (standardized
135 by the standard deviation) should be Gaussian with mean zero and unit variance,
136 with no skew or excess kurtosis. This criterion provides a straightforward test for
137 whether to accept a Gaussian growth model or explore alternatives. If the standard-
138 ized residuals are satisfactorily Gaussian, skip to the final step of the workflow.

139 There are many ways that growth data may deviate from Gaussian, and the na-
140 ture of those deviations can guide the search for a better distribution. Frequentist
141 tests such as the D'Agostino test of skewness (D'Agostino, 1970) and the Anscombe-
142 Glynn test of kurtosis (Anscombe and Glynn, 1983) could be used to diagnose
143 whether the aggregate distribution of standardized residuals deviates from normal-
144 ility (R package **moments** (Komsta and Novomestky, 2015)). However, the aggregate
145 distribution of standardized residuals may be misleading if properties such as skew
146 and kurtosis vary with size. For example, a change in the direction of skewness
147 from small to large sizes might produce zero overall skewness, but really requires a
148 distribution flexible enough to accommodate both positive and negative skew, such
149 as the skewed normal or Johnson S_U distributions. Alternatively, growth data may
150 lack skew but may exhibit leptokurtosis (in which case the t distribution may be a
151 good choice) or may shift from platykurtosis to leptokurtosis depending on initial
152 size (in which case the power exponential distribution may be a good choice). It is
153 therefore essential to visualize trends in distribution properties with respect to size,
154 either initial size (for simple models with only size-dependence) or expected future
155 size (for models with multiple fixed effects). In the case studies below, we rely on
156 quantile regression of the standardized residuals to visualize skew and kurtosis as
157 continuous functions of size or expected value. Fig. 1 includes guidance on how the
158 skew and kurtosis properties of the standardized residuals suggest options for an
159 appropriate growth distribution. In our case studies we take advantage of the many
160 distributions provided in the **gamlss** R package (Stasinopoulos et al., 2007), but any
161 other distributions with the necessary properties can be used.

- 162 3. *Refit the growth model using the chosen distribution.*

163 In models with multiple covariates and/or random effects, each potentially affecting
164 several distribution parameters (location, scale, skew, kurtosis) in different ways,

“refit the model” could entail a massive model selection process to identify the “right” or “best” non-Gaussian model. And with so many options, model uncertainty may be overwhelming and over-fitting becomes a significant risk even if precautions against it are taken. We therefore argue for adopting the more modest goal of remedying any evident defects in the Gaussian model. As we demonstrate below, the functional forms for the mean and standard deviation (or location and scale parameters) can often be carried over from the pilot Gaussian model into a non-Gaussian distribution, leaving skew and kurtosis as the targets for improvement.

Our recommendation for this step is based on the fact that parameter estimation using Gaussian regression models is generally robust to deviations from normality (Schielzeth et al., 2020), meaning that the mean of the Gaussian model is probably a good proxy for the mean of the non-Gaussian model (and if it is not, the next step in the workflow would catch that). The functional forms for skew and kurtosis of the non-Gaussian model can be guided by the qualitative features of the graphical diagnostics (e.g., skewness switches from positive to negative with size).

4. *Test the final model through graphical diagnostics comparing simulated and real growth data.*

A good model will generate simulated data that look like the real data. Again, it is important to inspect the properties of simulated data conditional on present size or expected future size, rather than examining the entire distribution. We provide examples below of informative comparisons between simulated and real data, based mainly on quantiles. If the simulated data do not correspond well with real data, alternative (possibly more flexible) growth distributions should be explored, or more complex functions relating distribution parameters to current size and other covariates. However, we again caution against a full-blown model selection exercise. Instead, alternative models should be chosen to remedy observable discrepancies between real and simulated size transition data, and at most slightly modified based on final diagnostics and statistical tests.

How should skewness and kurtosis be measured?

Improvement of a Gaussian model will involve scrutiny of skewness and kurtosis, so measurement of these properties warrants some attention. The standard measures of skewness and kurtosis (tail thickness) are based on the third and fourth central moments,



Figure 1: General workflow of recommendations for IPM 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 package `gamlss.dist`, except for the skewed generalized *t*, which is available in the package `sgt` (Davis, 2015).

197 respectively, of the distribution:

$$198 \quad \text{Skewness} = \frac{m_3}{\sigma^3}, \quad \text{Excess kurtosis} = \frac{m_4}{\sigma^4} - 3 \quad (1)$$

199 where $m_k = \mathbb{E}(X - \bar{X})^k$ is the k^{th} central moment of a random quantity X and σ^2 is the
200 variance (second central moment). A Gaussian distribution has zero skewness and zero
201 excess kurtosis.

202 The standard measures are easy to calculate but their use for choosing and eval-
203 uating growth models is hindered by their poor sampling properties. Because empirical
204 estimates involve high powers of data values, a few outliers can produce very inaccurate
205 estimates. Figure 2 shows a simulated example, where the underlying “data” are a sam-



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

ple of size 200 from a t distribution with 8 degrees of freedom; the true skew is 0, and the true excess kurtosis is 1.5. The distance between the largest and smallest estimates (indicated by the dotted red vertical lines), relative to the distance between the 5th and 95th percentiles, shows the broad extent of extreme values that can occur even with a large sample, especially for kurtosis.

We therefore use nonparametric (NP) measures of skew and kurtosis that are based on quantiles and thus are less sensitive to a few extreme data values. Let q_α denote the α quantile of a distribution or sample (e.g., $q_{0.05}$ is the 5th percentile). For any $0 < \alpha < 0.5$, a quantile-based measure of skewness is given by (McGillivray, 1986)

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

216 NP Skewness measures the asymmetry between the tails of the distribution above and
 217 below the median. The size of the upper tail can be measured (for any $0 < \alpha < 0.5$) by
 218 $\tau_U = q_{1-\alpha} - q_{0.5}$; for $\alpha = 0.05$ this is the difference between the 95th percentile and the
 219 median. The lower tail size is $\tau_L = q_{0.5} - q_\alpha$. The definition above is equivalent to

$$220 \quad \text{NP Skewness} = \frac{\tau_U - \tau_L}{(\tau_U + \tau_L)}. \quad (3)$$

221 An NP Skewness of ± 0.2 says that the difference in tail sizes is 20% of their total. The
 222 range of possible values is -1 to 1. Both $\alpha = 0.25$ (sometimes called “Kelly’s skewness”) and
 223 $\alpha = 0.1$ (“Bowley’s skewness”) are common choices. We used $\alpha = 0.1$, unless
 224 otherwise stated.

225 An analogous quantile-based measure of kurtosis (Jones et al., 2011) is

$$226 \quad \text{NP Kurtosis} = \frac{q_{1-\alpha} - q_\alpha}{q_{0.75} - q_{0.25}}. \quad (4)$$

227 For $\alpha = 0.05$, NP Kurtosis is the difference between the 95th and 5th percentiles, relative
 228 to the interquartile range. To facilitate interpretation, we scale NP Kurtosis relative to
 229 its value for Gaussian distribution, and subtract 1 so that the value for a Gaussian is
 230 zero. We call this “NP Excess Kurtosis”. The value for a Gaussian distribution is zero. A
 231 value of ± 0.2 means that the tails are on average 20% heavier (or lighter) than those of
 232 a Gaussian with the same interquartile range. We calculate NP Kurtosis using $\alpha = 0.05$
 233 unless otherwise stated, to focus on the tail edges, but again this is somewhat arbitrary.

234 Figure 2C,D illustrate how, applied to exactly the same simulated samples, the non-
 235 parametric measures produce a smaller fraction of highly inaccurate estimates caused
 236 by a few extreme values in the sample. But also note that, in contrast to the moment-
 237 based measures, numerically small values of the nonparametric measures (e.g., 0.1 or 0.2)
 238 should not be disregarded, because they are both scaled so that a value of 1 indicates
 239 extremely large departures from a Gaussian distribution.

240 Quantile-based estimation of skewness and kurtosis carries the added value that
 241 quantile regression methods may be used to derive these properties of size transitions
 242 as continuous functions of initial size or expected future size. In the examples below,
 243 we sometimes use the **qgam** package to fit smooth additive quantile regression models,
 244 which have the flexibility to accommodate nonlinear size-dependence in skewness and
 245 kurtosis. One risk of a gam-based approach is that fitted quantiles may be too “wiggly”
 246 without constraints on their complexity. In the examples below, we limit complexity by
 247 fitting splines with $k = 4$ or $k = 6$ basis functions. For the gam-averse, other quantile re-
 248 gression models may be equally suitable. For consistency with nonparametric skewness

249 and kurtosis, we similarly use quantile-based measures of location and scale, and use
250 quantile regression to visualize these as functions of size. Specifically, following Wan
251 et al. (2014),

252
$$\text{NP Mean} = \frac{q_{0.25} + q_{0.5} + q_{0.75}}{3} \quad (5)$$

253 and

254
$$\text{NP SD} = \frac{q_{0.75} - q_{0.25}}{1.35}. \quad (6)$$

255 1 Case study: Sea fan corals, *Gorgonia ventalina*

256 We begin with a simple example where current size is the only predictor of future size.
257 Bruno et al. (2011) developed an IPM to understand the rise and fall of a fungal pathogen
258 *Aspergillus sydowii* in Caribbean sea fan corals *G. ventalina*. The model was based on re-
259 peated observations of marked corals in permanent transects at several sites near Aku-
260 mal, Mexico, recording disease status (infected/uninfected) and the area of uninfected
261 tissue. The epidemic peak had passed and disease incidence was already low, so in-
262 fected fans were relatively infrequent. We therefore limit the analysis here to uninfected
263 individuals. Bruno et al. (2011) found statistically significant year and site effects, but
264 as those explained a very small fraction of the variation in growth increments, they
265 fitted a single growth model to data pooled across years and sites. We do the same
266 here. The pooled data set consists of 358 observed size transitions. The data exhibited
267 size-dependent variance in growth (change in area, cm^2). Bruno et al. (2011) chose to sta-
268 bilize the variance by cube-root transforming size, and then fitting the standard model
269 with Gaussian growth increments. Here we take a different approach, using natural log
270 transformation of area and modeling size-dependent variance.

271 With initial size as the only predictor, a simple way to fit a Gaussian model with
272 nonconstant variance is the `gam` function in `mgcv` library (Wood, 2017) using the `gaulss`
273 family. The mean and standard deviation are both fitted as smoothing spline functions
274 of initial size, and the `predict` function returns the fitted mean and also the inverse of
275 the fitted standard deviations with which we can compute the scaled residuals:

```
276 # XH is a data frame holding the data
277 # logarea.t0, .t1 denote initial and final values of log-transformed area
278 fitGAU <- gam(list(logarea.t1~ s(logarea.t0), ~ s(logarea.t0)),
279   data=XH, gamma=1.4, family=gaulss())
280 fitted_all = predict(fitGAU,type="response");
281 fitted_sd = 1/fitted_all[,2];
```

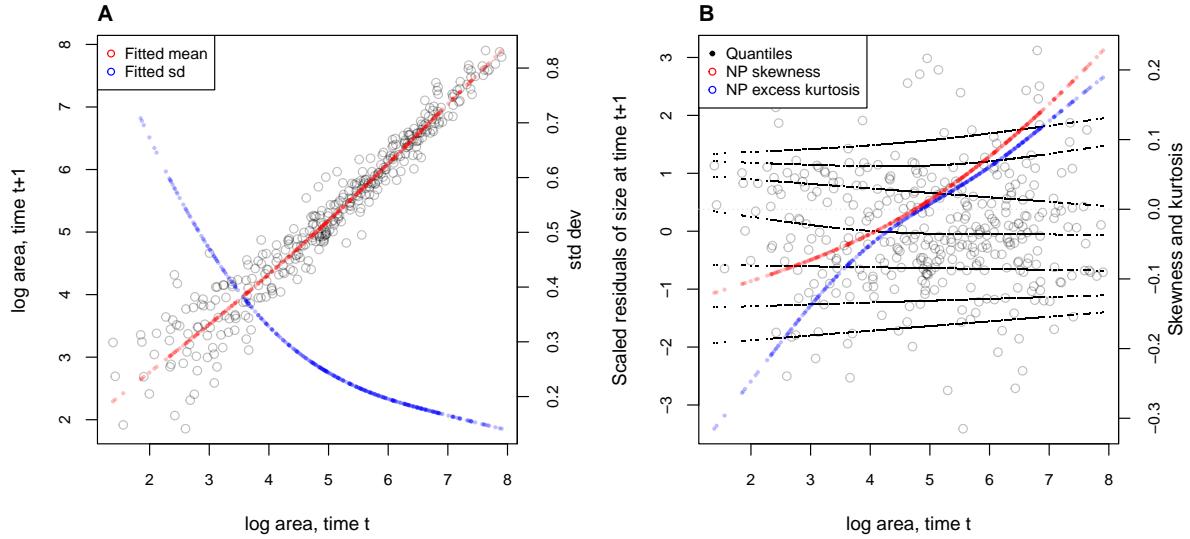


Figure 3: **A**, Size transition data for sea fan corals, *Gorgonia ventalina*, and fitted gam with mean (red) and standard deviation (blue) of future size conditional on current size. **B**, Quantile regressions of scaled residuals on size and nonparametric estimates of skewness (red) and excess kurtosis (blue) derived from them. Black lines in **B** show the 5th, 10th, 25th, 50th, 75th, 90th, and 95th quantiles. Figure made by script AkumalCorals_qgam.R.

282 scaledResids = **residuals**(fitGAU,type='response')/fitted_sd;
 283 Fig. 3A shows the log-transformed data and Gaussian model. The mean function (solid
 284 red curve) is visually nearly linear, but the fitted spline is strongly favored over a linear
 285 model for the mean ($\Delta AIC \approx 9$). The spline for standard deviation σ versus initial size
 286 reflects the evident greater variability in growth at smaller sizes.

287 There are no blatant signs of trouble in the pilot Gaussian model, but quantile re-
 288 gressions on the scaled residuals, and the NP Skewness and Kurtosis metrics derived
 289 from them (Eq. 3 and 4), suggest deviations from normality (Fig. 3B). Specifically, skew-
 290 ness switches from negative to positive across the size range, with smaller corals more
 291 prone to extreme shrinkage and larger corals more prone to extreme growth. Kurto-
 292 sis also changes direction over the size distribution, with thinner tails than Gaussian at
 293 small sizes and fatter tails at large sizes. The fitted nonparametric moments suggest that
 294 the upper and lower tails of size transition probabilities may differ by up to 20%, and the
 295 weight of the tails may be 20% greater or less than Gaussian, depending on initial size –
 296 not overwhelming deficiencies, but not trivial either. Are these deviations from normal-
 297 ity severe enough to warrant a second, non-Gaussian iteration of growth modeling? To
 298 answer that question, we simulated data from the fitted Gaussian model and examined

299 whether key properties of the simulated data are consistent with those of the real data –
300 this is the ultimate litmus test for a growth model’s adequacy and should be a standard
301 element of IPM construction, in our opinion. If the simulated data are not consistent
302 with the real data, it is time to choose a better distribution (Fig. 1). In this case, most
303 of 100 Gaussian model simulations are out of line with the skew at smallest sizes and
304 largest sizes, and the excess kurtosis observed at moderately large sizes (Fig. 4 CD). For
305 at least some parts of the size distribution, a non-Gaussian model would better capture
306 size transitions.

307 We sought a distribution that could accommodate the observed changes in the sign
308 of skewness and excess kurtosis. We chose the sinh-arcsinh (SHASH) distribution, a four-
309 parameter distribution that, conveniently, is included in **mgcv**’s **gam()** function: **SPE: I**
310 **made the SHASH model consistent with the Gaussian for location and scale, removing**
311 **the specification of k.**

```
312 fitSHASH <- gam(list(logarea.t1 ~ s(logarea.t0), # <- location  
313 ~ s(logarea.t0), # <- log-scale  
314 ~ s(logarea.t0,k=4), # <- skewness  
315 ~ s(logarea.t0,k=4)), # <- log-kurtosis  
316 data = XH, gamma = 1.4, family = shash, optimizer = "efs")
```

317 The fitted model’s mean and variance are nearly identical to the Gaussian (Fig. 4AB),
318 and the fitted trends in skewness and kurtosis are much less “wiggly” than the estimate
319 from the data (Fig. 4CD). Nonetheless, data simulated from the SHASH model are more
320 consistent with the real data, with more SHASH data sets matching or exceeding the
321 largest skewness and kurtosis values observed (Fig. 4CD). If one cares to quantify the
322 difference between models, the SHASH model is clearly favored by AIC ($\Delta AIC = 5.45$)
323 despite having twice as many parameters to fit.

324 What, then, have we gained by fitting a better growth model? Fig. 5A compares
325 the predicted distributions of subsequent size in the fitted model and Gaussian pilot
326 models, for the median size of a new recruit (leftmost pair of curves), the median ini-
327 tial size (central curves), and the 95th percentile of initial size in the data (rightmost
328 curves). The differences are small, and most pronounced for the smallest size, where re-
329 cruits are predicted to grow slightly larger under the SHASH model than the Gaussian
330 model. The direction of this difference was surprising, because the SHASH has negative
331 skew at small sizes in the data. However, the SHASH model also gives a better predic-
332 tion of mean growth at small sizes than the Gaussian model. At intermediate sizes the
333 predictions are nearly identical; at large sizes the SHASH has slightly lower standard

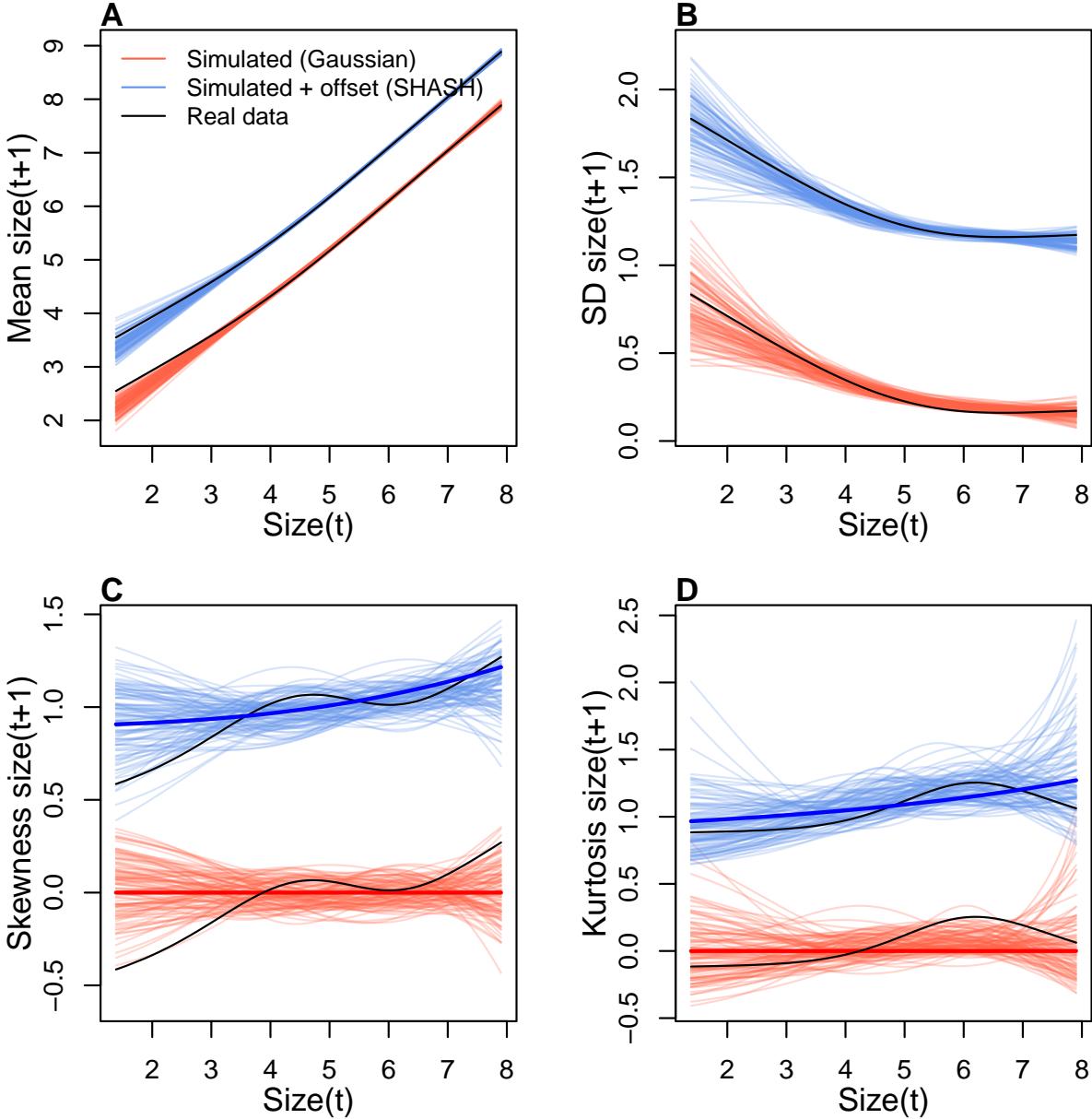


Figure 4: Comparisons among real coral data and data simulated from Gaussian and SHASH growth models for mean, standard deviation, NP skewness, and NP excess kurtosis of future size conditional on current size. Note that plotted values for the SHASH are offset by one unit to allow comparisons. In the skewness and kurtosis panels, the darker solid curves show the values for the fitted growth models. Figure made by script AkumalCorals_qgam.R.

334 deviation, but fatter tails (excess kurtosis). Fig. 5B shows the predicted steady-state size
 335 distributions resulting from a constant unit input of recruits. Again, the differences are

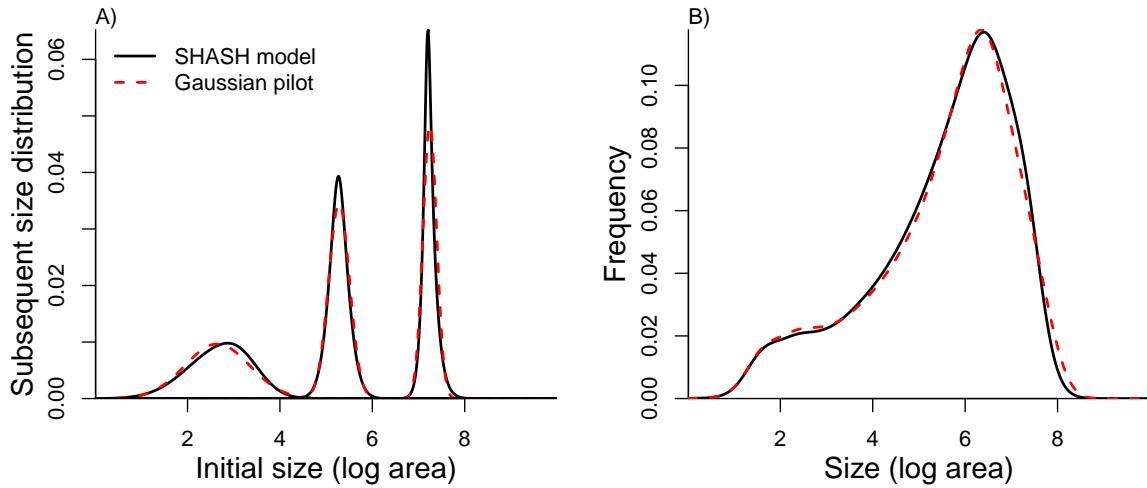


Figure 5: Comparisons between the fitted SHASH growth model (solid black curves) and the Gaussian pilot model (dashed red curves) for sea fans *G. ventalina*. A) Predicted frequency distributions of size in year $t + 1$ for three different values of size in year t . The leftmost pair of curves are for initial size equal to the median size of a new recruit (data from (Bruno et al., 2011)); central pair is for the median initial size of uninfected individuals; rightmost pair are for the 95th percentile initial size for uninfected individuals. B) Steady-state size distributions resulting from a constant unit input of new recruits. As in Bruno et al. (2011) we assume that larvae are very widely dispersed, so that the number of recruits arriving at any one location is independent of the local population abundance or structure. Size distribution of recruits was described by a kernel density estimate based on the measured sizes of known new recruits ($n = 9$). Figure made by script AkumalCoralsIPMs.R.

336 very subtle. Finally, the Gaussian and SHASH growth models predict very similar mean
 337 life span (17.7 and 17.9 years, respectively).

338 From these outputs, there is little evidence that improved modeling of coral growth
 339 meaningfully improved biological inferences from the IPM. One could argue that it was
 340 not worth the trouble, even though it was almost no trouble at all. But before fitting
 341 the SHASH model, we could not have known whether or not it would have made a
 342 difference.

343 In this case study we used `gam` to fit both the Gaussian and SHASH models because
 344 that obviated model selection on functions for mean, variance, and higher moments.
 345 However, `gam` should be used with caution. Nonparametric regression models notori-
 346 ously “wag their tails” because the ends of the fitted curve can be pulled close to the
 347 outermost data points. This is especially problematic for growth modeling, because data
 348 are typically sparse near the bounds of the size distribution. To minimize the risk of
 349 overfitting we specified the number of “knots” ($k=4$) and used `gamma=1.4` to overweight

model degrees of freedom as suggested by Gu (2013, sec. 3.2). But it is always important to plot the fitted splines and make sure they do not wag unrealistically. If they do, parametric regression may be a better choice.

2 Case study: tree cholla cactus, *Cylindriopuntia imbricata*

The next case study, focusing on the tree cholla cactus *Cylindriopuntia imbricata* at the Sevilleta Long-Term Ecological Research site in central New Mexico, adds a new feature on top of the simple size-dependent regressions in the previous study: random effects associated with temporal (year) and spatial (plot) environmental heterogeneity. This long-term study of cactus demography was initiated in 2004 and different subsets of the data have been analyzed in various IPM studies, all using Gaussian growth kernels (Compagnoni et al., 2016; Czachura and Miller, 2020; Elderd and Miller, 2016; Miller et al., 2009; Ohm and Miller, 2014). In fact, (Elderd and Miller, 2016) presented a Gaussian growth model fit to the cactus data as an example of a well fit growth function, based on a marginal distribution of residuals that appeared approximately Gaussian and posterior predictive checks (PPCs) of a Bayesian model that suggested consistency between the real data and data simulated from the fitted model (Fig. 4 in (Elderd and Miller, 2016)).

While PPCs and the associated “Bayesian P-value” are popular diagnostic tools, they are often considered to be too conservative (Conn et al., 2018; Zhang, 2014), failing to reject marginally bad models even though they are very effective in rejecting models that are terrible. The choice of discrepancy function (the statistic used to compare real and simulated data) can also be limiting: in our previous work, we used a discrepancy function focused on variance (the sum of the squared residuals), so we had a built-in blind-spot for mismatches in higher moments. In the clarity of hindsight, the PPC gave a false sense of security; the Gaussian was a poor choice all along.

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

We begin the growth modeling workflow, as above, with a generalized additive model with the mean and standard deviation of size in year $t + 1$ modeled as function of size in year t , with random intercepts for year and plot and assuming normally distributed residuals (`family=gaulss()`). The standardized residuals, accounting for size-

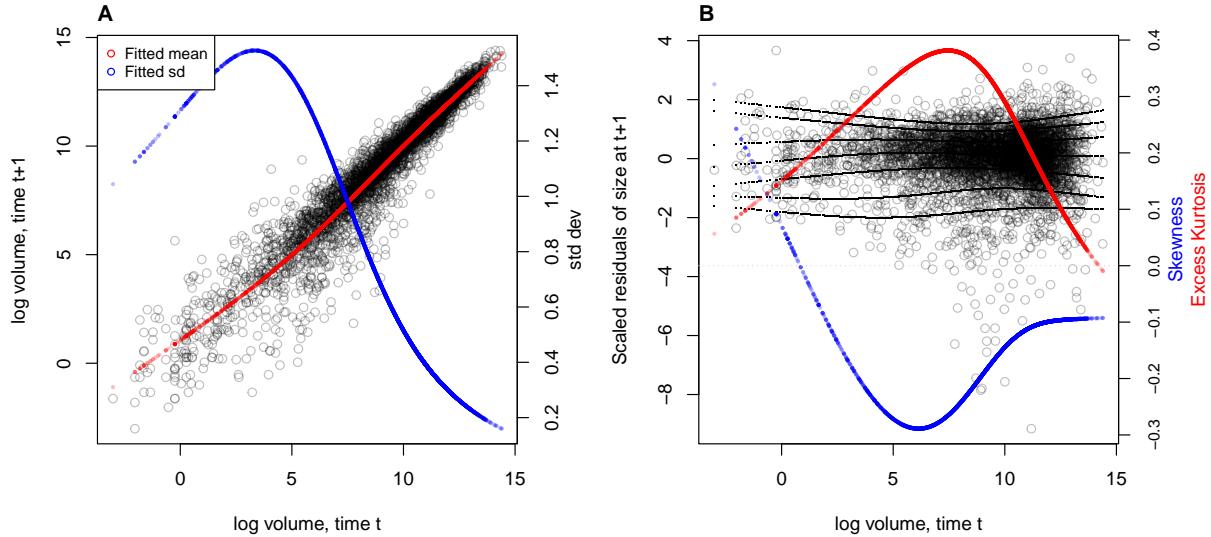


Figure 6: **A**, Size transition data for tree cholla cacti, *Cylindropuntia imbricata*, and fitted gam with mean (red) and standard deviation (blue) of future size conditional on current size. **B**, Quantile regressions of scaled residuals on size and nonparametric estimates of skewness (red) and excess kurtosis (blue) derived from them. Black lines in **B** show the 5th, 10th, 25th, 50th, 75th, 90th, and 95th quantiles. Figure made by script `cactus_growth_modeling_qgam.R`.

dependent residual variance (Fig. 6A), show clear signals of negative skew and positive excess kurtosis across most of the size distribution but strongest in the middle of the size distribution (Fig. 6B).

To better capture size transitions, we need a distribution with negative skew and positive excess kurtosis, but both of which may be negligible at some sizes. We first tried Johnson's S_U and then the skewed t distributions, both of which are limited to positive excess kurtosis. Both distributions provided some improvement over the Gaussian, but were not happy with the fit of either. Iterating through the workflow (Fig. 1), we arrived, again, at the SHASH distribution, which is more flexible than either the JSU or skewed t , capable of capturing a greater range of kurtosis for a given amount of skew, and vice versa (Steve's NPSkewKurtosisRanges.pdf). Furthermore, fitting the SHASH as a generalized additive model with `mgcv` allowed for flexible, non-monotonic size-dependence in skewness and kurtosis without the need for model selection on specific size-dependent functions; through iterations of trial and error, we found this flexibility was necessary to generate simulated data that compared favorably to the real data. The other distributions that we tried are not available as `mgcv` families, so we fit these with custom maximum likelihood functions, an approach we illustrate in the next case study.

401 The final growth model was similar to the SHASH gam in the coral case study, but
402 with random intercepts for the location parameter, representing spatial and temporal
403 heterogeneity:

```
404 fit_shash <- gam(list(logvol_t1 ~ s(logvol_t,k=4) +  
405   s(plot,bs="re") + s(year_t,bs="re")), # location  
406   ~ s(logvol_t,k=4), # log-scale  
407   ~ s(logvol_t,k=4), # skewness  
408   ~ s(logvol_t,k=4)), # log-kurtosis  
409   data = CYIM_grow,  
410   family = shash,  
411   optimizer = "efs")
```

412 The final SHASH model provided good correspondence between simulated and
413 real data, and provided more compelling improvement over the Gaussian model than
414 we saw in the coral case study (Fig. 7). The SHASH model over-estimated negative
415 skew at some sizes relative to the signal of skewness in the data (Fig. 7C), but the nature
416 of size-dependent skew in the data is not very biologically plausible and may instead
417 be driven by the tail-wagging tendency of gams. As in the coral case study, we see
418 that correctly modeling skewness and kurtosis improved estimation of the mean and
419 standard deviation (Fig. 7A,B), yielding a growth model that is clearly truer to the data
420 than the pilot Gaussian fit.

421 We explored how improved growth modeling influenced IPM results, leveraging
422 the plot and year structure of the study design to quantify spatial and temporal vari-
423 ance in fitness. We used the fitted random effects from the vital rate models to estimate
424 the asymptotic growth rate for each year (λ_t), centered on the average plot, and for
425 each plot (λ_p), centered on the average year. This allowed us to quantify demographic
426 variance associated with temporal and spatial heterogeneity. We found that the Gaus-
427 sian growth model tended to over-estimate λ_t , particularly in the harshest years (Fig.
428 8A), and thus under-estimated temporal variance in fitness ($Var(\lambda_{t(Gaussian)}) = 0.0018$,
429 $Var(\lambda_{t(SHASH)}) = 0.0023$). The opposite was true for plot-to-plot variation (Fig. 8B),
430 where the Gaussian model under-estimated λ_p and over-estimated spatial variance in
431 fitness ($Var(\lambda_{p(Gaussian)}) = 0.00015$, $Var(\lambda_{p(SHASH)}) = 0.000088$). Across both growth
432 models, fluctuations in fitness were stronger through time than across space. The
433 difference in temporal variance would suggest that Gaussian growth modeling would
434 lead to over-estimation of the stochastic growth rate λ_S , since temporal variance has
435 a negative influence on λ_S . However, this was not the case: stochastic IPMs based

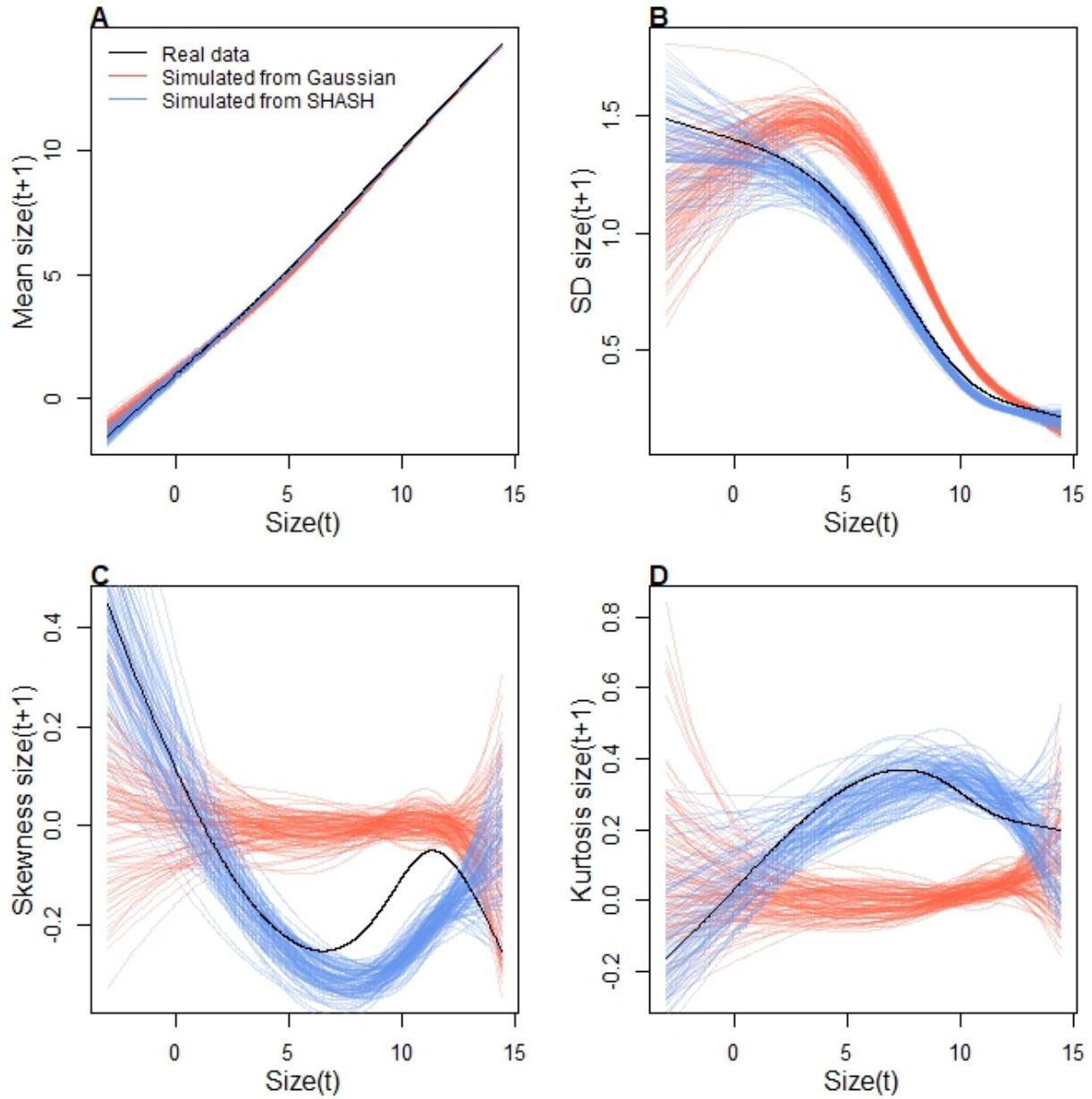


Figure 7: Comparisons among real cactus data and data simulated from Gaussian and SHASH growth models for mean, standard deviation, NP skewness, and NP excess kurtosis of future size conditional on current size. Figure made by script `cactus_growth_modeling_qgam.R`.

436 on Gaussian and SHASH growth models had nearly identical stochastic growth rates
 437 ($\lambda_S(\text{Gaussian}) = 0.9906$, $\lambda_S(\text{SHASH}) = 0.9909$). This is likely because temporal fluctua-
 438 tions in vital rates, which is where the SHASH growth model would make a difference,
 439 have a weaker influence on λ_S than the temporal fluctuations in size structure that they
 440 generate (Compagnoni et al., 2016; Ellis and Crone, 2013). Thus, depending on the target

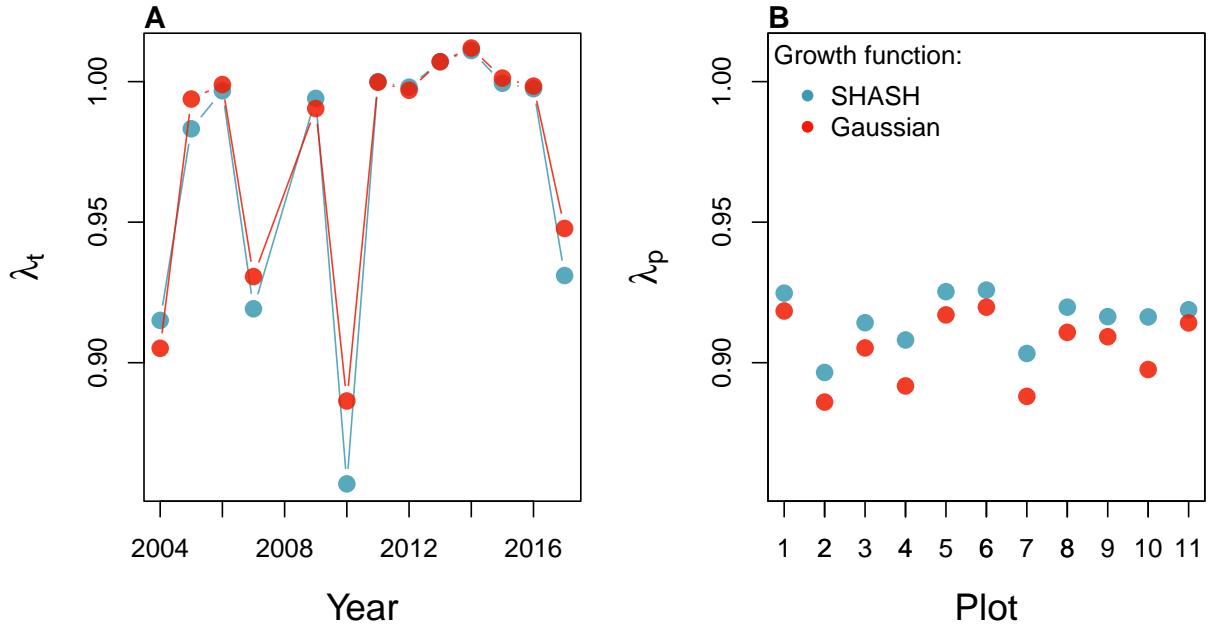


Figure 8: Temporal (A) and spatial (B) heterogeneity in fitness for the tree cholla cactus (*Cylindriopuntia imbricata*) predicted by IPMs using Gaussian or SHASH growth models. Figure made by script `cactus_growth_modeling_qgam.R`.

441 of one's analysis, modeling non-Gaussian size transitions with a Gaussian growth model
 442 could bias results in either direction, or make no difference at all.

443 3 Case study: creosotebush, *Larrea tridentata*

444 Our next case study comes from our studies of the woody shrub creosotebush (*Larrea tri-*
 445 *dentata*) at the Sevilleta Long-Term Ecological Research (LTER) site in central New Mex-
 446 ico, US. At this site as elsewhere in the Southwest US, creosotebush is encroaching into
 447 desert grassland habitats. The data described here were collected along transects span-
 448 ning grass-shrub ecotones to understand patterns of density dependence in creosotebush
 449 demography. Specifically, we asked whether fitness is maximized approaching zero den-
 450 sity at the leading edge of the expansion front (consistent with 'pulled' expansion), or
 451 whether there is a demographic advantage for shrubs at higher density due to positive
 452 feedbacks expected for ecosystem engineers (leading to 'pushed' expansion). Our pub-
 453 lished study (Drees et al., 2023) used a spatial integral projection model (SIPM) to predict
 454 the speed of shrub encroachment, assuming normally-distributed size transitions. Here
 455 we step through our suggested workflow to ask whether a non-Gaussian model would
 456 have been more faithful to the data, and how such an improvement would influence
 457 predictions for the speed of encroachment. We use this case study to illustrate several

458 new elements and challenges, including modeling skewness and kurtosis as functions of
459 expected future size (instead of initial size) and using distributions that are not available
460 as **mgcv** families. In fact, to diversify our use of software and illustrate alternatives, we
461 do not use **gam**'s for any element of this case study.

462 Growth data come from 522 shrubs censused longitudinally over four years (2013–
463 2017). Census individuals occurred along 12 replicate transects (200 to 600 m in length)
464 that spanned gradients of shrub density along shrub-grass ecotones. Size was measured
465 as volume of an elliptical cone based on height and width measurements; the size vari-
466 able of the IPM was the natural logarithm of volume (cm^3). For each census individual,
467 we recorded the size and density of all conspecifics within the five-meter transect “win-
468 dow” in which it occurred, and took the sum of all sizes within the window as a measure
469 of local density. The data are available in Ochocki et al. (2023).

470 As an initial Gaussian approach, we first fit a set of candidate generalized linear
471 mixed models, including transect as a random effect, that represented competing hy-
472 potheses for how size, density, and their interaction influence growth. Specifically, we fit
473 five candidate Gaussian models that included fixed effects of initial size only (model 1),
474 size and density (model 2), and size, density, and their interaction (model 3), allowing
475 for shrubs of different sizes to have different growth responses to local density. Models
476 4 and 5 mirrored models 2 and 3 but included second-order terms for density, allowing
477 for the possibility of non-monotonic density dependence. As in (Drees et al., 2023) we
478 pooled data across three transition years. Initial AIC rankings of these pilot models fa-
479 vor model 4 slightly over model 5 ($\Delta AIC = 0.8$) and significantly over all other models
480 ($\Delta AIC > 2$). However, these models were fit assuming constant variance, and inspection
481 of the residuals of the best model indicate this is not a safe assumption.

482 Unlike our previous case studies, here we have multiple fixed effects that may influ-
483 ence the variance of future size. In cases such as this, we recommend modeling variance
484 as a function of expected future size, rather than initial size as we did with the corals
485 and cacti. The expected (or “fitted”) values reflect the combined influence of all fixed
486 and random effects, and therefore implicitly account for multiple sources of variation in
487 the variance. While there are several convenient software packages for simultaneously
488 modeling Gaussian mean and variance as functions of independent variables (**mgcv** for
489 **gam** models as we saw above, **nlme** for linear models), **modeling variance as a function**
490 **of the mean is trickier because they cannot easily be fit simultaneously**². Here we us an
491 iterative re-weighting approach – which is not elegant, but it works. For Gaussian mod-

²*After I wrote this I discovered that nlme can fit residual variance as a function of fitted(.)*.

492 els, weights w_i can be used to indicate that the observations y_i vary in their dispersion
493 around the mean. In general, the iterative steps are:

1. Fit the expected value and normally-distributed residuals with constant variance:

$$y_i = \mu_i + \epsilon_i$$

$$\epsilon_i \sim N(0, \sigma)$$

2. Fit the standard deviation of the residuals as a function of the expected value.

Weights are derived as the inverse of the fitted variance:

$$\epsilon_i \sim N(0, f(\mu_i))$$

$$w_i = 1/f(\mu_i)^2$$

3. Re-fit the observation model, weighting the residual variance according to step 2:

$$y_i = \mu_i + \epsilon_i$$

$$\epsilon_i \sim N(0, \sigma \times \sqrt{w_i})$$

494 We iterated steps 2 and 3 until the weights did not change. In step 2, we modeled
495 the standard deviation as a simple linear function of the expected value ($\log(f(\mu_i)) =$
496 $\beta_0 + \beta_1 * \mu_i$) but other functions are possible, as is model selection among them. We
497 did this for all candidate models and, for fair AIC comparison, we re-fit all candidate
498 models with the same weights, estimated from the top model. The updated model
499 selection continued to favor model 4, but now with a stronger improvement over the
500 next-best model ($\Delta AIC = 3.0$).

501 The resulting Gaussian growth model predicts strong initial size-dependence and
502 weak and slightly nonlinear (but monotonic) negative density dependence (Fig. 9A).
503 The model accounts for non-constant variance through the fitted weights, which in-
504 dicate greater dispersion for smaller values of expected size ($\beta_1 = -0.21$; Fig. 9B).
505 mostly Quantiles of the standardized residuals indicate size-dependent mostly negative
506 skew and positive excess kurtosis, especially at smaller expected sizes (Fig. 9C).³ As a

³Note that there is still a variance trend in the standardized residuals—rather unsatisfying! I have been through this backwards and forwards and my take is that this is a product of the sample size imbalance between small and large plants. The quantile regression is doing its best. SPE: I think a lot of it has to do with the fitted SD function. `gam(family="gaulss")` says the standard deviation flattens out near the bottom, and using that SD function there is a smaller (but still unsatisfying) variance trend in the standardized residuals.

507 candidate for improvement, we turned to the Johnson's S_U (JSU) distribution, a four-
508 parameter, leptokurtic distribution capable of skew in either direction.

509 Following our suggested workflow, rather than re-fitting a JSU model from scratch,
510 we parameterize a model a model where the residuals from the Gaussian "pilot" model
511 are fitted by a JSU distribution. This relatively easy because the **gamlss.dist** package
512 provides a parameterization of the JSU in which the location parameter μ is the mean
513 and scale parameter σ is the standard deviation (Rigby et al., 2019). Using that, we
514 fitted the "hybrid" model by writing a likelihood function that uses the fitted mean and
515 standard deviation functions from Gaussian pilot model, and estimates the parameters
516 that control skewness and kurtosis as linear functions of predicted future size. The
517 "hybrid" likelihood looks like this [SPE: if we are going to use the spline SD function,](#)
518 [this will need to change:](#)

```
519 ## log_volume_t1 are the size obervations
520 ## GAU_fitted are the predicted future size from the best Gaussian model
521 ## pars is a vector of free parameters to be estimated
522 JSULogLik=function(pars){
523   dJSU(x=log_volume_t1,
524   mu=GAU_fitted,
525   sigma=exp(GAU_sd_coef[1]+GAU_sd_coef[2]*GAU_fitted),
526   nu = pars[1]+pars[2]*GAU_fitted,
527   tau = exp(pars[3]+pars[4]*GAU_fitted), log=TRUE)
528 }
```

529 The mean of the JSU is set to that of the best Gaussian model (`GAU_fitted`) and the
530 standard deviation is a function of the mean according to the coefficients (`GAU_sd_coef`)
531 estimated through iterative re-weighting. Based on diagnostics of the standardized resid-
532 uals (Fig. 9), JSU parameters that control skewness and kurtosis are defined as linear
533 functions of the mean, and those coefficients are estimated by maximum likelihood. This
534 approach relies on the robustness of Gaussian models fitted mean and variance to devia-
535 tions from normality. If one is skeptical of this approach, it is possible to simultaneously
536 re-fit all parameters of the JSU in a maximum likelihood framework. However, incorpo-
537 rating random effects into a custom likelihood model is non-trivial (we provide guidance
538 on one way to do this, using the "shrinkage" approach, in Appendix XX). Therefore a
539 key advantage of the hybrid approach is convenient retention of the fitted random ef-
540 fects and associated variance components, which get shuttled from the Gaussian model
541 into the non-Gaussian model without any fuss (it was critical that we used a parameter-

542 ization of the JSU for which `mu` is the mean and `sigma` is the standard deviation). And,
543 if this approach does not “work” (i.e., deviations from normality biased the fitted val-
544 ues of the Gaussian model) one would quickly find out through the simulation step of
545 the workflow. In this case, the hybrid JSU model performed well, generating simulated
546 data that aligned with the real data better than the best Gaussian model, particularly in
547 **standard deviation⁴** and kurtosis (Fig. 10). **The JSU model has exactly the same mean**
548 **and standard deviation of future size as the Gaussian, but Fig. 9 uses the quantile-based**
549 **nonparametric mean and standard deviation.** The results show that even though the
550 JSU was not fitted to match those, it comes closer than the Gaussian model as a result of
551 accounting for the skew and kurtosis.

552 The improvement of the JSU over the Gaussian growth model, while visually satis-
553 fying, had virtually no influence on SIPM results. Models using Gaussian or JSU growth
554 kernels had nearly identical, monotonic decreases in λ with increasing local density, and
555 nearly identical wave velocities (Fig. 11). This species has very low mortality risk once
556 established (mean remaining life expectancy of a median-sized shrub is 24,408 years)
557 and its population growth and wave expansion are limited by very low seedling recruit-
558 ment ((Drees et al., 2023)). Weak size-dependence in survival likely explains why the
559 improvement in growth modeling had little influence on SIPM predictions.

⁴I am a little mystified as to why the JSU is so much better. It is literally the same SD in both distributions. SPE: it's the same SD but not the same quantile-based nonparametric SD, and the JSU gets the nonparametric SD better. With the curves offset, you can see that in also does better at the NP mean.

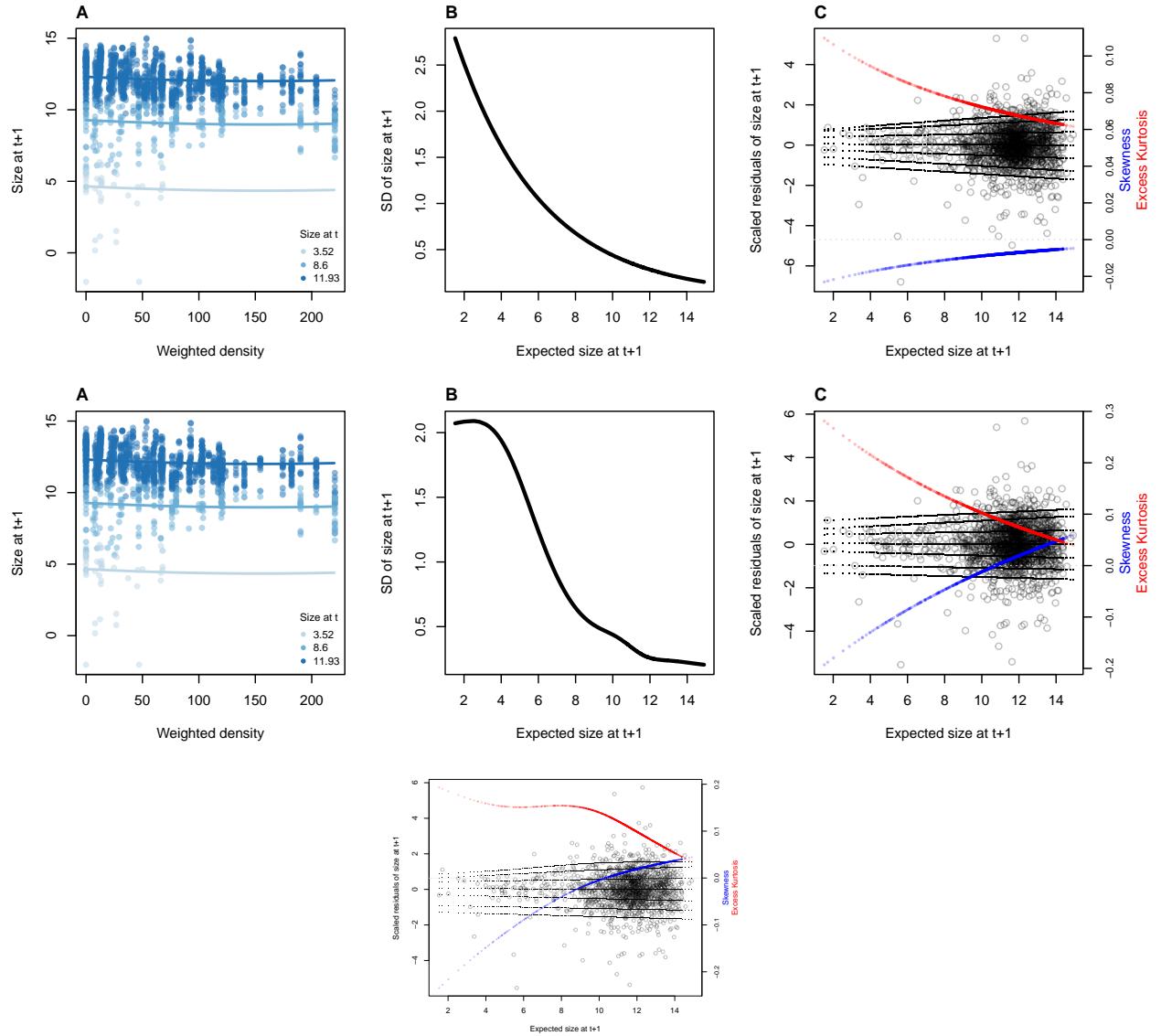


Figure 9: Two and 1/3 versions of the same figure. TOP, lmer growth model with log-linear model for SD as a function of fitted. MIDDLE, lmer growth model with spline SD as a function of fitted using gaulss, quantiles from rq (parametric). Bottom: rightmost panel redrawn with spline model for growth and SD using gaulss, and qgam fitting of residual quantiles. **A**, Creosotebush size transition data with respect to initial size (colors) and local weighted density (sum of sizes of all plants within a five-meter transect window). Size is quantified as the natural logarithm of plant volume (cm^3). **B**, Standard deviation of size at time $t + 1$ as a function of expected size at $t + 1$ (the fitted values), estimated by iterative re-weighting. **C**, Quantile regressions of scaled residuals on size and nonparametric estimates of skewness (blue) and excess kurtosis (red) derived from them. Black lines in **C** show the 5th, 10th, 25th, 50th, 75th, 90th, and 95th quantiles. All figures made by script `creosote_growth_modeling_rq.R`.

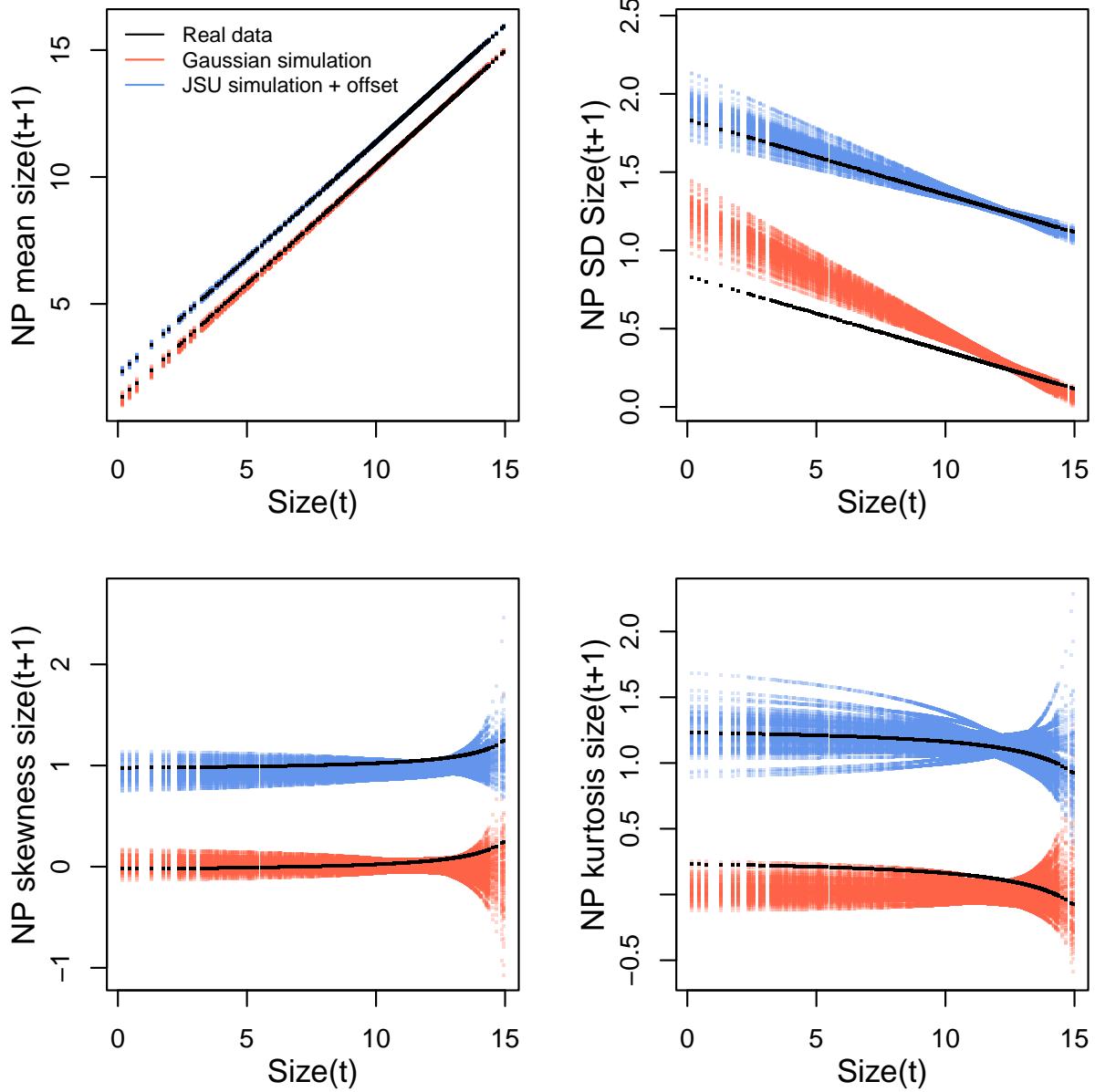


Figure 10: Comparisons between real creosotebush data and data simulated from Gaussian and JSU growth models for mean, standard deviation, NP skewness, and NP excess kurtosis of future size conditional on current size. Moments of the future size distribution are plotted with respect to initial size; their distribution is also conditional on density but initial size is by far the stronger predictor of future size, so we chose this visualization. Values for the JSU model (and the corresponding “real data” values) are offset vertically by one unit for comparison. Figure made by script `creosote_growth_modeling_qgam.R`.

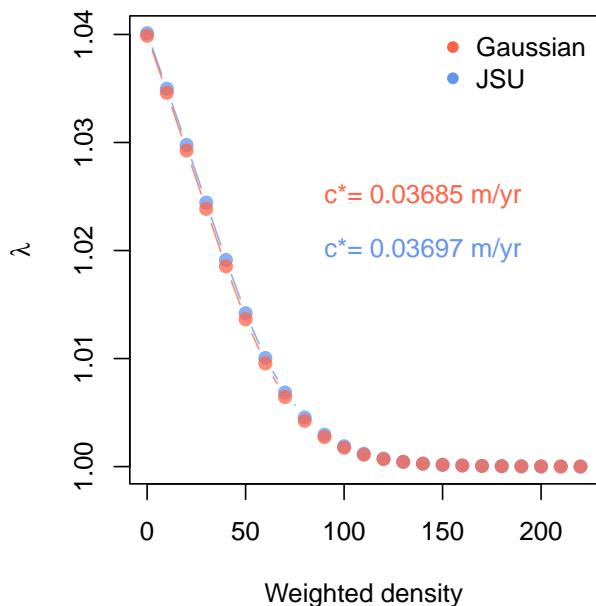


Figure 11: Density dependence in fitness (λ) and asymptotic velocity of the creosote encroachment wave (c^*) for Gaussian and JSU growth kernels. Weighted density is the sum of sizes ($\log(cm^3)$) of all conspecifics within a five-meter transect “window”. Figure made by script `creosote_growth_modeling_qgam.R`.

560 4 Case study: lady orchid, *Orchis purpurea*

561 Our final case study examines selection on life history strategies in the lady orchid *Or-*
562 *chis purpurea*. In a prior study, Miller et al. 2012 contrasted the growth trajectories from
563 year t to $t + 1$ for plants that did or did not flower in year t , as a way to quantify costs
564 of reproduction. The different growth kernels were then used in an IPM to quantify
565 evolutionarily stable life history strategies: the optimal flowering size that balances ben-
566 efits of flowering at larger sizes against the risk of dying before reaching those sizes.
567 The original study assumed a Gaussian distribution of size transitions and allowed for
568 non-constant variance with respect to initial size. Here we re-visit that analysis applying
569 our growth modeling workflow to derive improved growth kernels for flowering and
570 non-flowering orchids.

571 The data, originated by Dr. Hans Jacquemyn and used here with permission, come
572 from 368 plants in a Belgian population that was censused annually from 2003 through
573 2011 (for this reanalysis we are using data only from the “light” habitat). Size was mea-
574 sured as leaf area (cm^3) summed over all leaves, and we analyzed the natural logarithm
575 of total leaf area as the size variable of the IPM.

576 As a pilot Gaussian approach, we fit six candidate models in which the mean was
577 a function of initial size only, additive effects of initial size and flowering status, and
578 interaction between size and flowering, and the standard deviation was a function of
579 size only (models 1-3) or size and flowering status (models 4-6). All models included a
580 random intercept for year. As another variation on software and an alternative to two-
581 step fitting or iterative re-weighting, here we use `nlme::lme()`, which can simultaneously
582 fit linear predictors for mean and variance. For example, model 1 was:

```
583 orchid_GAU[[1]]<-lme(log_area_t1~ log_area_t,  
584 weights=varExp(form=~ log_area_t),  
585 random=~ 1|begin.year,data=orchid_grow,method="ML")
```

586 Model 3 (size \times flowering) was strongly favored, consistent with prior results that non-
587 flowering plants have a growth advantage over flowering plants. Growth variance de-
588 clined with initial size for both reproductive classes (Fig. 12A-B) and skewness and kur-
589 tosis of the standardized residuals indicate strong deviations from normality (Fig. 12C-
590 D). For most sizes, left skew and excess kurtosis were more severe for non-reproductive
591 plants, with tail imbalance ca. 10% of their total and tail weights 10–20% fatter than
592 Gaussian.

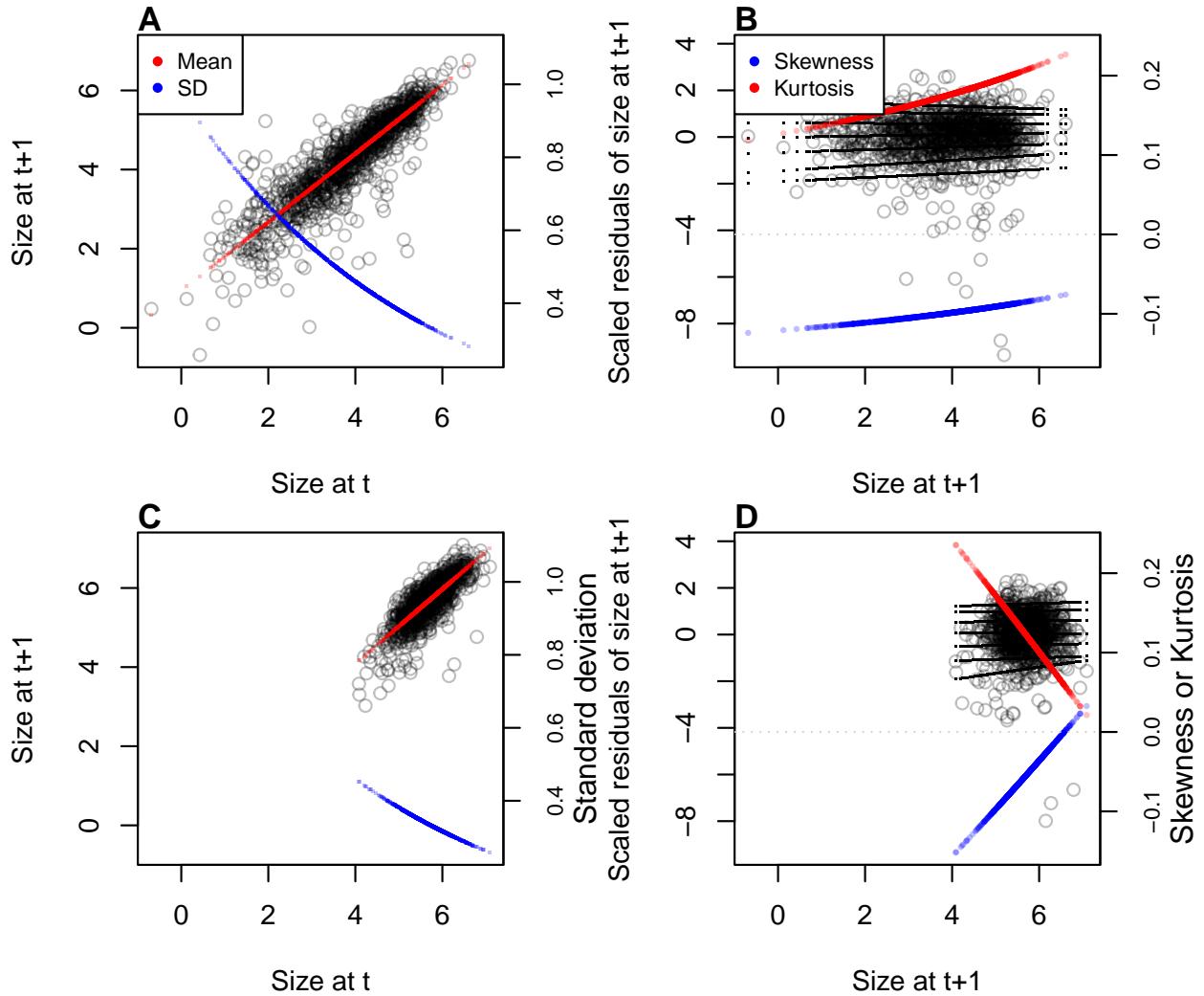


Figure 12

593 As improvements, we explored the skewed t and Johnson's SU distributions, both
 594 leptokurtic distributions with flexible skewness. We were happier with the skewed t ,
 595 which we fit in a similar way as we fit the JSU to the creosote data, setting the mean
 596 and standard deviation to the Gaussian fits and estimating free parameters controlling
 597 skewness and kurtosis:

```

598 ## log_area_t1 and log_area_t are the size obervations
599 ## flowering indicates reproductive status at time t (0 or 1)
600 ## GAU_fitted and GAU_sd are mean and standard deviation from lme
601 ## pars is a vector of free parameters to be estimated
602 SSTLogLik=function(pars){
603   dSST(x=log_area_t1,
```

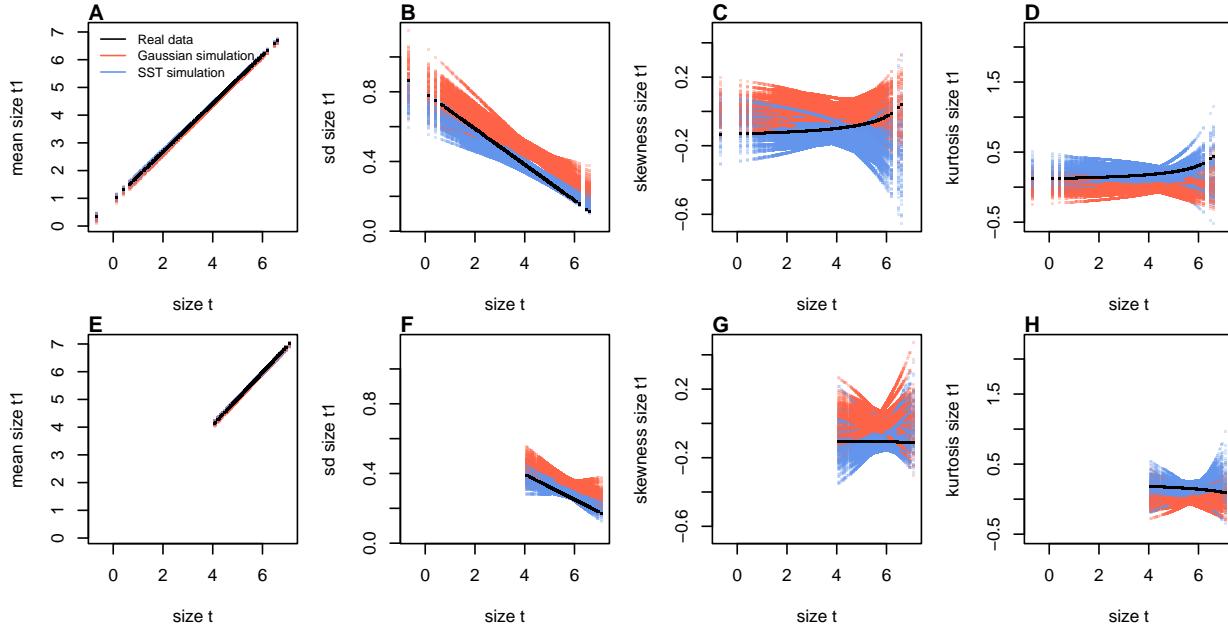


Figure 13: Comparisons between real orchid data and data simulated from Gaussian and skewed t growth models for mean, standard deviation, NP skewness, and NP kurtosis of future size conditional on current size. Top row (A-D) shows plants that were vegetative at the start of the transition year and bottom row (E-H) shows plants that were flowering at the start of the transition year. Figure made by script `orchid_growth_modeling_rq.R`.

```

604     mu=GAU_fitted,
605     sigma=GAU_sd,
606     nu = exp(pars[1] + pars[2]*log_area_t + pars[3]*as.logical(flowering) + pars[4]
607     tau = exp(pars[5] + pars[6]*log_area_t + pars[7]*as.logical(flowering) + pars[8]
608     log=TRUE)
609   }
610
611 gamlss.dist:dsST is a parameterization of the skewed  $t$  in which mu and sigma are the
612 mean and standard deviation, respectively. Based on diagnostics of the standardized
613 residuals (Fig. 12) we allowed nu and tau to vary by size and differ between flowering
614 and non-flowering plants (note that the tau parameter uses a  $\log(x - 2)$  link function).
615 Size transition data simulated from this model corresponded favorably to the real data,
616 much better than the pilot Gaussian model, including improvements in the standard
617 deviation5, skewness, and kurtosis of future size (Fig. 13).
```

Finally, we used the improved growth model to revisit key results of the original study. Miller et al. (2012) used the orchid IPM to estimate the evolutionarily stable strategy (ESS) as the mean size at flowering that maximizes lifetime reproductive success

⁵Again, the improvement here is surprising to me and I am unsure what to say about it.

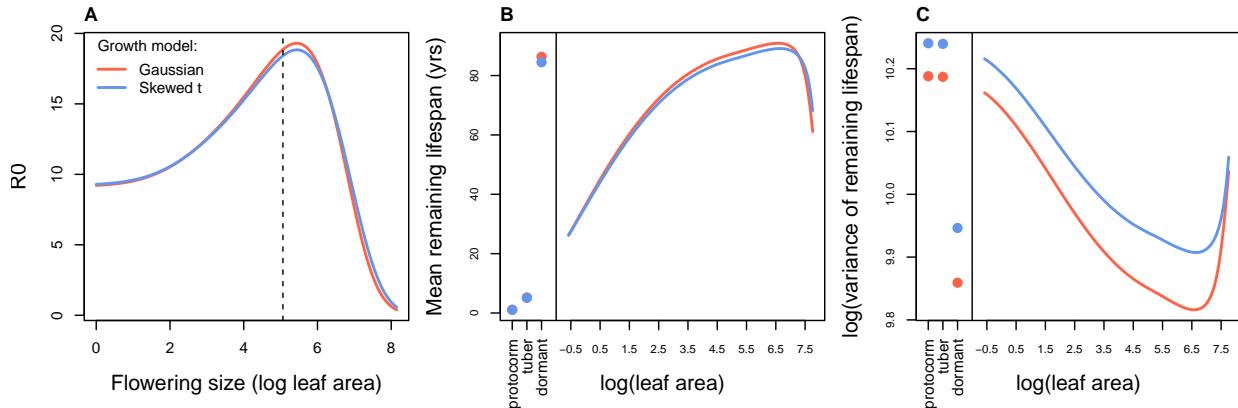


Figure 14: Orchid life history results from IPMs using Gaussian or skewed t growth models. **A**, Lifetime reproductive success (R_0) as a function of mean size of flowering. Dashed vertical line shows the observed mean flowering size. **B-C**, Mean and variance of remaining lifespan as a function of size or stage. The orchid IPM includes three discrete below-ground stages (protocorm, tuber, and dormant plant) in addition to continuous size of above-ground plants.

(R_0), given the constraint that flowering when small reduces growth and thus elevates mortality risk. Repeating that analysis here, we found that improved growth modeling has virtually no influence on predictions for optimal life history strategies (Fig. 14). ESS flowering sizes were nearly identical between IPMs with Gaussian vs skewed t growth models, and both aligned well with the observed mean flowering size (dashed vertical line in Fig. 14A). Extending beyond the original study, we also explored expected remaining lifespan for different ages and sizes (R package **Rage** (Jones et al., 2022)). Gaussian and skewed t growth models predicted nearly identical mean remaining lifespans across the stage and size distribution (Fig. 14B). However, the skewed t model predicted consistently greater variance in remaining lifespan, nearly 10% greater at some sizes.⁶ Thus, as we have seen in other case studies, the practical consequences of improved growth modeling depend on what one aims to learn from the IPM.

5 Discussion

Much of the appeal of integral projection models has stemmed from their embrace of continuous size structure through reliance on regression-based approaches, and the potentially complex fixed- and random-effect structures that these approaches allow. Using

⁶Do not believe this result! I have left it here as a placeholder because I would like to do this correctly. But I think there are problems with Rage's `life_expect_var()` function. The predicted variance declines linearly with matrix dimension.

familiar statistical tools and with relatively few parameters to estimate, IPM users can incorporate important sources of variation in demography and interrogate their influence on ecological and evolutionary dynamics. With this opportunity comes the burden of getting it right: IPMs are good models of the populations they are intended represent only insofar as the statistical models provide good fits to the underlying data. The growth sub-model is the trickiest part of “getting it right” because it defines a distribution of future size conditional on current size. Distributions have many properties – “moments” – and a good growth model should recapitulate the properties of real size transitions. The default assumption of normally distributed size transitions, employed overwhelmingly across 20+ years of IPM studies, is an arbitrary historical precedent. In four case studies (chosen simply because we had the data at our fingertips) and, we suspect, more broadly, skewness and excess kurtosis were common features of size transition data: shrinking was more common than growing, and large changes in size were more common than a Gaussian model would predict. Our most important message is that the standard assumption of normally-distributed size transitions should be abandoned and a more inquisitive process of growth modeling should take its place.

We have attempted to lay out a general workflow for what that process should look like, guided by visual diagnostics of standardized residuals. One implication of relying on visual diagnostics is that goodness of fit is in the eye of the beholder. This approach can empower IPM users to make informed choices, but it is not very prescriptive: we have not suggested any hard rules for when one or another distribution should be used, only that a good growth model should generate data that look like the real thing. Alternatively, model selection could be used to identify best-fitting growth distributions and best-fitting functions for higher moments. However, model selection among growth distributions with 3-5 parameters, each of which may be functions of state variables or fitted values, can quickly explode in complexity, and we are not convinced it is worth the trouble. It is possible to find a good growth model without worrying about which one is “best”.

In all of our case studies, non-Gaussian growth models always yielded more satisfying fits to size transition data than the Gaussian models published in those papers. However, much to our relief, none of these re-analyses yielded a “gotcha” result that overturned results of the original study. In this small sampling of case studies, improved growth modeling had only modest effects on IPM results. We caution against taking too much comfort in this outcome; we can imagine other scenarios in which the choice of the growth distribution could be more consequential. It is worth noting that three of our case studies focused on perennial plants and the fourth focused on corals,

672 which are demographically similar to perennial plants (heavy losses during recruitment
673 but high survival once established). Life cycles such as these may be relatively robust to
674 subtle features of the growth kernel. More systematic comparative analyses across may
675 provide insight into which types of species and life histories are more likely to exhibit
676 strong skewness and kurtosis of size transitions, and the conditions under which demo-
677 graphic analysis is more or less sensitive to these features of size transition. It is also
678 worth noting, as we saw in several case studies, that different outputs from the same
679 model can be more or less sensitive to the choice of growth distribution.

680 Some issues to be discussed.

- 681 • Many software options: lme4/maxLik, mgcv, rstan
- 682 • Comparison of our approach with beta regression method.
- 683 • We have emphasize growth but same principles apply to other continuous state
684 transitions, eg disease IPMs.

685 **Acknowledgements**

686 This research was supported by US NSF grants DEB-1933497 to SPE and DEB-1754468,
687 2208857, and 2225027 to TEXM.

688 **6 Authorship statement**

689 All authors discussed all aspects of the research and contributed to developing methods,
690 analyzing data, and writing and revising the paper.

691 **7 Data accessibility statement**

692 No original data appear in this paper. Should the paper be accepted, all computer scripts
693 supporting the results will be archived in a Zenodo package, with the DOI included at
694 the end of the article. During peer review, our data and code are available at https://github.com/texmiller/IPM_size_transitions.

696 **Literature Cited**

- 697 Anscombe, F. J. and Glynn, W. J. (1983). Distribution of the kurtosis statistic b_2 for
698 normal samples. *Biometrika*, 70(1):227–234.
- 699 Bates, D., Sarkar, D., Bates, M. D., and Matrix, L. (2007). The lme4 package. *R package
700 version*, 2(1):74.
- 701 Bruno, J. F., Ellner, S. P., Vu, I., Kim, K., and Harvell, C. D. (2011). Impacts of aspergillosis
702 on sea fan coral demography: modeling a moving target. *Ecological Monographs*,
703 81(1):123–139.
- 704 Compagnoni, A., Bibian, A. J., Ochocki, B. M., Rogers, H. S., Schultz, E. L., Sneck, M. E.,
705 Elderd, B. D., Iler, A. M., Inouye, D. W., Jacquemyn, H., et al. (2016). The effect of
706 demographic correlations on the stochastic population dynamics of perennial plants.
707 *Ecological Monographs*, 86(4):480–494.
- 708 Conn, P. B., Johnson, D. S., Williams, P. J., Melin, S. R., and Hooten, M. B. (2018). A guide
709 to bayesian model checking for ecologists. *Ecological Monographs*, 88(4):526–542.
- 710 Cooch, E. G. and White, G. C. (2020, accessed 5/17/2020). *Program MARK - a 'gentle
711 introduction'*. Available at phidot.org.
- 712 Coulson, T. (2012). Integral projections models, their construction and use in posing
713 hypotheses in ecology. *Oikos*, 121(9):1337–1350.
- 714 Crone, E. E. (2016). Contrasting effects of spatial heterogeneity and environmental
715 stochasticity on population dynamics of a perennial wildflower. *Journal of Ecology*,
716 104(2):281–291.
- 717 Czachura, K. and Miller, T. E. (2020). Demographic back-casting reveals that subtle
718 dimensions of climate change have strong effects on population viability. *Journal of
719 Ecology*.
- 720 D'Agostino, R. B. (1970). Transformation to normality of the null distribution of g_1 .
721 *Biometrika*, pages 679–681.
- 722 Davis, C. (2015). *sgt: Skewed Generalized T Distribution Tree*. R package version 2.0.
- 723 Drees, T., Ochocki, B. M., Collins, S. L., and Miller, T. E. (2023). Demography and
724 dispersal at a grass-shrub ecotone: a spatial integral projection model for woody plant
725 encroachment. *Ecological Monographs*, page e1574.

- 726 Easterling, M. R., Ellner, S. P., and Dixon, P. M. (2000). Size-specific sensitivity: applying
727 a new structured population model. *Ecology*, 81(3):694–708.
- 728 Elderd, B. D. and Miller, T. E. (2016). Quantifying demographic uncertainty: Bayesian
729 methods for integral projection models. *Ecological Monographs*, 86(1):125–144.
- 730 Ellis, M. M. and Crone, E. E. (2013). The role of transient dynamics in stochastic popula-
731 tion growth for nine perennial plants. *Ecology*, 94(8):1681–1686.
- 732 Ellner, S. P., Adler, P. B., Childs, D. Z., Hooker, G., Miller, T. E., and Rees, M. (2022).
733 A critical comparison of integral projection and matrix projection models for demo-
734 graphic analysis: Comment. *Ecology*, 103(10):e3605.
- 735 Ellner, S. P., Childs, D. Z., and Rees, M. (2016). *Data-driven Modeling of Structured Popula-*
736 *tions: A Practical Guide to the Integral Projection Model*. Springer, New York.
- 737 Gould, W. R. and Nichols, J. D. (1998). Estimation of temporal variability of survival in
738 animal populations. *Ecology*, 79:2531 – 2538.
- 739 Gu, C. (2013). *Smoothing Spline ANOVA Models*. Springer Science+Business Media, New
740 York, 2 edition.
- 741 Hadfield, J. D. et al. (2010). Mcmc methods for multi-response generalized linear mixed
742 models: the mcmcglmm r package. *Journal of Statistical Software*, 33(2):1–22.
- 743 Héault, B., Bachelot, B., Poorter, L., Rossi, V., Bongers, F., Chave, J., Paine, C. T., Wagner,
744 F., and Baraloto, C. (2011). Functional traits shape ontogenetic growth trajectories of
745 rain forest tree species. *Journal of ecology*, 99(6):1431–1440.
- 746 Jones, M. and Pewsey, A. (2009). Sinh-arcsinh distributions. *Biometrika*, 96:761 – 780.
- 747 Jones, M. C., Rosco, J. F., and Pewsey, A. (2011). Skewness-invariant measures of kurtosis.
748 *The American Statistician*, 65(2):89 – 95.
- 749 Jones, O. R., Barks, P., Stott, I., James, T. D., Levin, S., Petry, W. K., Capdevila, P., Che-
750 Castaldo, J., Jackson, J., Römer, G., et al. (2022). Rcompadre and rage—two r pack-
751 ages to facilitate the use of the compadre and comadre databases and calculation of
752 life-history traits from matrix population models. *Methods in Ecology and Evolution*,
753 13(4):770–781.
- 754 Komsta, L. and Novomestky, F. (2015). Moments, cumulants, skewness, kurtosis and
755 related tests. *R package version*, 14(1).

- 756 Link, W. A. and Nichols, J. D. (1994). On the importance of sampling variance to inves-
757 tigations of temporal variation in animal population size. *Oikos*, 69(3):539 – 544.
- 758 Louthan, A. M., Keighron, M., Kiekebusch, E., Cayton, H., Terando, A., and Morris, W. F.
759 (2022). Climate change weakens the impact of disturbance interval on the growth rate
760 of natural populations of venus flytrap. *Ecological Monographs*, 92(4):e1528.
- 761 McGillivray, H. (1986). Skewness and asymmetry: measures and orderings. *Annals of
762 Statistics*, 14:994–1011.
- 763 Metcalf, C. J. E., Ellner, S. P., Childs, D. Z., Salguero-Gómez, R., Merow, C., McMahon,
764 S. M., Jongejans, E., and Rees, M. (2015). Statistical modelling of annual variation for
765 inference on stochastic population dynamics using Integral Projection Models. *Methods
766 in Ecology and Evolution*, 6:1007–1017.
- 767 Miller, T. E. (2020). Long-term study of tree cholla demography in the los pinos
768 mountains, sevilleta national wildlife refuge. [https://doi.org/10.6073/pasta/
769 dd06df3f950afe4a4642306182237d13](https://doi.org/10.6073/pasta/dd06df3f950afe4a4642306182237d13).
- 770 Miller, T. E., Louda, S. M., Rose, K. A., and Eckberg, J. O. (2009). Impacts of insect
771 herbivory on cactus population dynamics: experimental demography across an envi-
772 ronmental gradient. *Ecological Monographs*, 79(1):155–172.
- 773 Miller, T. E., Williams, J. L., Jongejans, E., Brys, R., and Jacquemyn, H. (2012). Evolution-
774 ary demography of iteroparous plants: incorporating non-lethal costs of reproduction
775 into integral projection models. *Proceedings of the Royal Society B: Biological Sciences*,
776 279(1739):2831–2840.
- 777 Ochocki, B. M., Drees, T., and Miller, T. E. (2023). Density-dependent demography of
778 creosote bush (*larrea tridentata*) along grass-shrub ecotones. <https://doi.org/10.6073/pasta/ca53c16f16dcf9fb11f3ee99ea5445ac>.
- 780 Ohm, J. R. and Miller, T. E. (2014). Balancing anti-herbivore benefits and anti-pollinator
781 costs of defensive mutualists. *Ecology*, 95(10):2924–2935.
- 782 Ozgul, A., Childs, D. Z., Oli, M. K., Armitage, K. B., Blumstein, D. T., Olson, L. E., Tul-
783 japurkar, S., and Coulson, T. (2010). Coupled dynamics of body mass and population
784 growth in response to environmental change. *Nature*, 466(7305):482–485.

- 785 Peterson, M. L., Morris, W., Linares, C., and Doak, D. (2019). Improving structured
786 population models with more realistic representations of non-normal growth. *Methods*
787 in Ecology and Evolution
- 788 Plard, F., Schindler, S., Arlettaz, R., and Schaub, M. (2018). Sex-specific heterogeneity
789 in fixed morphological traits influences individual fitness in a monogamous bird
790 population. *The American Naturalist*, 191(1):106–119.
- 791 Rees, M., Childs, D. Z., and Ellner, S. P. (2014). Building integral projection models: a
792 user's guide. *Journal of Animal Ecology*, 83(3):528–545.
- 793 Rigby, R. A., Stasinopoulos, M. D., Heller, G. Z., and De Bastiani, F. (2019). *Distributions*
794 for modeling location, scale, and shape: Using GAMLSS in R. CRC press.
- 795 Salguero-Gómez, R. and Casper, B. B. (2010). Keeping plant shrinkage in the demo-
796 graphic loop. *Journal of Ecology*, 98(2):312–323.
- 797 Schielzeth, H., Dingemanse, N. J., Nakagawa, S., Westneat, D. F., Allegue, H., Teplitsky,
798 C., Réale, D., Dochtermann, N. A., Garamszegi, L. Z., and Araya-Ajoy, Y. G. (2020).
799 Robustness of linear mixed-effects models to violations of distributional assumptions.
800 *Methods in ecology and evolution*, 11(9):1141–1152.
- 801 Schultz, E. L., Eckberg, J. O., Berg, S. S., Louda, S. M., and Miller, T. E. (2017). Native
802 insect herbivory overwhelms context dependence to limit complex invasion dynamics
803 of exotic weeds. *Ecology letters*, 20(11):1374–1384.
- 804 Stasinopoulos, D. M., Rigby, R. A., et al. (2007). Generalized additive models for location
805 scale and shape (gamlss) in r. *Journal of Statistical Software*, 23(7):1–46.
- 806 Stubberud, M. W., Vindenes, Y., Vøllestad, L. A., Winfield, I. J., Stenseth, N. C., and Lan-
807 gangen, Ø. (2019). Effects of size-and sex-selective harvesting: An integral projection
808 model approach. *Ecology and Evolution*, 9(22):12556–12570.
- 809 Wan, X., Wang, W., Liu, J., and Tong, T. (2014). Estimating the sample mean and stan-
810 dard deviation from the sample size, median, range and/or interquartile range. *BMC*
811 *medical research methodology*, 14:1–13.
- 812 Williams, J. L., Miller, T. E., and Ellner, S. P. (2012). Avoiding unintentional eviction from
813 integral projection models. *Ecology*, 93(9):2008–2014.

814 Wood, S. (2017). *Generalized Additive Models: An Introduction with R.* Chapman and
815 Hall/CRC, 2 edition.

816 Zhang, J. L. (2014). Comparative investigation of three bayesian p values. *Computational
817 Statistics & Data Analysis*, 79:277–291.

Appendices

S.1 The Jones-Pewsey distribution

Jones and Pewsey (2009) introduced a simple, tractable generalization of the Normal distribution with two additional parameters determining asymmetry (skewness), and tail weight (kurtosis) which can be either lighter or heavier than the Gaussian. It is defined as a transformation of a $\text{Normal}(0,1)$ random variable using the hyperbolic sine function (\sinh) and its inverse (asinh), as follows. The distribution family's base probability density $f_{\epsilon,\delta}$ is the probability density of the random variable $X_{\epsilon,\delta}$ where

$$Z = \sinh(\delta \text{ asinh}(X_{\epsilon,\delta}) - \epsilon) \quad (\text{S.1})$$

and Z has a $\text{Normal}(0,1)$ distribution. Equivalently,

$$X_{\epsilon,\delta} = \sinh\left(\frac{1}{\delta} \text{ asinh}(Z) + \frac{\epsilon}{\delta}\right). \quad (\text{S.2})$$

Parameters $\delta = 1, \epsilon = 0$ give the $\text{Normal}(0,1)$ distribution. Skewness has the sign of ϵ , and $\delta > 0$ controls tail weight, with heavier than Gaussian tails for $\delta < 1$ and lighter than Gaussian tails for $\delta > 1$. A formula for the density $f_{\epsilon,\delta}$ is given by Jones and Pewsey (2009, eqn. 2). The general four-parameter family with location parameter μ and scale parameter σ is defined as the probability densities of $\mu + \sigma X_{\epsilon,\delta}$. We refer to this as the JP distribution family.

As is unfortunately the case for most four-parameter distributions μ is not the mean, σ is not the standard deviation, ϵ is not the skew and δ is not the kurtosis. All else being equal, larger μ gives a larger mean, larger σ gives a higher standard deviation, higher ϵ gives higher asymmetry, and higher δ gives heavier tail weight. But each moment is jointly determined by all four parameters.

The main advantage of the JP distribution is that the attainable combinations of skewness and kurtosis are very broad, compared to other four-parameter families, and come very close to the theoretical limits on kurtosis as a function of skewness (Jones and Pewsey, 2009, Fig. 2). Additionally, being a transformation of the Normal makes it very simple to generate random numbers from the distribution, and to compute probability density, cumulative distribution, and quantile functions. There are also simple analytic formulas for the first four moments (Jones and Pewsey, 2009, p. 764) which we use below to define a centered and scaled version in which μ and σ are the mean and standard deviation.

848 The definition (S.2) shows that the distribution depends on ϵ only through the ratio
849 ϵ/δ . We have found that this property can be problematic for estimating distribution
850 parameters. Even with good sized ($n = 250$ or 500) data sets generated from the distri-
851 bution with known parameters, both maximum likelihood and Bayesian estimation were
852 unstable for some values of ϵ and δ , occasionally yielding estimates far from the truth.
853 One cause was a ridge in the (ϵ, δ) likelihood surface with a constant of ϵ/δ . Another is
854 that when δ is large, changes in ϵ have little effect.

855 To avoid that problems, we reparameterize the distribution as follows:

856
$$X_{\lambda, \tau} = \sinh(e^{-\tau} \operatorname{asinh}(Z) + \lambda). \quad (\text{S.3})$$

857 Thus, the two parameterizations are related by

858
$$\delta = e^\tau, \epsilon = \delta\lambda = e^\tau\lambda. \quad (\text{S.4})$$

859 The definition of τ allows it to take any real value, with negative values giving thinner
860 than Gaussian tails and positive values giving fatter than Gaussian tails. λ also can take
861 any real value, and the distribution's skew has the same sign as λ . Because the sinh
862 function is nonlinear, it is still the case that the skew depends on τ as well as λ , but the
863 "crosstalk" between the kurtosis and skew parameters is weaker. As a result, we found
864 that maximum likelihood estimation of parameter values was generally more reliable if
865 the distribution is parameterized in terms of τ and λ .

866 S.2 Estimating mixed-effects models using shrinkage

867 Ecologists often fit demographic and other statistical models that include random effects
868 terms to quantify variation among years, spatial locations, individuals, etc. Random
869 effects are a natural choice when interest centers on the magnitude of variation (e.g., how
870 much does mortality vary among years?) rather than individual values (e.g., mortality
871 in 2013). They also allow each estimate to "borrows strength" from others, so that (for
872 example) the estimate from a year with small sample size (and thus large sampling
873 variability) is shifted towards the center of the overall distribution.

874 Specialized software is often used to fit such models, such as the **nlme**, **lme4**, **mgcv**
875 and **gamm4** libraries in R, but these only allow a small subset of the distribution families
876 we want to consider for modeling growth increments (the **gamLss** package allows many
877 distribution families, but in our experience, even when random effects are simple in
878 structure the fitting algorithms often fail to converge or fail to find the global optimum).

879 One way past this limitation is Bayesian estimation, using STAN with user-written
880 (or borrowed) code for the chosen growth distribution (see section XX for an example).
881 In this appendix we describe another option, introduced by Link and Nichols (1994)
882 and Gould and Nichols (1998): fitting a fixed-effects model by Maximum Likelihood,
883 followed by shrinkage of coefficient estimates. None of the ideas here are original. The
884 material overlaps Appendix S1 of Metcalf et al. (2015), but for completeness we make
885 it self-contained. Appendix D of Cooch and White (2020) (written by K.D. Burnham)
886 provides more details and examples in the context of capture-recapture analysis.

887 Here we explain shrinkage using a simple model based on our analysis of *Pseu-*
888 *doroegneria spicata*. That model includes random effects for between-year variation in
889 the slope and intercept of future size (log area) as a function of initial size. To keep
890 the example simple, we assume that initial size and year are the only covariates, and
891 we assume that growth increments follow a skew-Normal distribution with noncon-
892 stant variance and constant skew parameter. Code for this example is in the script
893 `SimpleShrinkageExample.R`. The first part of the script generates an artificial data set
894 by fitting the model to a subset of the growth data (20th century Control plots), and
895 randomly generating new “size next year” values for each individual in the actual data
896 set. The second part contains the “data” analysis.

897 As in our *P. spicata* analysis, we assumed that that the skew and kurtosis parameters
898 were functions of the location parameter; this dominated ($\Delta AIC \approx 30$) the alternate
899 model with skew and kurtosis depending on initial size. The analogous Gaussian model,
900 with constant variance, could be fitted as follows using `lmer`:

901 `lmer(new.size ~ init.size + (init.size|year), data=growthData, REML=TRUE);`
902 where `growthData` is a data frame holding the data with year as an unordered factor.
903 For our skew-Normal model, we instead use maximum likelihood with all between-year
904 variation included as fixed effects. The appropriate design matrix is easily constructed
905 using the `model.matrix` function:

906 `U = model.matrix(~ year + init.size:year - 1, data=growthData)`

907 If there are T years, the matrix `U` specified in this way has $2T$ columns corresponding to
908 n annual intercepts and T annual slopes.

909 Using this design matrix, we can readily write a log likelihood function for use with
910 the `maxLik` package, with a log link function for the variance because it is necessarily
911 positive:

912 `LogLik=function(pars,new.size,U){`

```

913     pars1 = pars[1:ncol(U)]; pars2=pars[-(1:ncol(U))];
914     mu = U%*%pars1;
915     sigma = exp(pars2[1]+pars2[2]*mu);
916     dSN1(new.size, mu=mu, sigma=sigma, nu=pars2[3], log=TRUE)
917 }

```

918 Parameters and their standard errors can then be estimated with `maxLik`, starting
919 from a random guess:

```

920   start=c(runif(ncol(U)), rep(0,3))
921   out=maxLik(logLik=LogLik,start=start, new.size=simData$new.size,U=U,
922     method="BHHH",control=list(iterlim=5000,printLevel=1),finalHessian=TRUE);
923   coefs = out$estimate; # parameters
924   V = vcov(out); SEs = sqrt(diag(V)); # standard errors

```

925 In real life we would repeat the optimization several times with several different starting
926 values, to be confident that the optimal parameter values had been found.

927 Focus now on the year-specific intercept parameters $\hat{a}_t, t = 1, 2, \dots, T$. We can view
928 the year-specific estimates \hat{a}_t as consisting of unobserved true values a_t plus sampling
929 error:

$$930 \quad \hat{a}_t = a_t + \varepsilon_t \quad (\text{S.5})$$

931 Because of the sampling errors, the sample variance of the estimates \hat{a}_t is an upward-
932 biased estimate of the true across-year variance in the parameter. That is undesirable if
933 the model will be used to project how temporal variability affects population dynamics.
934 However, maximum likelihood estimation gives us an approximate variance-covariance
935 matrix \hat{V} of the sampling errors, V in the code above. With that information, we can
936 estimate the parameters of a random effects model for the intercept parameters, and
937 thereby improve the year-specific estimates and the estimate of the across-year variance.

938 The model is as follows. We make the standard mixed-models assumptions that the
939 a_t are drawn independently from some fixed distribution with unknown variance σ^2 .
940 We also assume that the estimates \hat{a}_t are unbiased, that is

$$941 \quad \mathbb{E}(\varepsilon_t | a_t) = 0. \quad (\text{S.6})$$

942 These are optimistic assumptions, but not excessively optimistic. Some degree of tem-
943 poral correlation will often be present, and as we explain at the end, it is theoretically
944 possible to account for it. Maximum likelihood parameter estimates are not unbiased,
945 but if the assumptions of maximum likelihood are satisfied the bias is asymptotically

946 negligible compared to the standard error (the bias scales as the inverse of sample size,
 947 the standard error as the square root of the inverse of sample size).

948 Let S^2 denote the sample variance of the estimates \hat{a}_t . It can then be shown that

$$949 \quad \mathbb{E}(S^2) = \sigma^2 + \frac{1}{T} \sum_{t=1}^T \mathbb{E}Var(\varepsilon_t) - \frac{1}{T(T-1)} \sum_{i=1}^{j-1} \sum_{j=1}^T \mathbb{E}Cov(\varepsilon_i, \varepsilon_j). \quad (\text{S.7})$$

950 This is eqn. (1) in Gould and Nichols (1998) in our notation, without the term that results
 951 from temporal autocorrelation.

952 The terms besides σ^2 on the right-hand are the expected impact of sampling error
 953 on the across-year variance of the parameter estimates; their presence makes S^2 a biased
 954 estimated of σ^2 . However, all of those terms correspond to entries in the variance-
 955 covariance matrix V . We can therefore use our estimated variance-covariance matrix \hat{V}
 956 to removes the bias due to sampling variability:

$$957 \quad \hat{\sigma}^2 = S^2 - \frac{1}{T} \sum_{t=1}^T \hat{V}_{t,t} + \frac{1}{T(T-1)} \sum_{i=1}^{j-1} \sum_{j=1}^T \hat{V}_{i,j}. \quad (\text{S.8})$$

958 $\hat{\sigma}^2$ estimates the variance of the distribution from which the a_t are assumed to be drawn.

959 Using that estimate, we can adjust the year-specific estimates to reduce the ex-
 960 pected impact of sampling error. Depending on your purposes, there are two possible
 961 adjustments. The first option is the one used in the popular capture-recapture analysis
 962 software Mark Cooch and White (2020),

$$963 \quad \tilde{a}_t = \bar{a}_t + \sqrt{\frac{\hat{\sigma}^2}{\hat{\sigma}^2 + \hat{V}_{t,t}}} (\hat{a}_t - \bar{a}_t). \quad (\text{S.9})$$

964 The name “shrinkage” comes from the fact that each estimate is adjusted towards the
 965 overall mean, with larger adjustments of values that have higher estimated sampling
 966 error variance, $\hat{V}_{t,t}$. This shrinkage estimate has the property that the expected sample
 967 variance of the adjusted estimates \tilde{a}_t is very close to $\hat{\sigma}^2$, so the \tilde{a}_t approximate the actual
 968 amount of parameter variation.

969 The second is to replace \hat{a}_t by the least-squares estimate of a_t under the additional
 970 assumption that the a_t are drawn from a Gaussian distribution; this is given by

$$971 \quad \tilde{a}_t = \bar{a}_t + \frac{\hat{\sigma}^2}{\hat{\sigma}^2 + \hat{V}_{t,t}} (\hat{a}_t - \bar{a}_t). \quad (\text{S.10})$$

972 This option is theoretically preferable if the Gaussian assumption is reasonable, and you
 973 are more interested in year-specific values rather than across-year variance. However,
 974 Metcalf et al. (2015) found that even (S.9), which does less shrinkage, resulted in a small
 975 downward bias in the temporal variance of population growth rates. This argues for
 976 always using the first option, and we do the same here.

977 We differ from MARK, however, in using (S.8) rather than an iterative method
 978 that takes (S.8) as its starting estimate and refines the estimate by using weighted least
 979 squares based on the current estimate. Metcalf et al. (2015) found, in simulation studies,
 980 that the iterative method was either slightly beneficial or wildly inaccurate. We therefore
 981 advise against it.

982 Finally, as mentioned above, the estimate of σ^2 can account for temporal autocor-
 983 relation in the a_t . When present, those correlations add a term to eqn. (S.7) (see eqn.
 984 (1) in Gould and Nichols (1998)), which can be estimated from the sample autocorre-
 985 lation of the \hat{a}_t . We do not recommend doing this (and therefore omit the formulas)
 986 because the autocorrelations can only be reliably estimated if they fall to nearly zero
 987 within lag $m \ll T$, in which case the autocorrelation term is small (specifically, $O(m/T)$).
 988 Otherwise, the random error from using poorly estimated autocorrelations is likely to
 989 outweigh the small bias from omitting that term.

990 The take-home message is that estimating random effects from the regression coef-
 991 ficients is very simple:

```

992 # Variance-covariance matrices for intercepts and slopes
993 V1 = V[1:T,1:T]; V2 = V[(T+1):(2*T),(T+1):(2*T)];
994 # Extract year-specific intercepts, center them to zero
995 fixed.fx = coefs[1:T]; fixed.fx = fixed.fx-mean(fixed.fx);
996
997 # Estimate sigma^2
998 var.hat = mean(fixed.fx^2) - mean(diag(V1)) +
999             (sum(V1)-sum(diag(V1)))/(2*T*(T-1));
1000
1001 # Shrink deviations from the mean
1002 shrinkRanIntercept = fixed.fx*sqrt(var.hat/(var.hat + diag(V1)));
1003
1004 # Do it all again for the slopes
1005 fixed.fx2 = coefs[(T+1):(2*T)]; fixed.fx2 = fixed.fx2-mean(fixed.fx2);
1006 var2.hat = mean(fixed.fx2^2) - mean(diag(V2)) +
1007             (sum(V2)-sum(diag(V2)))/(2*T*(T-1));
  
```

```
1008 shrinkRanSlope = fixed.fx2*sqrt(var2.hat/(var2.hat + diag(V2)));
```

1009 The figure below shows the results for one artificial PSSP “data” set, having $T = 22$
1010 years and growth measurements on about 175 individuals/year on average. The true
1011 random year effects (the ones used to generate the data) are recovered with good accu-
1012 racy and no bias. In particular there is no sign of extreme values being pulled in too
1013 far towards the mean, which would cause an S-shaped graph of estimated versus true
1014 values.

