Nonlinear Ordinal Regression to Predict Bud Dormancy Requirements and Bud Burst in Deciduous Trees

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In review

Conflict of interest statement

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest

Author contribution statement

GB designed and fit the model. SS designed the experiment, LA established the experiment and collected the data with the assistance of DF and EF. GB, EL, NB, IC, EF and SS wrote the manuscript.

Keywords

Abstract

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Most experimental studies on tree dormancy use chilling treatments, after which shoots are exposed to heat. Dormancy completion is typically registered when a certain percentage of buds in a shoot have burst, and climatic requirements are compressed into summary statistics using temperature-based chill and heat models. However, this methodology does not consider chilling requirement and bud burst as a continuous, sequential, and time dependent process that is particular for each bud in a shoot. Moreover, the implicit assumption in such studies that chill and heat accumulation are independent processes is contradicted by known interactions between chill accumulation and heat needs.

As an alternative, we propose to model bud progression through dormancy and bud burst using a Bayesian hierarchical nonlinear ordinal regression model, in which a single latent parameter μ drives movement through observed developmental stages. As μ increases, the probability of occupying each stage (i.e. dormant, 'green tip' and leaf-out) changes, according to thresholds that define the transitions (θ). μ is linked to heat and chill accumulation via a logistic function. This allows for a nonlinear, saturating effect of chilling on bud development, and constitutes a robust analytic method for deriving chill saturation points.

The model was trained and tested using data from 14,400 individual buds from 48 trees of 8 cherry cultivars, which were exposed to ten levels of chilling and subsequently to homogeneous heat conditions. Cultivars showed differences in their relative sensitivity to chill and heat effects and in the uncertainty around these parameter estimates. Results suggest strong differentiation of cultivars by both chilling requirements and responsivity to heat accumulation. This methodology shows promise in providing robust, analytically-derived estimates of phenological responses, which are crucial for predicting plasticity under changing climate conditions, making this dormancy model a promising tool for assessing adaptation strategies for deciduous orchards.

Ethics statements

(Authors are required to state the ethical considerations of their study in the manuscript, including for cases where the study was exempt from ethical approval procedures)

Does the study presented in the manuscript involve human or animal subjects: No

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12 **Abstract**

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16 and heat models. However, this methodology does not consider chilling requirement and bud burst as
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24 (θ). μ is linked to heat and chill accumulation via a logistic function. This allows for a nonlinear,
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27 The model was trained and tested using data from 14,400 individual buds from 48 trees of 8 cherry
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30 uncertainty around these parameter estimates. Results suggest strong differentiation of cultivars by
31 both chilling requirements and responsivity to heat accumulation. This methodology shows promise in
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33 predicting plasticity under changing climate conditions, making this dormancy model a promising tool
34 for assessing adaptation strategies for deciduous orchards.

35 **Keywords: chilling, temperate trees, climate change, dormancy release, warm winter, bud-break**

36 **1   Introduction**

Deciduous trees from temperate and boreal climates undergo a period of dormancy during the cold season, which enables them to survive unfavorable winter conditions (Faust et al., 1997). During dormancy, the meristem of the buds or any other parts of a plant is unable to undergo cell division and expansion (Rohde and Bhalerao, 2007; Cooke et al., 2012). In order to resume growth, trees require exposure to certain environmental stimuli. While some authors have demonstrated an important role of photoperiod in dormancy release (Ibanez et al., 2010; Kozarewa et al., 2010), the rest-breaking behavior of deciduous fruit and nut trees appears to be driven almost exclusively by temperature (Luedeling et al., 2011; Cooke et al., 2012; Benmoussa et al., 2017; Cook et al., 2017). As tree buds progress through their rest period, they require exposure to cool and subsequent warm conditions to overcome the dormant state (Egea et al., 2003; Harrington et al., 2010; Luedeling et al., 2013; Guo et al., 2015; Benmoussa et al., 2017).

In accordance with these requirements, the dormancy period is often conceptualized as consisting of a phase of endodormancy, during which buds accumulate 'chill', and a period of ecodormancy, when tree-specific chilling requirements (CR) have been met and buds begin to accumulate heat, until they break to initiate leaf or flower development (Lang, 1987; Lang et al., 1987). While this general pattern is widely accepted, many questions still surround the physiology and genetics of the dormancy-breaking process (Campoy et al., 2011). Accordingly, there is substantial uncertainty about how to quantify chill and heat accumulation (Luedeling, 2012), whether chill and heat requirements are independent (Luedeling et al., 2009b) or interact with each other (Darbyshire et al., 2016), and during what periods chill and heat accumulate (Luedeling and Gassner, 2012).

Many researchers have made use of phenology observations, derived either from long-term monitoring programs or from experiments under controlled conditions, to estimate the chilling and heat requirements of trees (Ruiz et al., 2007; Alburquerque et al., 2008; Zhang and Taylor, 2011; Luedeling et al., 2013; Guo et al., 2015) and to produce prediction models for spring phenology (Chung et al., 2011; Parker and Abatzoglou, 2018). However, evaluating such records is not trivial, because buds do not change visibly during most of the dormancy season. When they finally break, buds have already fulfilled both their chilling and heat requirements, which makes it difficult to derive reliable information on each of these climatic needs, or on the way they may have interacted. Studies that have produced such information have usually relied on tenuous assumptions about chill and heat accumulation during dormancy, e.g. that buds fulfill chill and heat requirements sequentially (Luedeling et al., 2009b), or that commonly used chill models are biologically meaningful enough to perform accurately in artificial temperature treatments (Guo et al., 2014). The potential errors that these assumptions introduce are rarely accounted for but may well be substantial (Luedeling et al., 2009a; Luedeling and Brown, 2011).

Another implicit assumption of most evaluations of phenology data is that trees respond as homogeneous units that pass certain development thresholds, e.g. the transition from endodormancy to ecodormancy, at a clearly defined time, after exposure to climatic stimuli. In reality, however, trees usually have buds in different developmental stages. While the entire population of all buds can be summarized at the tree level, e.g. in the developmental stage "about 40% of flowers open" on the BBCH scale for cherries (stage 65; (Meier et al., 1994)), it seems more plausible that every bud undergoes its own progression through dormancy.

We propose a modeling approach that recognizes that phenological development does not happen in all buds simultaneously. At any given observation time, a tree or shoot contains buds in different stages of development. This poses practical problems during phenology observations, where observers often assign a single development stage to entire trees or shoots. Such assignments are particularly

86 challenging in years with irregular tree development, e.g. as a result of insufficient chill accumulation,
87 when bud development within individual trees can be very heterogeneous (Erez, 2000; Ghrab et al.,
88 2014). Besides causing challenges in deciding on the state of tree development, failure to account for
89 within-tree variation in bud development also discards valuable information that could be used to
90 further our understanding of tree development stages, their timing, and their responses to climatic cues.
91 We present an approach that considers buds on a tree as a population, in which each bud follows its
92 own development trajectory.

94 In fact, the various phenology classification scales that are in use today are largely oriented towards
95 the bud scale. Even though some tree-scale stages are included (e.g. '50% flowers open'), most stage
96 denominations refer to the state of individual buds (e.g. 'green tip'), not trees or shoots (Meier et al.,
97 1994). For a bud, it is relatively easy to unambiguously assign such a stage at any point in time, and
98 each bud follows a clearly defined trajectory from bud formation to the final stages of leaf or fruit
99 development. Our phenology modeling approach is based on observations of all buds on a tree or twig,
100 in which the state of each bud is recorded. These data are summarized into the percentages of buds in
101 each phenological stage along its development trajectory.

103 The distribution of development stages within the population of buds shifts over time. During the cold
104 season, virtually all buds of deciduous trees are dormant. Gradually, buds then transition into more
105 advanced development stages, as their dormancy is broken, and they resume active growth. Over time,
106 increasing shares of the buds assume progressively advanced development stages. Our analysis is based
107 on this shift over time of the proportions of buds in different phenological states.

109 Progress through dormancy manifests itself as a gradual shift in the probability of each bud reaching
110 certain development stages. This probability shift is likely driven by a continuous dormancy
111 progression process, the rate of which depends on chill and heat accumulation. By adopting this
112 perspective of the dormancy process, precise and objective phenological data can be collected at any
113 point in time, by assessing the distribution of development stages among the total population of buds
114 on a tree or branch. For the majority of buds, developmental stages can usually be assigned without
115 much ambiguity. At the tree level, this is much more difficult, with a potentially strong influence of
116 observer bias, and a high risk of inaccuracy arising from infrequent observations that may miss
117 important tree-level stages.

119 To avoid assumptions about whether chill and heat accumulate sequentially (Luedeling et al., 2009b),
120 in parallel or whether they interact (Harrington et al., 2010; Pope et al., 2014), we designed our model
121 in a way that allowed the data to define which of these situations applies. Mathematically, we describe
122 the coupling of a chill- and heat-modulated continuous process with a probabilistic prediction model
123 for phenological stages by a nonlinear ordinal regression, which is described in the following section.

2 Methods

2.1 Modeling the progression of tree buds through dormancy

127 We conceptualize the trees' progression through the dormant phase as a continuous process, throughout
128 which the probability of observing individual phenological stages gradually shifts, according to how
129 much chill or heat has accumulated. The underlying biological processes can thus be described by a
130 continuous development model, which is linked with a probabilistic prediction model for each bud's
131 phenological stage (McKinley et al., 2015).

132

2.1.1 Probabilistic interpretation of phenology observations

134 We note that in any given observation (i), the proportion of the total number of buds (n_i) that finds
135 itself in a particular development state (j, with J being the total number of states) is the result of n_i
136 random draws from a set of probabilities (p_{ij}, with $j = [1,…,J]$) that, for each bud, defines the likelihood
137 of being in each of the states. This set of probabilities defines a multinomial distribution, which is
138 responsible for producing the distribution of phenological states observed during observation i. This
139 observed distribution can be denoted by Y_i, which consists of J elements Y_{ij} that define the number of
140 buds in each state j out of the total of J states. In the present analysis, we include J=3 states:
141 1='dormant', 2='green tip' and 3='leaf-out'. Using 'Mult' to stand for 'multinomial distribution', the
142 process that produces the data collected during a phenology observation event can thus be described
143 by:

144

$$Y_{ij} \sim Mult(n_i, \boldsymbol{p}_i) \tag{1}$$

146

147 Changes in the distribution of buds across the development stages over the course of the dormancy
148 season result from shifts in the probabilities of a bud being in these stages, with a continuous decrease
149 of the likelihood of being dormant and a gradual increase in the chance of assuming a more advanced
150 state (Figure 1). Data recorded during each observation i thus corresponds to a particular set of
151 probabilities $\boldsymbol{p}_i$ (consisting of j elements p_{ij}) that corresponds to the development state of the tree at the
152 time of the observation. The development shown in Figure 1 is difficult to describe mathematically,
153 because the share of buds in each stage increases and then decreases again, and the sum of all the
154 proportions needs to make up 100%. It is therefore convenient to consider, for every state j, the
155 cumulative probability (γ_{ij}) of a bud being in either the particular state of interest or in one of the earlier
156 states (Figure 2).

157

158 Note that each of the cumulative probabilities decreases monotonically through time, which is easier
159 to describe mathematically than the hump-shaped curves shown in Figure 1. The relationship
160 between the probabilities p_{ij} and the cumulative probabilities γ_{ij} is defined by:

161

$$p_{ij} = \begin{cases} \gamma_{ij} & for\ j = 1 \\ \gamma_{ij} - \gamma_{i(j-1)} & for\ j = 2, …, J-1 \\ 1 - \gamma_{i(J-1)} & for\ j = J \end{cases} \tag{2}$$

163

164 We build a population-based tree phenology model by describing the development of these cumulative
165 probabilities over time. This is achieved by evaluating distributions of bud states at different points in
166 time (i 1-4 in Figure 2) and relating them to tree development through regression analysis. Probability
167 data is difficult to handle in a regression equation, because all individual bud state probabilities must
168 be between 0 and 1, and all the probabilities have to add up to 1. We therefore apply a logit
169 transformation, which projects probability values onto the full numeric scale (-infinity to +infinity)
170 (Figure 3).

171

172 This logit transformation is described by:

173

$$logit(\gamma) = \log\left(\frac{\gamma}{1-\gamma}\right) \tag{3}$$

175

4

176 **2.1.2 Relating phenology observations to tree development**

177 The transformed cumulative probabilities of buds being in particular phenological states can be
178 correlated with any variable μ that describes the tree's progress through the dormancy period.
179

$$logit(\gamma) \sim \mu \tag{4}$$

181

182 The scale of this development-tracking variable (μ) can be divided by a series of thresholds (Θ) that
183 mark the transitions between development stages (Figure 4). In other words, the variable that describes
184 the progression of dormancy will pass several thresholds (Θ_1 to Θ_4 in Figure 4) during bud
185 development, at which the buds transition to the next development stage.
186

187 For computing the (log-transformed) cumulative probability of a bud being in or having passed a given
188 development stage j, we have to subtract the value of the development-tracking variable from the
189 threshold value Θ_j that corresponds to this stage. This correlation can thus be expressed as:
190

$$logit(\gamma_{ij}) \sim \theta_j - \mu_i \tag{5}$$

192

193 By converting this value back to the probability scale, we can extract the cumulative probability of
194 buds being in the corresponding stage or in an earlier stage. After doing this for all of the classes, we
195 obtain the predicted value of the share of buds in each state.
196

197 **2.1.3 Describing tree development during dormancy**

198 The question remains, what development-tracking variable (μ) can be used to correlate the logit-
199 transformed cumulative probabilities with. Tracking the progression of tree buds through dormancy is
200 challenging, because during most of this development, buds do not change visibly. While it is well
201 established that buds respond to chill and heat accumulation, it is not clear how to precisely measure
202 each of these. It is also not clear in what way chill and heat are related. Many studies assume that the
203 accumulation of heat follows complete fulfillment of the chilling requirement (Luedeling et al., 2009b),
204 but this is probably an oversimplification. Some studies assume that chill and heat accumulate in
205 parallel (Landsberg, 1974), but it seems unlikely that this is true during the entire dormancy season.
206

207 The most plausible conceptualization is a partial overlap between chill and heat accumulation (Pope et
208 al., 2014), with evidence pointing to a minimum amount of chill that is essential, a transition period,
209 in which additional chill reduces the amount of heat that is required, and a maximum useable amount
210 of chill (chill saturation), after which additional chill is no longer effective (Harrington et al., 2010).
211 Rather than choosing one of these models, we use a formulation that accommodates all three scenarios
212 and allows observed data to define which situation applies.
213

214 We conceptualize the breaking of dormancy as a gradual transition between a state in which heat does
215 not affect buds and a state where it is fully effective. The responsiveness to heat follows a sigmoidal
216 curve, in which the period between the minimum chilling requirement and the maximum effective chill
217 is characterized by an increase in heat effectiveness (Figure 5). The mathematical formulation of this
218 relationship can be done in a way that allows the shape of this curve to vary in terms of steepness and
219 position. For example, in a situation of purely sequential fulfillment of chilling and heat requirements,
220 the increase could be very steep, so that the transition zone of increasing heat effectiveness disappears
221 (Figure 6a). If chill and heat accumulated in parallel and with full efficiency all throughout dormancy,
222 the slope would be moved to the very beginning of dormancy (Figure 6b). In an intermediate situation,

223 which would correspond to the Chill Overlap Model, we would expect to find a moderate slope at an
224 intermediate chill accumulation level (Figure 6c).
225
226 Mathematically, the basic relationship between heat and tree development during an observation i is
227 described by:

$$\mu_i = Heat_i * \alpha * f(Chill_i) \tag{6}$$

231 In this equation, $Heat_i$ is the heat accumulated at observation time i, while α is a conversion factor that
232 translates between the effect of heat accumulation and the modification in heat effectiveness introduced
233 by the function $f(Chill_i)$. Since tree development does not only depend on heat accumulation but is also
234 affected by the vigor of the observed tree or the particular twig that is sampled, we decompose α into
235 components that account for this variation:

$$\alpha = \alpha_{INTERCEPT} + \alpha_{TREE} + \alpha_{TWIG} \tag{7}$$

239 This disaggregation ensures that μ_i can be considered as an independent and identically distributed
240 random variable. To describe the effect of chill accumulation on heat effectiveness, we use a
241 formulation of the standard logistic growth curve function (Figure 5). Characteristic features of this
242 function are an asymptotic maximum value (in this case 1 for maximum heat effect), as well as two
243 inflection points: β describes the transition towards the period of maximum sensitivity to additional
244 chill, and η marks the transition towards the asymptote, where chill effects start to decline.
245
246 This relationship can be described as:

$$f(Chill_i) = f(Chill_i, \beta, \eta) = (1 + \exp(-\beta - \eta * Chill_i))^{-1} \tag{8}$$

250 Depending on the value of the parameters β and η, this equation can be used to describe situations of
251 sequential accumulation of chill and heat (Figure 6a), parallel accumulation (Figure 6b) and
252 overlapping accumulation, with chill levels determining heat effectiveness (Figure 6c).
253
254 The inclusion of the logistic growth curve in the second level of the overall model allows for
255 considerable flexibility in discovering the point of saturation for chill effects in the phenological
256 development response. Instead of determining a hard threshold point, as in a linear plateau model, the
257 growth response to chilling is assumed to take a sinusoidal shape. This model assigns α the role of
258 mapping the maximum potential influence of chilling onto the growth curve of buds, and that of the
259 ceiling rate of responsivity to heat (at chilling saturation, the formula approaches $\mu = Heat*\alpha$). The
260 location (β) and rapidity (η) values define the transition between zones of small effect (insufficient
261 chill, with minimal effect of additional units), strong effect (insufficient chill, with rapid growth
262 increase from additional units), and again small effect (sufficient chill, with minimal effect of
263 additional units).
264
265 The features of the logistic growth curve are well studied and provide convenient mathematically
266 determined points for standard assessment of response features across models using the logistic
267 function. One such response feature is the "asymptotic deceleration point" (ADP), as defined by Passos
268 et al. (2012), the third root of the fourth derivative, which indicates the final transition towards the
269 asymptote. After this point is reached, there is very little response to any further movement along the
270 curve. In this scenario, the ADP can be interpreted as the point after which there is an insignificant

271 accumulation of additional benefit from chilling. It is used here to assess chill saturation. Passos et al.
272 (2012) found the closed form of this root as:

273

274
$$\text{ADP} = -[\log(5 - 2\sqrt{6}) + \beta]/\eta \tag{9}$$

275

276 which provides a convenient equation for direct translation of estimated parameters into saturation
277 thresholds.

278

279 ### 2.1.4 Modeling chill and heat accumulation

280 What remains is to define variables for tracking chill and heat accumulation. For chill, researchers have
281 developed a number of models, including the "Chilling Hours Model" (Bennett (1949); Weinberger
282 (1950)), the "Utah Model" (Richardson et al. (1974)) and the "Dynamic Model" (Fishman et al.
283 (1987a), Fishman et al. (1987b) and Erez et al. (1990)). All of these approaches have proven useful
284 tools for orchard management, but they have not performed well in warm Mediterranean climates and
285 in a changing environment (Luedeling, 2012), and they are not based on robust physiological
286 understanding (Luedeling, 2012). Acknowledging these shortcomings, we chose the Dynamic Model
287 for this analysis, since it has usually outperformed the other models in comparative analyses (Ruiz et
288 al., 2007; Luedeling et al., 2009a; Zhang and Taylor, 2011; Benmoussa et al., 2017).
289 For heat accumulation, we use the Growing Degree Hours approach by Anderson et al. (1986), which
290 is commonly applied in fruit tree phenology studies. It should be noted here, however, that these models
291 are the most credible models to date, but they are unlikely to accurately describe chill and heat
292 accumulation and thus constitute possibly substantial sources of error.

293

294 ## 2.2 Phenology data collection

295 ### 2.2.1 Plant material, forcing conditions and experimental design

296 In this experiment, 960 twigs were collected from 8 cherry (*Prunus avium* L.) varieties established in
297 a commercial orchard with fully mature trees between 5 and 7 years old, grafted onto Colt rootstock.
298 The orchard is located in Río Claro, Region del Maule, Chile (35°24' S, 71°24' O). In the orchard, six
299 trees of each of the following varieties were used as twig donors: "Bing", "Lapins", "Rainier",
300 "Regina", "Santina", "Skeena", Sweetheart" and "Kordia" (48 trees in total). In each tree, a total of 20
301 one-year old twigs were randomly tagged on May 17, 2017 between 1.5 m to 3 m above the ground
302 around the canopy. Twigs were tagged so that two twigs per tree were harvested at 10 different
303 sampling dates during winter, according to the following chill levels (in CP) recorded in the orchard:
304 16 (May 17th), 26 (May 29th), 31 (June 8th), 37 (June 14th), 42 (June 21st), 47 (June 28th), 52 (July 5th),
305 57 (July 11th), 63 (July 19th), and 70 (July 26th). All selected twigs were between 30 and 50 cm in length
306 and 4 – 6 mm in diameter. Twigs were transported to the deciduous fruit tree laboratory at the Escuela
307 de Agronomía of the Pontificia Universidad Católica de Valparaíso. Upon arrival in the lab, twigs were
308 disinfected with a solution of sodium hypochlorite (0.5% v/v) and cut at the bottom while submerged
309 in distilled water to avoid cavitation. Twigs were then placed in containers with a solution of 250 mL
310 of sucrose (5% p/v) and transferred to a forcing chamber (environmental conditions: 21±0.71°C, 65%
311 relative humidity, 16/8 h photoperiod, 50 µmol m^{-2} s^{-1} metal halide cold white light), where they were
312 kept for eight weeks, resulting in a total forcing of 20,000 GDH.

313

314 The experimental design was a randomized complete block with a split plot factorial structure. The
315 main-plot was the date of twig harvest, which is analogous to chill received in the field, while the sub-

316 plot was the variety. Six blocks were used with two sub-samples in the sub-plot (two shoots per
317 sampling date, per variety repetition).
318

2.2.2 Monitoring of vegetative phases and forcing chamber temperature

320 Temperature data were recorded using six Hobo® sensors located in representative trees of the
321 experiment and compared to the meteorological station of San Pedro, Molina, which is part of Chile's
322 National Agroclimatic Network (https://www.agromet.cl/) and located 21 km from the orchard. Winter
323 chill was estimated from April 1, 2017, which coincided approximately with natural leaf fall. Heat
324 accumulation (in GDH) was calculated, in both field and forcing chamber, according to Anderson et
325 al. (1986). Temperature data in the forcing chamber was monitored with two Hobo® sensors located
326 inside the chamber. Chill accumulation was quantified in Chill Portions (CP) according to the Dynamic
327 Model (Erez et al., 1990), using a function contained in the "chillR" package (Luedeling, 2018) for R
328 (R Core Team, 2017).
329

330 Upon arrival in the forcing chamber, length and diameter of each twig were recorded. Additionally,
331 each bud of each twig was individually identified from top to bottom. The phenological stage of each
332 bud was recorded once per week as bud without budburst, bud at BBCH-scale stage 08 (green tips) and
333 bud at BBCH-scale stage 11 (bud break).
334

335 In September 2017, a visual inspection in the orchard was done to record the moment when 50% of
336 buds had reached phenological stage BBCH 08 (green tip) for assessment of model predictive capacity
337 using field measurements of chill and heat accumulation (in CP and GDH, respectively).
338

2.2.3 Dormancy release monitoring

340 For comparability with prior literature (Egea et al., 2003; Ruiz et al., 2007; Alburquerque et al., 2008),
341 data were processed according to a "dormancy release" heuristic (hereafter, "DRH"). In this heuristic,
342 twigs are observed at 21 days in the incubator, and are classified as "active" if 50% of the buds express
343 green tip or more advanced phenological development, and "inactive" if this threshold is not met. The
344 minimum chill accumulation required to become active is considered the critical chill sufficiency level.
345 This heuristic was applied to each set of chill accumulations within each set of repetition-subsample
346 twigs, yielding 12 measurements per variety. Means and standard deviations were then sampled from
347 these derivative measurements for comparison of the DRH with the model.
348

2.3 Data analysis

2.3.1 Model fitting

351 Models were separately fit (completely unpooled between varieties) using the dataset from beginning
352 of observation at phenological state 0 (dormant) to termination of observation at phenological state 2
353 (leaf out). Growing Degree Hours and Chill Portions covariates were scaled to facilitate model
354 convergence (GDH scale factor: 4648; CP scale factor: 14.35). Model fitting was achieved through a
355 Markov Chain Monte Carlo (MCMC) Bayesian sampling procedure, in which initial estimates for all
356 model parameters are iteratively sampled until the distribution of samples defines a model that
357 optimally describes the observed data. Even in the fitted model, all parameters are described by
358 distributions (the posterior distributions), which allow considering uncertainties about the true model
359 parameters. These uncertainties can be interpreted as error estimates for the tree development
360 characteristics that are derived from the analysis.

361
362 Uninformative priors were used for all model variables and each model was compiled and sampled
363 with the Stan MCMC library using the "RStan" package in R (R Core Team, 2017). MCMC chains
364 and posterior samples were inspected using the "shinystan" package in R (R Core Team, 2017). Model
365 specifications, diagnostics, and Stan code are available in a public GitHub repository
366 (https://github.com/graemebaird/cherry_chill_nlm).
367

368 **2.3.2 Posterior predictive distributions**

369 Simultaneous during MCMC sampling for model parameters, posterior predictive distributions of bud
370 state (Y_{rep}) were sampled for assessment of in-sample model predictive capacity. For each
371 observation's posterior predictive distribution, the mode (most frequently predicted ordinal outcome
372 from all iterations of Y_{rep}) was used for comparison against original data.
373

374 **2.3.3 Posterior predictions of vegetative phases**

375 Weather data and visual inspections of 50% dormancy release (50% of observed buds at green-tip or
376 further) from donor trees in the commercial orchard were used to evaluate the predictive accuracy of
377 the model fits in each variety. Median posterior simulations of bud activity probability were generated
378 for daily heat and chill observations to estimate the predicted date when the activity probability (i.e.
379 for a simulated ordinal outcome $\hat{Y}$, activity probability is $\Pr(\hat{Y} \neq 0)$) exceeded 50%.
380

381 **2.3.4 Comparing heat sensitivity between varieties**

382 The asymptote parameter α serves as a coefficient for the maximum linear growth-rate relationship
383 between heat and μ. However, as each variety was modeled separately, each cut point θ_j in the ordinal
384 model was estimated simultaneously with α, and any comparison of growth rates using α alone
385 would be confounded by differences in the values of θ_j, as the absolute distance that μ needs to
386 traverse between cutpoints works in concert with growth rate α to estimate the phenological stage.
387 This can be worked around by creating a transformed alpha-ratio (AR) parameter for each variety
388 v,
389

390 $$AR_v = \alpha_v/\theta_{v1} \tag{10}$$

391
392 standardizing the growth rate α by the value of the first cutpoint θ_1, normalizing the heat responsivity
393 by the latent estimations of "distance" between cutpoints. AR can then be compared across varieties as
394 a standardized measurement of heat sensitivity and growth rate.
395

396 **3   Results**

397 For all 8 cherry cultivars, all parameters in all models converged to relatively tight estimates with no
398 convergence problems, indicating that the model and data structures are well matched, and some
399 differentiation between varieties was indicated (Table 1).
400

401 **3.1   Hypothesized chill saturation differences between cultivars**

402 The Bayesian approach to model fitting provides posterior parameter distributions once the model is
403 fit to data. Since the asymptotic deceleration point (ADP) is a linear transformation of these parameters,

404 their distributions can be used to derive posterior distributions for the ADP. These distributions allow
405 defining probability distributions and confidence intervals for biologically relevant dormancy
406 parameters, such as the ADP, which can be interpreted as a cultivar's chilling requirement (CR). A
407 more common definition of the chilling requirement found in the literature is the amount of chill needed
408 for 50% budbreak, termed the Dormancy Release Heuristic (DRH) in this paper. Also for this metric,
409 posterior distributions and confidence intervals for its value were computed.

411 The posterior distributions indicate overlap between ADP and DRH (See Table 2 for means and their
412 95% credible intervals (CI), or Figure 7 for plotted distribution densities). ADP estimates generally
413 spanned a 4-5 CP 95% CI, although Kordia, Santina, Bing, and Regina had relatively larger CI's,
414 indicating variability in varietal responses. ADP-estimated chilling requirements were generally
415 clustered into low (~33 CP; Skeena, Lapins), medium (~35CP; Regina, Santina, Sweetheart, Bing) and
416 high (~38CP; Kordia, Rainier), and 3 of 8 DRH means were captured by the 95% CI ADP ranges.

3.2 Comparing parameters between varieties

419 The ADP calculation is only dependent on β and η in the logistic function, and direct examination of
420 these parameters provides no additional information for our research objectives. Additionally, by using
421 the alpha-ratio (AR) transformed parameter, differences between estimations of maximum possible
422 responsivity to heat (i.e. α) are scaled by the latent cutpoints, thus capturing both estimations of heat
423 responsivity and phenological transitions in the continuous variable μ. As such, an overall view of all
424 relevant posterior samples can be taken by examining the relationship between AP and ADP, as plotted
425 in Figure 8.

427 A strong (-0.768) Pearson correlation between AR and ADP between varieties indicates a negative
428 relationship between varietal responsivity to heat accumulation and chilling saturation, in which
429 varieties that require fewer Chill Portions to achieve saturation also exhibit a rapid response to heat
430 accumulation and thus a faster growth rate. Conversely, a moderate (0.357) Pearson correlation
431 between α and saturation within variety-specific posterior distributions likely indicates the general
432 difficulty in parameter inference, when γ could be progressed either by increased heat sensitivity (larger
433 α) or lower saturation requirements.

3.3 Model posterior predictions

436 Posterior predictions of bud state generally matched the nonlinear heat/chill interaction pattern found
437 in the original data, but with consistently higher estimates of heat accumulation required to reach
438 greentip (Figure 9).

3.4 Estimated vs actual bud activity dates

441 The posterior predictions of bud activity given field-linked chill (in CP) and heat (in GDH) data
442 performed poorly, at best estimating roughly half of the actual 50% bud activity that was observed in
443 the field, and frequently less (Table 3). Varieties with higher AR ratios tended to reach 50% bud activity
444 sooner.

4 Discussion

447   **4.1   Progress in dormancy modeling**

448   The use of a ordinal regression model combined with a nonlinear formulation of the trees' response to
449   chill and heat accumulation constitutes a significant advance in the way tree dormancy is modeled. The
450   focus on the entire population of buds rather than the aggregate phenology of the whole tree allows
451   generation of nuanced data on a tree's state, e.g. capturing the heterogeneous development that can be
452   induced by chill deficiency. It also raises the precision and objectivity of phenological observations,
453   because it is much easier to unambiguously classify the status of individual buds than that of trees.
454
455   Bud-scale observations combined with the concept of phenological development as a continuous
456   process allow accurate and precise assessment of the state of a tree's development at any point in time.
457   This is a significant improvement over tree-scale observations, which are often only conducted at
458   intervals of several days or weeks, and then produce estimates that are relatively imprecise and can be
459   subject to considerable observer bias.
460
461   Using a flexible model structure that can accommodate all commonly used concepts of the relationship
462   between chill and heat accumulation (sequential, parallel or overlapping) eliminates the need for
463   assumptions about this critical issue, which previous studies attempting to model tree dormancy have
464   had to make (Kramer, 1994; Chuine et al., 1999; Chuine, 2000; Hanninen and Kramer, 2007;
465   Chmielewski et al., 2011; Pope et al., 2014; Darbyshire et al., 2016; Darbyshire et al., 2017). While we
466   found clear evidence of an interaction between accumulated chill and the trees' heat requirements for
467   cherry cultivars in Chile, use of our methodology could clarify this relationship for other species and
468   other locations.
469

470   **4.2   Detecting chill sufficiency via a non-linear form**

471   In accordance with previous findings, we found strong evidence for a distinct saturation point in the
472   effect of chill accumulation on bud vigor in all varieties, evidenced both by the good fit of the non-
473   linear component to the data and by the estimations of saturation location (ADP). The use of the ADP
474   location to determine saturation is a relatively arbitrary choice; Passos et al. (2012) outline a number
475   of alternatives to find similar results. Importantly, by fitting these models using a Bayesian framework,
476   we were able to determine a distribution-based, rather than point-based, estimate of chill sufficiency
477   for each variety, and propagate this distributional uncertainty through calculation of the ADP with β
478   and η, retaining all model information through the process. This allows for an assessment of data
479   uncertainty regarding the chill sufficiency estimates, as seen in the ADP brackets of Figure 9, and
480   significant adaptability to modifications to the underlying model structure, as long as posterior
481   estimates of β and η remain available.
482
483   Further, the general overlap of the ADP 95% credible intervals with the 50% dormancy release method
484   estimates indicates both that our estimates of chill sufficiency using non-linear modeling do not deviate
485   markedly from estimates obtained with a prior methodology and that the 50% method is surprisingly
486   adequate for capturing a complex non-linear relationship using a fairly simple heuristic-based
487   approach.
488

489   **4.3   Advantages to continuous development modeling**

490   A significant advantage of this model for detecting chill effects is its use of the entire dataset. The
491   range of heuristics recommended for detection of chill sufficiency is broad, both in specification of

11

492 observation time (10 days (Egea et al., 2003; Ruiz et al., 2007; Alburquerque et al., 2008), 14 days, 21
493 days) and in phenological stage (bud swelling (Alburquerque et al., 2008), greentip (Egea et al., 2003),
494 leaf-out). By modeling the entire dataset, the arbitrary component of observation/stage selection is
495 avoided, producing parameter estimates and sufficiency estimates which are more easily comparable
496 across datasets, even given experimental design differences in observation frequency and phenological
497 measurements. This feature opens up considerable possibility for direct comparison of data between
498 experiments or even synthesis of observations between experiments via additional layers to the multi-
499 level model structure.
500
501 Aside from flexibility in the non-linear component, the use of a latent continuous variable to represent
502 phenological development allows additional flexibility in representation of an arbitrary number of
503 phenological stages. While in this dataset we restricted observations to three phenological stages, the
504 model is easily expandable to additional stages. This expandability provides potential for moving
505 beyond incubator data to predicting in-field phenology, such as flowering and fruiting dates, and to
506 more credible assessments of both chill sufficiency and heat sensitivity.
507

4.4 Compensatory effects of chilling and warming

509 Aside from chill sufficiency, the model fits also provide insight into the influence of heat on bud
510 development. It has been posited (Harrington et al., 2010; Pope et al., 2014; Darbyshire et al., 2016)
511 that there is potential for compensatory adaptation of phenology in cherry trees, i.e. that in the absence
512 of sufficient chill accumulation, additional heat accumulation may provide additional vigor that
513 accelerates phenological development to overcome any penalty incurred by chill insufficiency. The
514 alpha-ratio (AR) parameter provides a method for examining the relative sensitivity of each variety to
515 heat accumulation (GDH) during the observation period, standardized for comparability.
516
517 The negative correlation between AR and ADP indicates that, among the cultivars analyzed in our
518 study, varieties with lower detected chilling requirements also expressed a higher level of sensitivity
519 to heat – not only do they need less chill to reach maximum growth potential, their maximum growth
520 rate is generally higher. These findings suggest a weakening of any compensatory effects that may
521 occur via a double penalty, as varieties with higher chilling requirements will also need more heat to
522 progress to more advanced phenological stages.
523

4.5 Inability to recover field bud activity

525 Estimating field bud activity primarily served as a test of our ability to capture heat sensitivity, as the
526 orchard conditions produced chill accumulation far in excess of all varieties' inferred requirements,
527 and thus all posterior predictions were driven by heat. The differences between range and rapidity of
528 heat accumulation observed in the field (~7000 GDH over 10 weeks) versus those observed in the
529 incubator (~20000 GDH over 5 weeks) very likely biased the model to underestimate bud sensitivity
530 to heat accumulation. This, along with the model's structural conflation of time with heat (there is no
531 component allowing the progression of time to drive μ, only heat accumulation), resulted in a poor
532 estimation of field bud activity – although it can be noted that the varieties with highest AR values
533 (Bing, Lapins, Rainier) reached 50% budbreak earlier, suggesting a valid overall ranking of heat
534 sensitivity between cultivars. While unsurprising, considering the difference between field conditions
535 and incubator conditions, our difficulty in predicting budburst in the orchard highlights the restriction
536 that the experimental design places on our ability to directly estimate heat responsivity under field

537 conditions. It should also be noted that neither the Dynamic Model nor the Growing Degree Hours
538 concept, which interact to set the pace of development progress, are likely to be completely accurate,
539 which may have contributed to our difficulty to predict budburst in the field.
540

4.6   Potential future work

542 This methodology presents a promising foundation for future work in modeling and predicting the
543 climatic requirements of deciduous fruit trees such as cherries. For fruit production, this is a critical
544 task in light of the impact global climate change may have on deciduous tree crop production regions
545 (Luedeling et al., 2011; Darbyshire et al., 2014). While our study and prior work reliably demonstrate
546 the existence of a non-linear response to chill accumulation (Harrington et al., 2010; Pope et al., 2014),
547 the strict nature of this relationship in regards to real-world scenarios is poorly defined, especially
548 regarding the potential compensatory effects of increased heat accumulation via a warmer growing
549 season.
550

551 Some important components are missing from this experiment and model structure. As noted, to
552 credibly estimate the impact of heat accumulation on bud development, future work should incorporate
553 varying temperature regimes, either through on-farm observations of bud development or via
554 manipulation of incubator environments. Additionally, a decomposition of growth into both a heat-
555 and time-mediated process would allow for a more rational assessment of their individual effects and
556 may provide a more feasible means to predict on-farm phenological development and determine the
557 relative impact of growing season heat accumulation.
558

559 This paper represents a first-in-kind attempt to extend phenological modeling approaches already
560 extant in the ecology literature (Clark et al., 2014) to the field of horticulture. Even though this model
561 was performed with data from cherries, many other deciduous orchard production systems depend on
562 adequate accumulation of winter chill and face similar issues in determining varietal requirements and
563 adaptation to shifting temperature regimes (Dennis, 2003; Luedeling, 2012). Extending this model type
564 to these systems may provide valuable information for future planning.
565

5   Conclusions

567 The phenology data we collected could accurately be described by a nonlinear ordinal regression that
568 conceptualized progression through dormancy as a continuous process at the level of individual buds,
569 which is driven by heat, with heat effectiveness modulated by a chill-dependent sigmoidal function.
570 Besides producing a good fit for the data, this modeling approach has several conceptual advantages
571 over commonly used methods: 1) by using buds rather than trees as observational units, it raises the
572 precision of observations; 2) by considering the population of all buds on a tree or branch, it adds
573 nuance to recordings of phenological states; 3) by interpreting phenological development as a
574 continuous process, it allows full use of observations taken at any point in time; 4) by using a flexible
575 formulation of chill and heat accumulation, it reduces the need for assumptions about the relationship
576 between both requirements; and 5) by using Bayesian procedures, it provides confidence intervals for
577 agroclimatic needs, which are more credible than precise numbers.
578

579 We hope that these innovations will add conceptual clarity to future attempts to understand and model
580 phenology and enable studies that address uncertainties that remain. For example, it is still unclear how
581 to best quantify chill and heat, at what points in time the chilling and forcing periods begin and end,

582 and whether chill and heat accumulate in the same way all through dormancy. While many of these
583 issues may not be completely unraveled any time soon, we hope that a focus on bud-scale analyses and
584 the concept of phenology development as a continuous process that occurs in each individual bud will
585 facilitate targeted research to narrow critical knowledge gaps.
586

587 **6   Conflict of interest**

588 The authors declare that this research was conducted in the absence of any commercial or financial
589 relationships that could be construed as a potential conflict of interest.
590

591 **7   Author contributions**

592 GB designed and fit the model. SS designed the experiment, LA established the experiment and
593 collected the data with the assistance of DF and EF. GB, EL, NB, IC, EF and SS wrote the manuscript.
594

595 **8   Acknowledgments**

599

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735

736

Variety	α	β	η	θ_1	θ_2
Bing	1.918 (0.097)	-3.597 (0.325)	2.342 (0.229)	3.646 (0.090)	6.592 (0.126)
Kordia	1.815 (0.106)	-5.681 (0.578)	2.933 (0.321)	4.147 (0.117)	6.342 (0.144)
Lapins	1.971 (0.058)	-5.164 (0.408)	3.302 (0.269)	3.449 (0.085)	6.177 (0.117)
Rainier	1.859 (1.227)	-6.275 (0.546)	3.174 (0.081)	3.140 (0.081)	5.712 (0.109)
Regina	2.092 (0.979)	-5.223 (0.789)	3.077 (0.455)	3.880 (0.107)	6.939 (0.150)
Santina	1.882 (0.108)	-3.406 (0.433)	2.305 (0.293)	4.603 (0.116)	6.640 (0.139)
Skeena	2.010 (0.091)	-4.968 (0.477)	3.089 (0.310)	3.886 (0.096)	6.585 (0.128)
Sweetheart	1.884 (0.088)	-6.059 (0.692)	3.347 (0.394)	3.801 (0.093)	6.032 (0.118)

737

738 Table 1 Coefficients of the ordinal model fitted to phenology data for 8 cherry cultivars in Chile.
739 Coefficients are presented as means and standard deviations (in parentheses). Note that all parameters
740 are fit to scaled covariates (GDH scale factor: 4648; CP scale factor: 14.35).

741

Variety	Asymptotic Deceleration Point			Dormancy Release Heuristic		
	Mean	5%L	95%H	Mean	5%L	95%H
Rainier	38.6	35.2	42.2	31.8	29.8	33.9
Lapins	32.5	30.7	34.5	29.7	26.3	33.2
Sweetheart	35.8	33.4	39.3	32.2	29.3	35.2
Bing	36.1	32.7	39.9	31.6	29.7	33.4
Kordia	39.1	36.0	43.4	37.5	32.7	42.3
Regina	35.0	32.5	39.4	30.9	28.7	33.1
Skeena	33.8	31.5	36.8	33.1	30.6	35.7
Santina	35.6	31.9	40.6	35.2	32.5	37.9

742

743 Table 2 Means and 90% confidence intervals (described by their lower and upper bounds; 5%L and
744 95%H) for two interpretations of the chilling requirements of cherry cultivars in Chile based on a
745 ordinal regression model: the asymptotic deceleration point (ADP) of chill effectiveness and the 50%
746 dormancy release heuristic (DHR).

747

Variety	Field date	Field GDH	Estimated proportion of active buds at field date
Lapins	09-sept	5637	0.23
Bing	08-sept	5560	0.19
Rainier	09-sept	5637	0.27
Regina	17-sept	6500	0.25
Kordia	17-sept	6500	0.15
Skeena	17-sept	6500	0.23
Santina	17-sept	6500	0.11
Sweetheart	10-sept	5687	0.16

748
749   Table 3 Estimated versus observed 50% bud activity dates.

750 Figure 1 Schematic illustration of the progression of the population of buds on a tree through
751 dormancy and subsequent development stages, illustrated by changes in the percentage of buds in
752 each state over time.
753
754 Figure 2 Schematic illustration of the development through the dormancy period of cumulative
755 probabilities ($\gamma_1 - \gamma_5$) for buds being in a particular stage or any of the previous stages. Dotted lines
756 marked 1 through 4 show observation times (i), at which the percentage of buds in each stage is
757 recorded.
758
759 Figure 3 Illustration of the logit transformation applied to cumulative probabilities (γ).
760
761 Figure 4 Schematic illustration of a generic bud development tracking variable (μ), with a series of
762 thresholds marking the transition points between tree development stages.
763
764 Figure 5 Illustration of the sigmoidal heat effectiveness curve used in the regression analysis, and
765 significance of the parameters β and η of the logistic growth function.
766
767 Figure 6 Different forms of the sigmoidal curve, corresponding to a) the sequential model, b) the
768 parallel model and c) the overlap model of chill and heat accumulation.
769
770 Figure 7. Critical chilling requirements as determined by the asymptotic deceleration point (ADP)
771 calculation from the non-linear model and by measuring minimum chill accumulation to reach 50%
772 bud activity at 21 days in the incubator (the "dormancy release heuristic"; DRH). Posterior distributions
773 of ADPs are presented as density histograms for each variety. Mapped on top of the density histograms,
774 DRH means are presented as black dots and DRH standard deviation upper and lower bounds are
775 presented as error bars.
776
777 Figure 8 Posterior mappings of the asymptotic deceleration point (ADP) and alpha-ratio (AR)
778 transformed parameters of dormancy-breaking models for 8 cherry cultivars in Chile. The ADP
779 constitutes an approximation of the trees' chilling requirement (in Chill Portions) and the alpha-ratio
780 describes their sensitivity to heat (larger values indicating greater sensitivity). The central ellipse plot
781 maps the boundaries of the 95% credible intervals (the upper and lower boundaries that contain 95%
782 of the total distribution of posterior samples) of the AR (x-axis) and ADP (y-axis) on two-dimensional
783 space. Density histograms of the posterior distributions are plotted opposite their corresponding axes.
784 A gradient of differentiation between varieties is visible within each component (histograms) and as
785 covarying parameters (ellipses).
786
787 Figure 9 Relationship between chill accumulation, heat needs and budburst for 8 cherry cultivars in
788 Chile. Solid black lines mark the bud heat requirement (in Growing Degree Hours – GDH) required to
789 reach greentip stage across the observed spectrum of chill accumulation (in Chill Portions – CP) for
790 the raw data (black line: mean, grey shading: standard deviation boundaries) and model simulated data
791 (Y_{rep}, red line). The dashed black line shows the budburst % as observed after 21 days under forcing
792 conditions (right axis). Model estimated asymptotic deceleration point medians (red vertical solid line)
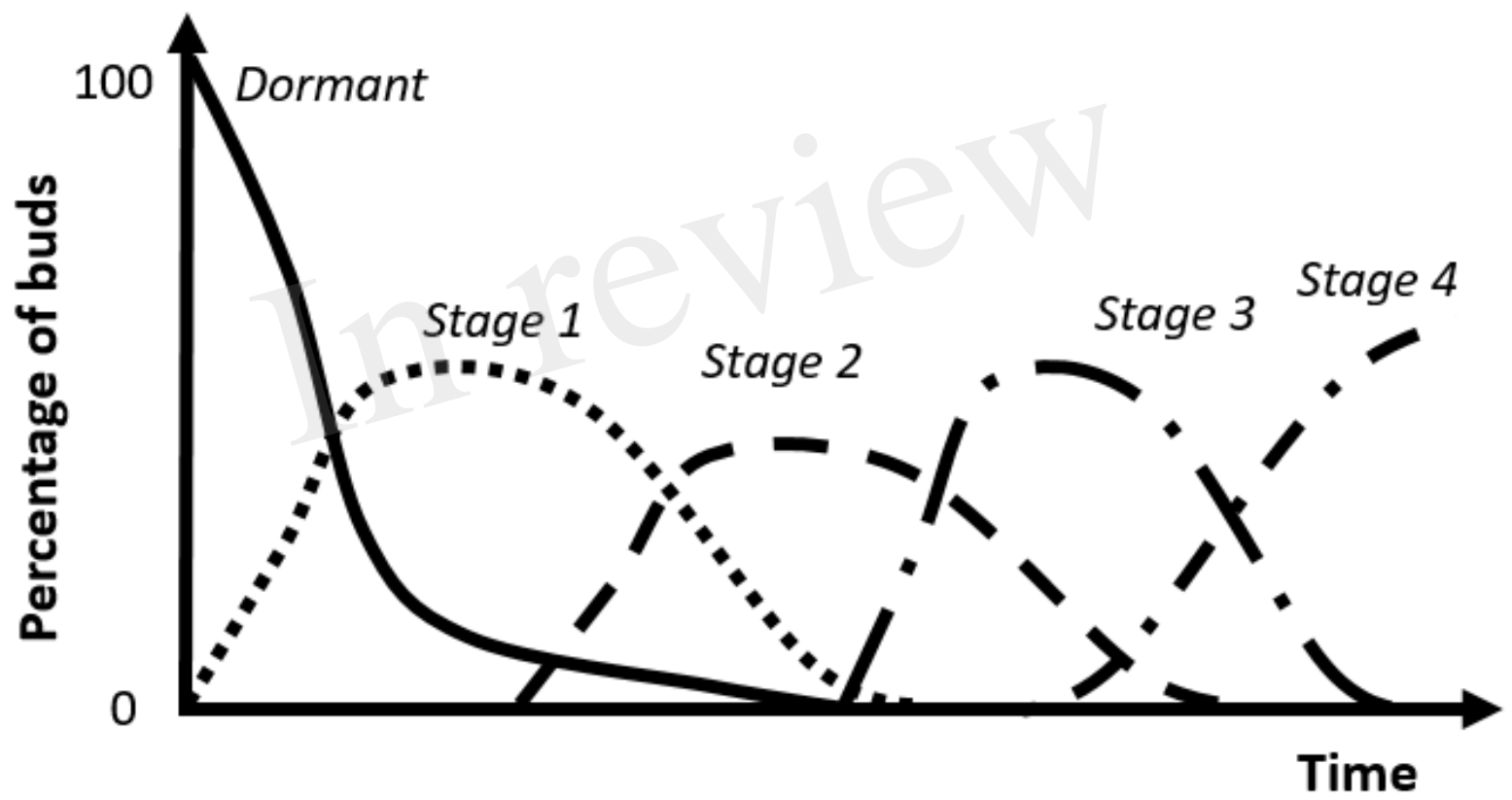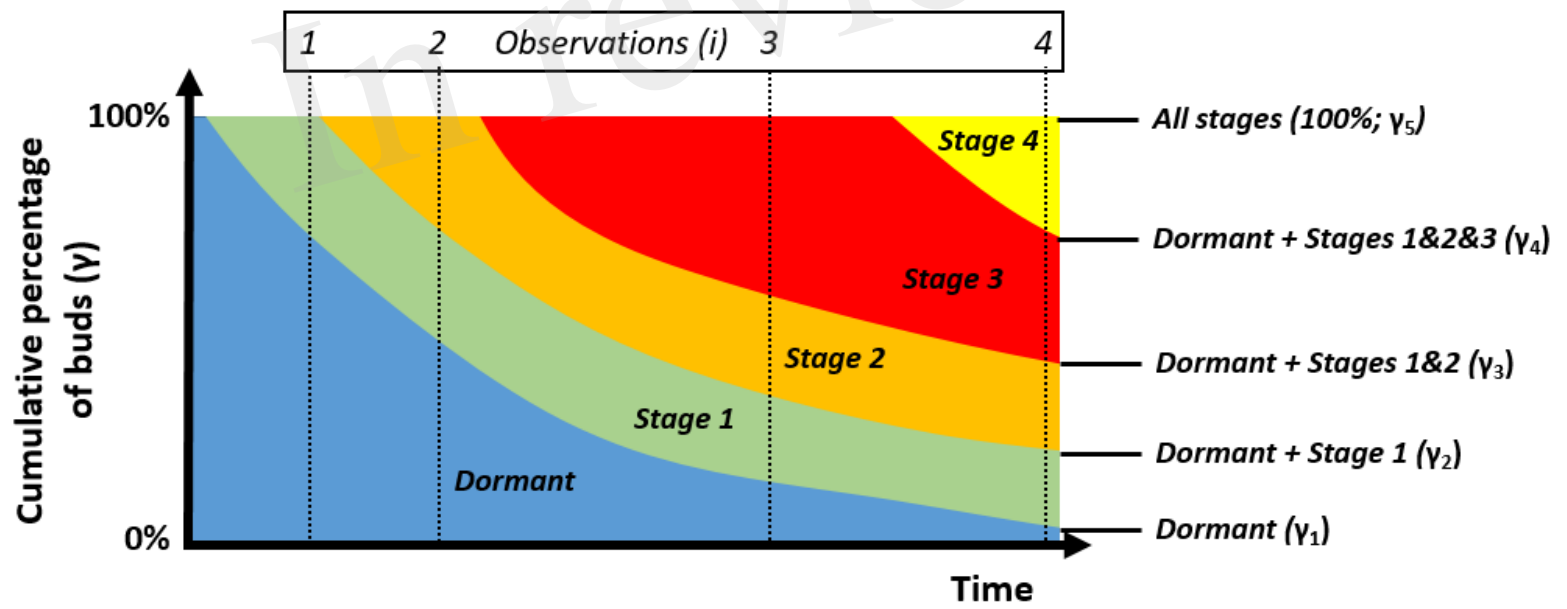793 and 95% credible intervals (red vertical dotted lines).
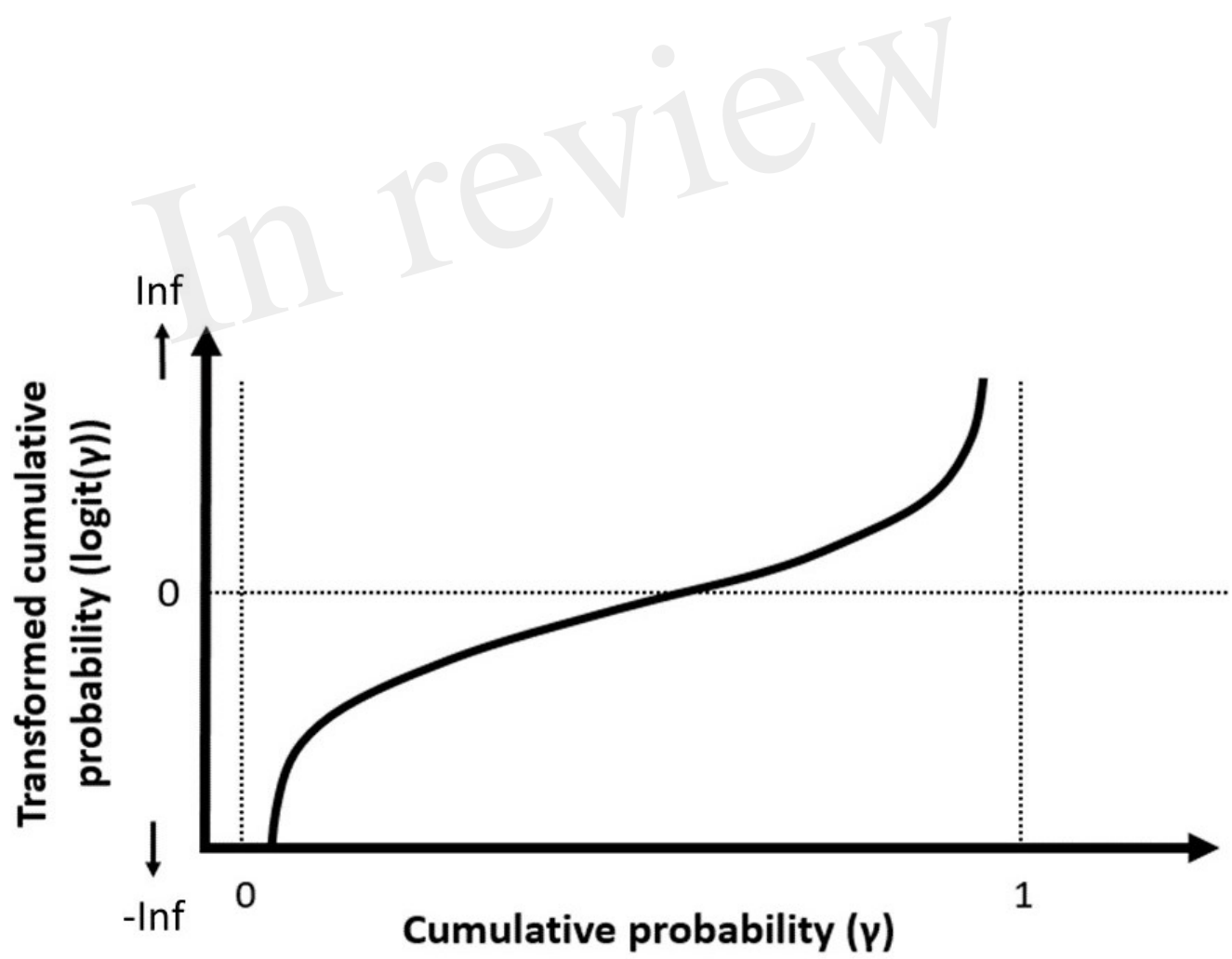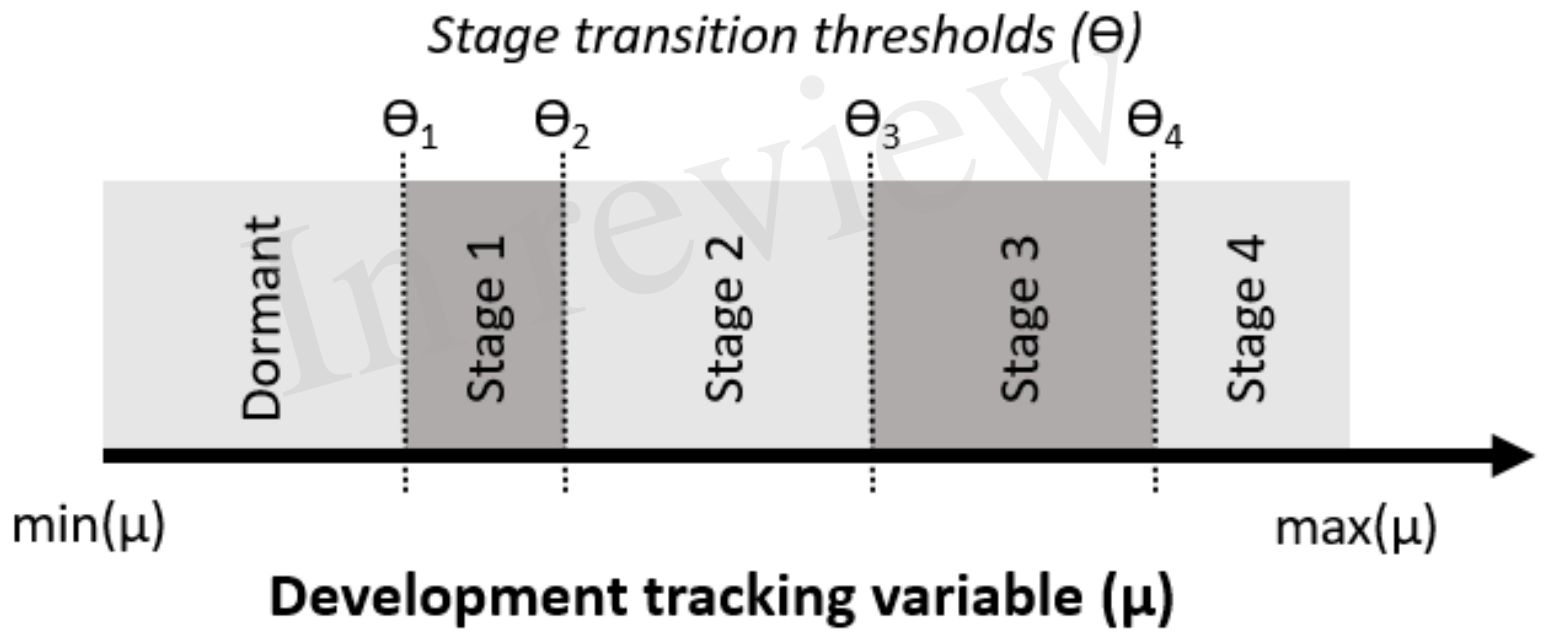
Figure 1.JPEG

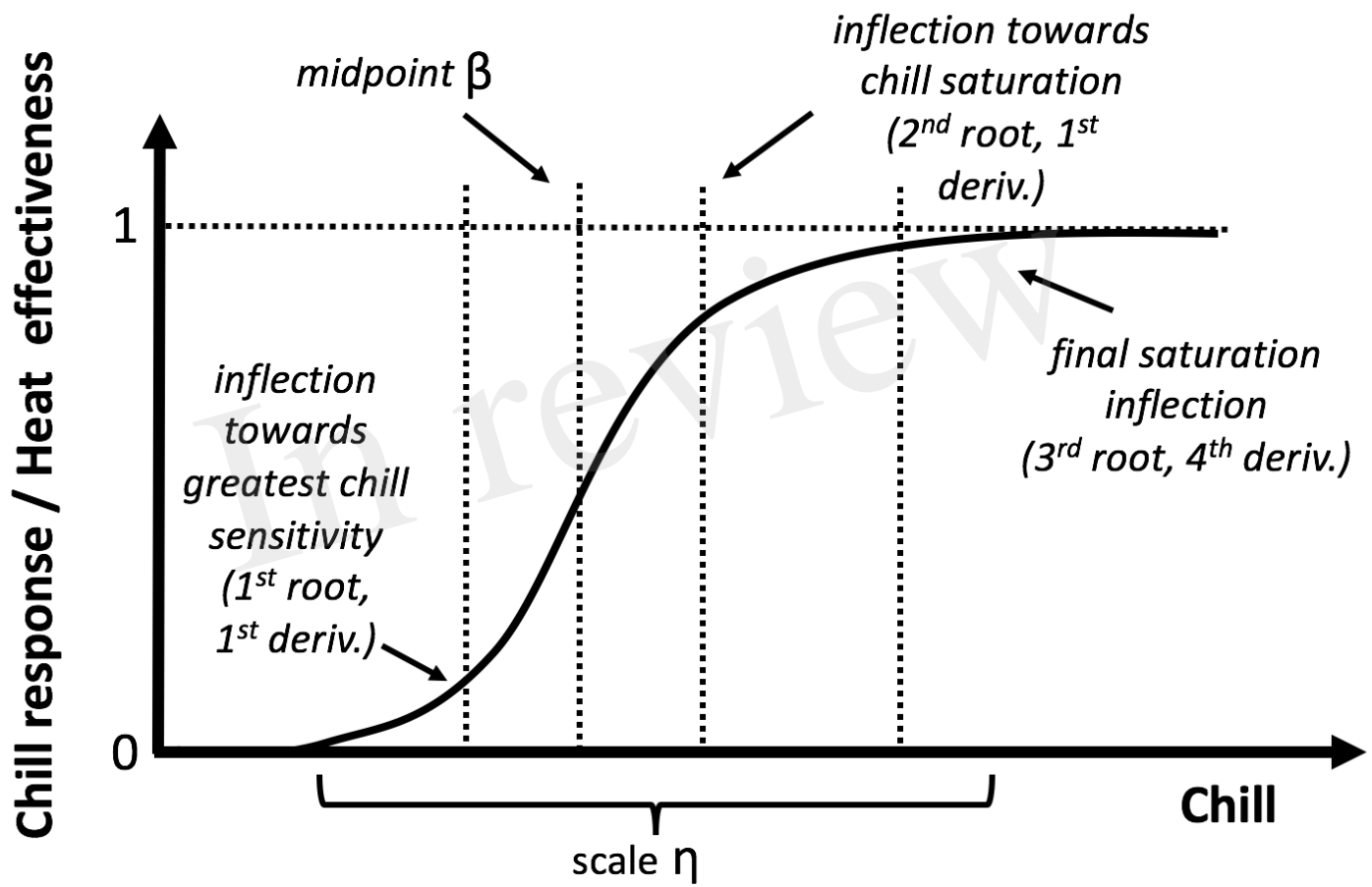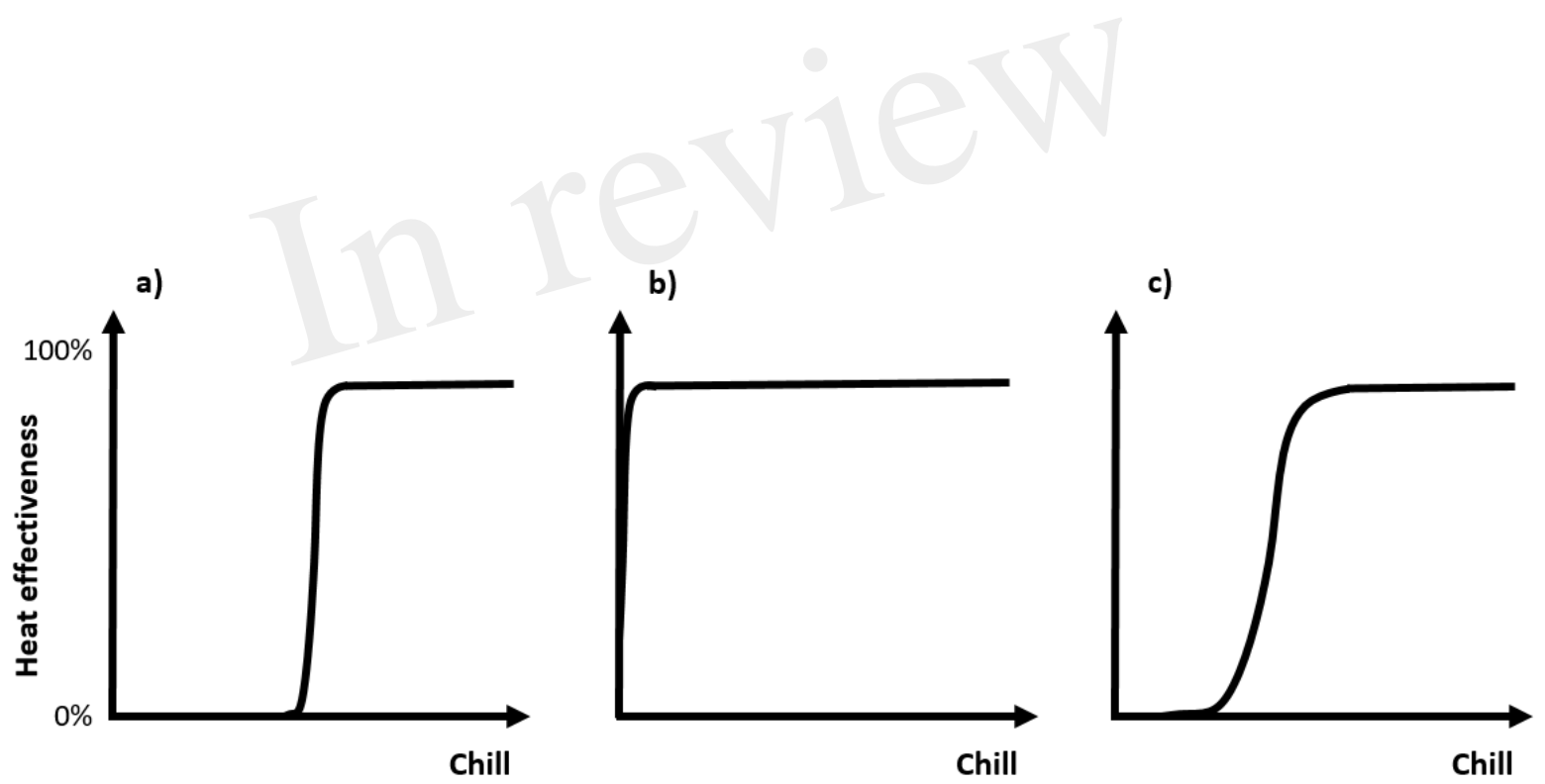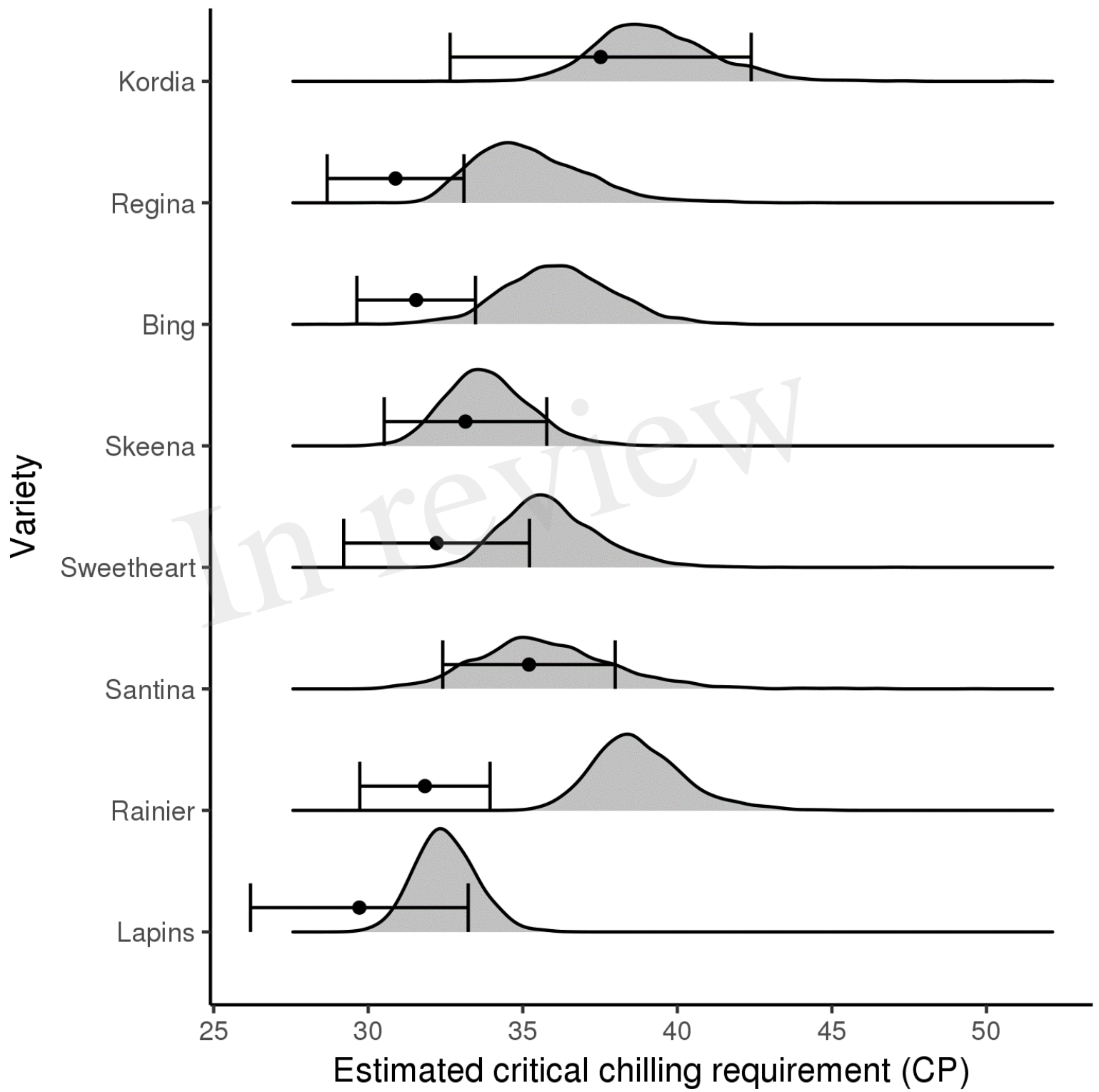Figure 2.JPEG

Figure 3.JPEG
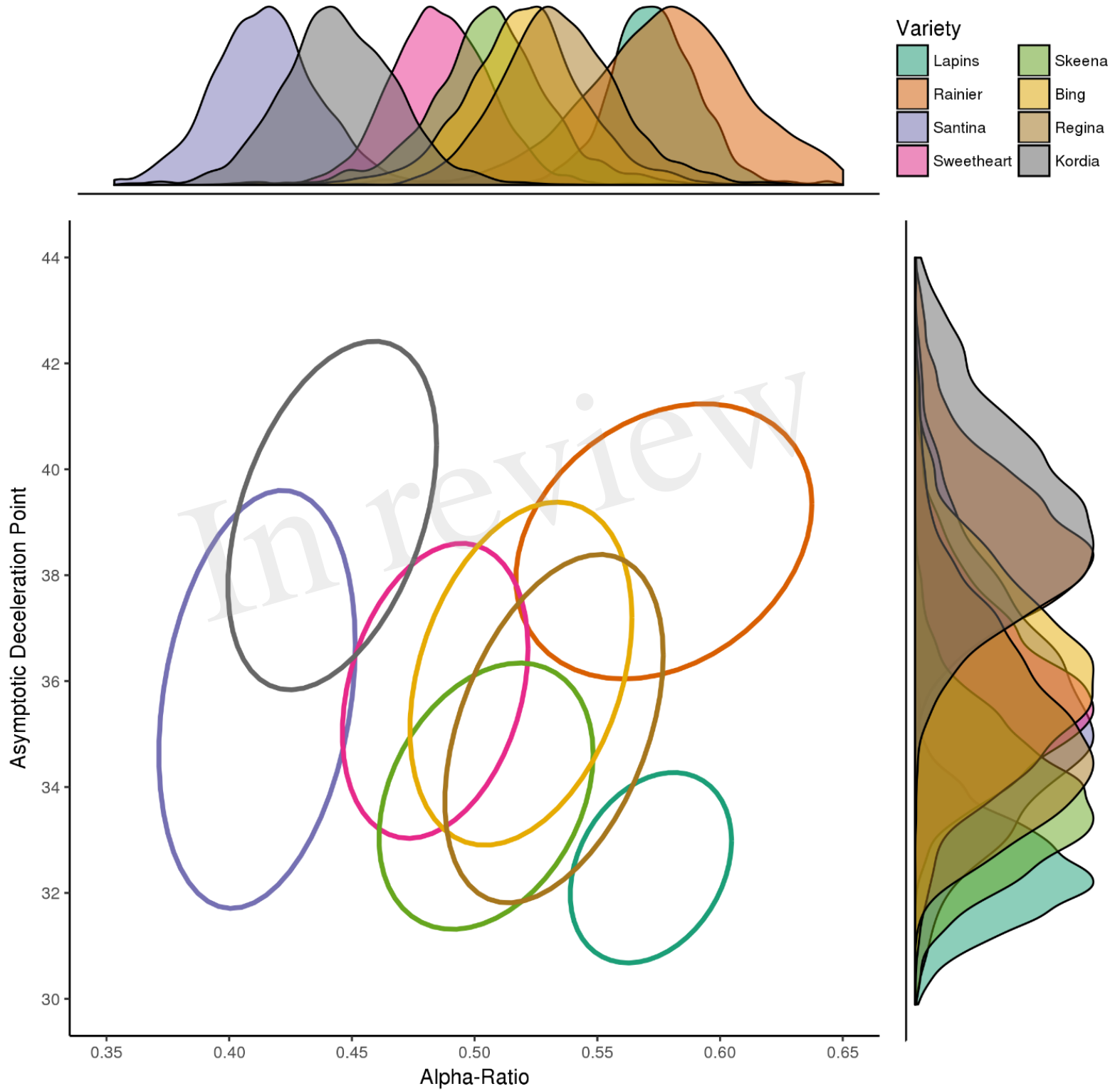
Figure 4.JPEG

Figure 5.JPEG

Figure 6.JPEG

Figure 7.JPEG

Figure 8.JPEG

Figure 9.JPEG