

1 **Contributions of dynamic environmental signals during life-cycle transitions**  
2 **to early life-history traits in lodgepole pine (*Pinus contorta* Dougl.)**

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15 **Running title:** Environment and life-history strategies

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23 **Abstract**

24 Environmental signals are important triggers in the life-cycle transitions and play a crucial role in  
25 the life-history evolution. Yet, very little is known about the leading ecological factors contributing  
26 to the variations of life-history traits in perennial plants. This paper explores both the causes and  
27 consequences for the evolution of life-history traits (i.e., seed dormancy and size) in lodgepole  
28 pine (*Pinus contorta* Dougl.) across British Columbia (B.C.), Canada. We selected 83 lodgepole  
29 pine populations covering 22 ecosystem zones of B.C. and through their geographic coordinate,  
30 197 climatic variables were generated accordingly for the reference (1961-1990) and future (2041-  
31 2070) periods. We found that dynamic climatic variables rather than constant geographic variables  
32 are the true environmental driving forces in seed dormancy and size variations and thus provide  
33 reliable predictors in response to global climate change. Evapotranspiration and precipitation in  
34 the plant-to-seed chronology are the most critical climate variables for seed dormancy and size  
35 variations, respectively. Hence, we predicted that levels of seed dormancy in lodgepole pine would  
36 increase across large tracts of B.C. in 2050s. Winter-chilling is able to increase the magnitude of  
37 life-history plasticity and lower the bet-hedge strategy in the seed-to-plant transition; however,  
38 winter-chilling is likely to be insufficient in the north of 49°N in 2050s, which may delay  
39 germination while unfavourable conditions during dry summers may result in adverse  
40 consequences in the survival of seedlings owing to extended germination span. These findings  
41 provide useful information to studies related to assessments of seed transfer and tree adaptation.

42

43 **Key words:** life-history evolution; dynamic environmental signals; seed dormancy; seed size;  
44 climate change; lodgepole pine

45 **INTRODUCTION**

46 In the context of global climate change, species have responded by tracking the environment for  
47 which they are best suited through local adaptation, range shift, range reduction, or a combination  
48 of these (Walther et al., 2002;Parmesan and Yohe, 2003;Cleland et al., 2007;Breshears et al., 2008).  
49 Knowledge about traits that vary with ecological niches should therefore help predict how these  
50 traits may evolve under climate change. Life-history traits, known as fitness components due to  
51 predictable monotonic relationship with fitness, are related to the timing and success of  
52 development, reproduction, and senescence throughout the life cycle (Calow, 1998). Ecological and  
53 genetic trade-offs constrain the combinations of the life-history traits through evolution (Adler et  
54 al., 2014), which involves an adaptation to environments and is shaped by natural selection.

55         Climate change has already altered the timing of major life-history transitions, such as seed  
56 germination timing (from seed to plant). Timing is directional and completely asymmetric and the  
57 timing of seed germination is the earliest life-history trait that is expressed and sets the context for  
58 the traits that follow (Donohue et al., 2010). It is controlled by the level of seed dormancy, whereby  
59 dormant seeds await germination cues for dormancy release (Finch-Savage and Leubner-Metzger,  
60 2006;Baskin and Baskin, 1998). Moreover, early developmental stages of plants are more sensitive  
61 to environment perturbations than adult stages and represent a major bottleneck to regeneration  
62 from seeds (Johnsen and Skrøppa, 1996;Hedhly et al., 2009). At the core of plant regeneration,  
63 temperature and water availability (or precipitation) are critical drivers for a plant's distribution  
64 (Woodward and Williams, 1987). Hence, climate-changed plant regeneration will be manipulated  
65 in both temperature- and moisture-controlled ecosystems (Walter and Breckle, 2002) and much of  
66 plant regeneration climate research has been directed at tundra and boreal forest, and treeline  
67 ecotones (reviewed in (Walck et al., 2011)).

68           Seed size is another important life-history trait and subject to changing environmental  
69 settings. In the palaeontological scale, fossil data suggest that seed size remains small across all  
70 plants until the Cretaceous period (124 MYA). Seed size begins to increase after the limit of the  
71 Cretaceous-Tertiary period (65 MYA). One of the most popular explanations is that climate change  
72 gives rise to seed size variation, which took place during that period (Eriksson et al., 2000). In the  
73 ecological time scale, empirical studies lend supports to the impact of environment on seed size  
74 variation. Since the early 1950s, effects of environmental stimuli, such as, temperature and  
75 photoperiod on seed size and weight have been noted. *Chenopodium polyspermum* L. seeds from  
76 mother plants grown in long days have lower germination frequency and thicker seed coats when  
77 compared to seeds from short days (Pourrat and Jacques, 1975). Large seed size with more  
78 provisions stored for seedlings may be favorable in variable environments (Venable and Brown,  
79 1988). Seed plants have a general trend of increasing embryo to seed ratio (E:S) in morphological  
80 seed dormancy and the shift in E:S is likely a heterochronic change, having vital implications to  
81 life history of seed plants (Forbis et al., 2002). *A priori*, the environment plays a crucial role in  
82 life-history traits in general and seed size in particular.

83           Adaptive phenotypic plasticity underpins rapid phenological shifts in response to climate  
84 change and evolve when cues reliably predict fitness consequences of life-history decision  
85 (Simons, 2014). This was evident by the performance of seedlings produced by central European  
86 trees growing in central Norway as they expressed phenology similar to that of their adjacent  
87 ecotype and were exceedingly different from those produced at their original habitat (Skrøppa et  
88 al., 2010). Differences in adaptive traits between populations are inconsistent with the Mendelian  
89 genetic framework and probably modulated by epigenetic mechanisms (Yakovlev et al., 2012).  
90 Germination-cuing under favorable conditions is similar within species; however, these conditions

91 do not persist throughout the seasons. Likewise, populations growing in different ecological niches  
92 may have different degrees of exposure to unfavourable environments. As such, the prevention of  
93 germination of some seeds even under favourable conditions would be of significance. When  
94 environments fluctuate unpredictably, "bet-hedging" strategy (Slatkin, 1974) is expected to spread  
95 germination over time to reduce the risk of outright extinction. This results in the evolution of  
96 traits that maximizes the geometric-mean fitness by reducing fitness variance over generations  
97 (Gillespie, 1977). To date, much of the evidence for bet-hedging remains restricted to simple life-  
98 history plants (e.g., annuals) (Childs et al., 2010).

99         A continuously changing environment is constantly selecting for new adapted genotypes  
100 resulting in greater genetic diversity (Jump et al., 2009). Adaptive evolution characterized by the  
101 genetic architecture allows population persistence in the long term (Lande and Shannon, 1996).  
102 However, sustained directional selection due to climate change could potentially eliminate a  
103 proportion of the genetic variation needed for continued adaptation. To date, it remains unclear  
104 whether adaptive evolution can keep pace with climate change (Etterson and Shaw, 2001).

105         Life-history strategy for long-lived organisms is influenced primarily by survival (Adler et  
106 al., 2014). Evergreen coniferous forests in the Pacific Northwest are unique among the Northern  
107 Hemisphere temperate forests in their species composition and high productivity (Waring and  
108 Franklin, 1979). Our study species, lodgepole pine (*Pinus contorta* Dougl.), is an aggressive  
109 pioneer species distributed over wide geographic and ecologic ranges across British Columbia,  
110 Canada and is therefore expected to display a wide spectrum of dormancy variation owing to  
111 adaptation to diversified local habitats (Plomion et al., 2007). Cone and seed production in  
112 lodgepole pine is not as cyclic as in many other conifers. Cone drop soon after seed maturation is  
113 commonly observed in coastal areas but lodgepole pine growing in the interior tends to be

114 serotinous, indicating that mature cones do not drop or open to release seeds unless exposed to  
115 fluctuating high temperature during prolonged hot summer and low fall temperatures or due to fire  
116 or insect damage (Fowells, 1965;Owens et al., 1981, 1982). Most serotinous cones take several  
117 years to open and seeds are released in large quantities, consequently, any seed collection made  
118 from a single tree consists of a mixture of different seed-crop years. Before the cones eventually  
119 open, seeds are wrapped and sealed by scales and sticky resin without exposure to any germination  
120 cues (such as moisture, oxygen, etc.); thus we assumed that seed dormancy in lodgepole pine is  
121 least affected over its natural storage period.

122         Seed dormancy is an intrinsic attribute affecting regeneration dynamics and seed size is  
123 one of the vital determinants for the evolution of seed dormancy. The objectives of this study are  
124 to evaluate the contributions of local environmental effects during life-cycle transitions to seed  
125 dormancy and size variations of lodgepole pine populations across British Columbia, Canada and  
126 to predict how life-history traits evolve locally under ongoing climate change. Studies of seed  
127 dormancy and size allow investigating the relationship between these two life-history traits and  
128 their relationship with environments in life-cycle transitions. This study can also contribute to  
129 providing the missing empirical evidence of bet-hedging strategy in long life-history plants.

130

## 131 **METHODS**

### 132 *Plant materials, and current and future climate data*

133 The 83 lodgepole pine seed lots used were representative of 83 different populations covering 22  
134 ecosystem zones. The seed lots are distributed throughout the species' natural range across British  
135 Columbia (B.C.), Canada encompassing coastal area and interior regions with a spatial grid over  
136 latitudinal range from 49 to 60°N and longitudinal range from 115 to 132°W, which consist of  
137 tundra, boreal and temperate forests, and treeline ecotone ecosystems (Fig. S1). The studied

138 populations were selected primarily based on two important climate variables; namely, mean  
139 annual temperature (MAT) and annual heat moisture index (AHM) (Fig. S2) (Wang et al., 2006)  
140 and geographic variables, including longitude, latitude, and elevation were also considered.

141 Climate data (197 climatic variables) of the 83 studied sites for the reference normal period  
142 1961-1990 were generated using ClimateWNA version 4.85 (a software package used for regional  
143 climate predictions using historical weather station data and global circulation models) (Wang et  
144 al., 2012). The same 197 climatic variables for the future period between 2041 and 2070 (or 2050s)  
145 were also projected using ClimateWNA. The future climate data were downscaled to point  
146 locations using a delta approach (Wang et al., 2012). We used three Representative Concentration  
147 Pathways (RCP) 2.6, 4.5 and 8.5 from the CGCM4 model output of the phase 5 of the Coupled  
148 Model Intercomparison Project (CMIP5), generated by the United States National Center for  
149 Atmospheric Research. The CCSM4 model output was included in the Intergovernmental Panel  
150 on Climate Change (IPCC) Fifth Assessment Report (AR5) (Stocker and Randall, 2013).  
151 Moreover, CCSM4 is close to the average in both temperature and precipitation increases in the  
152 study areas (B.C.). In the prediction of seed dormancy indicators across B.C. for the reference  
153 period and 2050s, climate data were generated for each pixel at the spatial resolution of  $800 \times 800$   
154 m using ClimateWNA. The full list of climatic variables is given in Table S1 and the four most  
155 relevant variables for the present study were *Eref07* and *\_summer* (July and summer hargreaves  
156 reference evaporation estimated based on temperature and solar radiation), *DD\_0\_summer*  
157 (summer degree-days below  $0^{\circ}\text{C}$ ), *PPT07* and *10* (July and October precipitation (mm)), and  
158 *Tmax07* (July maximum mean temperature ( $^{\circ}\text{C}$ )).

### 159 *Life-history traits' measurement*

160 Germination parameters were estimated from cumulative germination curves fitting a  
161 mathematical function known as the four-parameter Hill function (El-Kassaby et al., 2008). Core  
162 germination parameters include dormancy index (*DI*, the difference of areas under germination  
163 curves (*AUC*) of control and treated seed), germination capacity (*GC*, the final germination  
164 fraction), time to germination (time at the onset of germination), and germination speed (*GS*, the  
165 time required to achieve 50% germination of the total germinated seed) (graphically represented  
166 by Figure S3, (Liu and El-Kassaby, 2015)). To simulate winter chilling in the soil seed bank and  
167 retain natural seed dormancy, seed germination was manipulated with or without 21-day moist-  
168 chilling treatment under 3°C in lightproof chamber. Germination assay was performed as  
169 previously described (Liu et al., 2013b) and seed size was measured as the average of 1000-seed  
170 weight collected from each study site.

### 171 *Data analysis and visualization*

172 To investigate which climatic variables can most explain the observed patterns of seed dormancy  
173 and size variations, partial least squares (PLS) analyses was conducted using SAS® (vers. 9.3;  
174 SAS Institute Inc., Cary, NC) (Jose Crossa et al., 2013). The goal of PLS regression is to analyse  
175 multivariate response based on a large set of explanatory variables (i.e., climatic variables). This  
176 technique combines features from principle component analysis (PCA) and multiple regression  
177 (Abdi, 2007;Carrascal et al., 2009). PLS regression is particularly suitable when the matrix of  
178 predictors has more variables than observations, and when there is multicollinearity among N  
179 values. Using the machine-learning algorithm (i.e., PLS), important climate variables can be  
180 identified through a process of model optimization and there is no needed to explain the  
181 contribution of climate variables in the initial input dataset. In the PLS biplot, the angles between  
182 the environment vectors proximately correspond to the correlation coefficients among the



183 environments. The cosine of the angle between two vectors approximates the correlation between  
 184 them and the length of the vectors is proportional to the standard deviation within respective  
 185 environments or genotypes (Yan, 2001; Yan and Tinker, 2006). Virtually, an ideal environment  
 186 has the longest vector of all test environments (most discriminating and informative) and is closely  
 187 located on the abscissa (most representative) (Liu and El-Kassaby, 2015). As a comparison, PCA  
 188 for explanatory variables and canonical correlation analysis (CCA) dealing with both explanatory  
 189 and response variables were also performed (Liu and El-Kassaby, 2015). To examine how seed  
 190 dormancy and size varied in ecosystem zones, the two variables were analyzed collectively using  
 191 multivariate analyses (MANOVA) with the aid of general linear model (GLM) procedure in SAS  
 192 (Manly, 2005; Tabachnick and Fidell, 2012). To investigate how the most correlated climatic and  
 193 geographic variables affect life-history traits, hierarchical models were established using PROC  
 194 MIXED in SAS with errors split into population and ecosystem zones but having unequal  
 195 variances at the population level (West et al., 2007; Raudenbush and Bryk, 2001). The most  
 196 correlated climatic variables through the PLS analysis were used and the model was expressed as  
 197 follows:

$$(life\text{-}history\ trait)_{ij} = (\beta_0 + \epsilon_j) + \beta_k \times P_{kij} + \beta_l \times T_{lij} + \epsilon_{ij} \quad [1]$$

198 where  $i$  and  $j$  represent two levels, namely,  $i^{\text{th}}$  population within  $j^{\text{th}}$  ecosystem zone;  $P_{kij}$  and  $T_{lij}$   
 199 represent the  $k^{\text{th}}$  precipitation- and  $l^{\text{th}}$  temperature-based variable in  $i^{\text{th}}$  population within  $j^{\text{th}}$   
 200 ecosystem zone, respectively;  $\epsilon_j$  and  $\epsilon_{ij}$  represent errors from the ecosystem zone and population  
 201 level, respectively. Intercept ( $\beta_0 + \epsilon_j$ ) and coefficients ( $\beta_k$  and  $\beta_l$  ( $k, l = 1, 2, 3, \dots$ )) were estimated  
 202 using our experiment data. Analogously, fitting models using longitude, elevation, and latitude as  
 203 independent variables were established. Using the foregoing climatic model for the reference  
 204

205 period and 2050s via CCSM4 RCP 4.5, *DI* values were estimated for each pixel across BC at the  
206 resolution of  $800 \times 800$  m and mapped across B.C for visualization.

207 To investigate the phenotypic plasticity of timing of seed germination, Pearson's product-  
208 moment correlation was calculated. The mean phenotypic plasticity of timing of seed germination  
209 is the magnitude of the average response of the population genotypes to specific environments and  
210 calculated as a population's mean *AUC* in the chilling manipulation minus its corresponding value  
211 in the control (i.e., *DI*). To investigate the range of possible plastic response to dormancy and to  
212 determine its genetic contribution to the phenotypic variance, the following linear model was used:

$$213 \quad DI_{ij} = \mu + G_i + E_j + GE_{ij} + \varepsilon \quad [2]$$

214 where  $DI_{ij}$  is dormancy index of  $i^{\text{th}}$  genotype in  $j^{\text{th}}$  environment,  $\mu$  is the overall mean,  $G_i$  is the  
215 effect of the  $i^{\text{th}}$  genotype,  $E_j$  is the effect of the  $j^{\text{th}}$  environment,  $GE_{ij}$  is the interaction of  $i^{\text{th}}$  genotype  
216 with  $j^{\text{th}}$  environment, and  $\varepsilon$  is the random error. The range of phenotypic plasticity is interpreted  
217 as  $G \times E$  variation ( $V_{G \times E}$ ) and the extent of genetic control of a trait was calculated by broad-sense  
218 heritability ( $H^2 = V_G / (V_G + V_{G \times E} + V_\varepsilon)$ ).

219 To evaluate bet-hedge strategy in seed germination, two potential traits were tested, i.e.,  
220 germination capacity and time to germination. Specifically, germination capacity was the subject  
221 of Cohen's classic bet-hedging model (Cohen, 1966), in which dormancy is expected to evolve in  
222 proportion to the probability of encountering a 'bad' year, which corresponds to no chilling  
223 manipulation in this study. Time to germination in a 'bad' or 'good' year (i.e., no chilling vs.  
224 chilling) represents within-season variation, which has been shown to be advantageous when  
225 germination success is unpredicted within season (Simons, 2009). The standard deviation (STD)  
226 for these two traits in a 'good' and 'bad' year was also calculated to measure the amount of  
227 variation across studied populations.

228

## 229 **RESULTS**

### 230 *Life-history traits strongly correlated with climatic variables in the plant-to-seed transition*

231 Partial least squares (PLS) analyses for seed dormancy and weight indicated that the first and  
232 second components accounted for 15 and 13%, and 18 and 9% of the total variation, respectively  
233 (Fig. S4). The 15 most correlated climatic variables with respect to life-history traits were  
234 correlated with environmental factors related to temperature (Fig. 1). This indicates that  
235 temperature plays a major role in the development of life-history traits (Liu and El-Kassaby, 2015).  
236 By contrast, the PCA analysis showed several temperature-based variables which were  
237 intrinsically correlated (Fig. S5). In addition, the PLS analyses classified the 83 population habitats  
238 into 21 and 20 major categories for seed dormancy and weight, respectively (blue arrows in Figure  
239 S4).

240 The first canonical correlation analysis (CCA) was significant across all statistical tests  
241 (Table S2A). Seed dormancy and weight had moderate (0.66) and very strong (0.90) correlations  
242 with climate, moderate (0.59) and high (0.74) correlations with life-history traits (i.e., combination  
243 of seed dormancy and weight), and moderate (0.53-0.55) correlation with geographic variables  
244 (Table 1A). This implies that the climatic variables were more important than the geographic  
245 variables in variations of life-history traits. Based on respective covariate matrices for ‘life-history  
246 traits’, ‘climatic ecology’, and ‘geographic ecology’ canonical variates, 62.35 and 47.11%, 62.85  
247 and 45.06%, 14.80 and 6.82% of variance were explained by their corresponding canonical  
248 variates for the same group of variables and the other group of variables (Table 1B). Furthermore,  
249 multivariate analyses showed that ecosystem zones were significant for seed dormancy and weight,  
250 and had moderate correlation ( $R^2 = 0.55-0.56$ ,  $P < 0.0001$ ) with life-history traits (Table 2).

251 In the hierarchical model for seed dormancy using climatic variables, the climatic variables  
252 *Eref07*, *Eref\_summer*, and *DD\_0\_summer* were significant (Table 3A). This indicates that summer  
253 moisture and temperature, the period corresponding to the plant-to-seed transition, played an  
254 important role in the development of seed dormancy. The intercept including error from ecosystem  
255 zones was not significant (Table 3A). For seed weight, variables *PPT07* and *PPT10*, *Tmax07*, and  
256 intercept were significant (Table 3B), indicating that July temperature and precipitation and  
257 October precipitation were important to seed weight. Ecosystem zones, representing ecological  
258 boundaries in geography, had a greater impact on the variation of seed weight than that of seed  
259 dormancy. In the geographic variable-based hierarchical model for seed dormancy, only longitude  
260 and intercept were significant (Table S4A and Fig. S6A). For seed weight, longitude, elevation  
261 and intercept were significant (Table S4B and Fig. S6B), indicating that longitude was an  
262 important geographic factor in life-history traits and geographic factors had greater influence on  
263 the variation of seed weight than seed dormancy. Considering all these results collectively, life-  
264 history traits were significantly influenced by precipitation as well as temperature in the plant-to-  
265 seed chronology, and roughly distributed in a longitude pattern.

#### 266 ***Prediction of life-history traits in response to climate change***

267 Using current climate data, seed dormancy predicted had a moderate linear relationship ( $R^2 = 0.47$ ,  
268  $P < 0.0001$ ) with that observed (Fig. 2), which was used for the correction of the climate scenario  
269 predicted in 2050s. Seed dormancy predictions using three greenhouse gas emission scenarios  
270 (RCP2.6, 4.5, and 8.5) showed that *DI* in 2050s would increase (Fig. 2). In general, the spatial  
271 pattern of *DI* across the entire province showed that the seed dormancy in the south of B.C. would  
272 pronouncedly increase and the territory previously not suitable for pines to establish (grey area in  
273 1970s) is expected to shrink in 2050s, which are responses to climate change (Fig. 3). In addition,

274 seed weight ‘predicted’ had a low moderate linear relationship ( $R^2 = 0.34$ ,  $P < 0.0001$ ) with  
275 observed values (Fig. S7).

### 276 *Correlated response in plasticity to timing of seed germination after ‘winter-chilling’*

277 Among the 83 lodgepole pine populations, variance of seed dormancy was significantly explained  
278 by genotype and environment (Table 2B). Estimate of broad-sense heritability ( $H^2$ ) was 0.54  
279 corresponding with the observed variance component for genotypes (Table 2B), indicating that  
280 genetic components have moderate influence on seed dormancy variation. In response to  
281 significant  $G \times E$  interaction (Table 2B), a plot of the reaction norms of  $AUC$  showed a range shift,  
282 nonparallelism, and crossing between moist-chilling and control (Fig. 4), where  $G \times E$  accounted  
283 for 39% of the variance and was attributed to crossing of reaction norms (Table 2B), indicating  
284 that environments changed the adaptive values of the life-history trait.

285  $AUC$  and phenotypic plasticity under chilling treatment had a moderate correlation ( $R^2 =$   
286  $0.53$ ,  $P < 0.0001$ ) (Fig. 4), indicating that populations that germinated after chilling treatment were  
287 more plastic. However, when no treatment prior to germination was applied, they yielded a weak  
288 and not statistically significant correlation ( $R^2 = 0.04$ ,  $P = 0.3479$ ) (Fig. 4). Therefore, germination  
289 after the chilling treatment was able to increase the magnitude of phenotypic plasticity, which was  
290 a response to subsequent predictable environments.

### 291 *Expression of bet-hedge under manipulated environmental uncertainty*

292 Relative to ‘bad-year’ simulation, ‘good-year’ resulted in higher and uniform germination capacity  
293 and shorter time to germination across the 83 populations (Fig. 5). The standard deviation (STD)  
294 of germination capacity and time to germination were evenly distributed on the two sides of  
295 respective average line for both good- and bad-year across populations (Fig. 5) and ‘good-year’  
296 had lower average STD germination capacity and STD time to germination (Fig. 5). This indicates

297 that, though bet-hedge is a risk strategy for unpredictable environments, ‘good-year’ can lower the  
298 risk by means of allowing higher germination capacity and shorter time to germination across  
299 populations.

300

## 301 **DISCUSSION**

302 Climate change is accelerating plant life-cycle transitions in coordination with the seasons. In life-  
303 cycle transitions, the environment plays a critical role in the development of life-history traits and  
304 in response to environmental stimuli, intrinsic mechanisms of genetics, epigenetics, phenotypic  
305 plasticity, bet-hedge strategy, and adaptive evolution take effect (Fig. 6). In this study, we found  
306 that seed dormancy and size were most correlated with evapotranspiration, and precipitation and  
307 maximum mean temperature during the plant-to-seed transition, respectively, using 83 lodgepole  
308 pine populations across British Columbia (B.C.), Canada. We predicted that the range of seed  
309 dormancy variation would increase across B.C. in 2050s. Moreover, winter-chilling can increase  
310 the magnitude of life-history plasticity (predictable factor) and lower the bet-hedge strategy  
311 (unpredictable factor). However, future climate may bring about insufficient winter-chilling  
312 required to decay seed dormancy, thus resulting in adverse consequences for the timing of  
313 phenology and the growth and establishment in lodgepole pine. This study allowed us to gain  
314 insights in the role of dynamic environments in shaping life-history characteristics.

### 315 ***Environmental conditions in the plant-to-seed transition***

316 In the plant-to-seed chronology, the sexual reproduction of plants is vulnerable to climate change  
317 as influenced by the maternal environment (Hedhly et al., 2009;Donohue, 2009;Schmitt et al.,  
318 1992), and temperature is involved in both genetically-based and environmentally-induced  
319 parental effects (Lacey, 1996). Global warming has resulted in an upward shift in species optimum

320 elevation and latitude (Chen et al., 2011; Lenoir et al., 2008; Parmesan and Yohe, 2003), an  
321 observation similar to that reported by Parmesan C. (2006) as she pointed out that the best places  
322 to seek potential changes in species ranges is at their altitudinal and latitudinal treelines (Parmesan,  
323 2006). This suggested that climatic variables are the real causes of species' responses to  
324 environmental signals. Compared with last three decades, the Pacific Northwest is expected to  
325 warm about 0.8-2.9°C by mid-century (Leung et al., 2004; Duffy et al., 2006; Mote et al., 2008),  
326 and 1.5-5.4°C by the end of the century (Mote et al., 2008). Warming in this region will be  
327 probably greater in summer (3.9°C on average) than in winter (2.7°C) (Mote et al., 2008).

328         In the hierarchical model for seed dormancy, the climatic variable, summer degree-days  
329 below 0°C (*DD\_0\_summer*) was not equal to zero only for 16 out of the total 83 study populations  
330 and was projected to be zero for 80 populations in 2050s. We performed approximation by  
331 removing *DD\_0\_summer* from the model and the result of seed dormancy projection could be  
332 interpreted as: given the current-future difference in July hargreaves reference evaporation (*Eref*)  
333 is more than one third higher than that in summer *Eref* (Jun.-Aug. period), seed dormancy will  
334 increase in 2050s, and if such a difference is less than one third higher, seed dormancy will  
335 diminish. These results also suggest that the allocation of summer *Eref* in July (i.e., seed  
336 development period) was critical in the development of seed dormancy.

337         The ecosystem zones were significant in analyses of life-history traits using MANOVA  
338 (Table 2A) but not significant for seed dormancy and weight models (Table S2). This indicates  
339 that dynamic climatic variables are true driving effects on modulating life-history traits. On the  
340 other hand, gene flow as a single pollen grain carries half the number of alleles and may yield  
341 effective distance spanning from a few centimetres to thousands of kilometres (Nathan et al., 2008).  
342 The 'abundant center' model, which deals with the spatial distribution for populations across

343 species' ranges and its evolutionary potential, also has implications (Volis et al., 2014;Etterson  
344 and Shaw, 2001;Parmesan, 2006), that is, compared with core populations, locally adapted  
345 peripheral populations had lower adaptive potential and were outperformed in the novel  
346 environment. Ecosystem zones like other geographic variables are not individual units to classify  
347 life-history traits.

348 A number of ecologically and evolutionary relevant genes have been identified in  
349 Arabidopsis and some annuals, such as *FLC* (Flowering Locus C), *SCR/SP11* (S-locus Cysteine-  
350 Rich protein/ S-locus Protein 11) (Shimizu et al., 2011;Amasino, 2010), as they provide genetic  
351 diversity in adaptive evolution. Moreover, both seed dormancy (genes in ABA and GA signalling  
352 circuit) and flowering (such as *FLC*) were modulated by epigenetic mechanisms (Müller et al.,  
353 2012;Chinnusamy et al., 2008;Bossdorf et al., 2008). This indicates that epigenetic changes play  
354 a significant role in evolution and ecology and the environment signals acting on genes by  
355 epigenetic modification were crucial for life-history traits. In recent years, much progress has been  
356 made in uncovering genes operating on different seed compartments i.e., embryo, endosperm, and  
357 seed coat, which modulate seed development (Le et al., 2010). Processes that regulate seed size  
358 and development are coordinated across several morphologically distinct sub-regions (Belmonte  
359 et al., 2013) and the complex cross-talk and integration of signals from different components of  
360 the seed together determine its final size (Garcia et al., 2005).

### 361 ***Temperature signals in winter-chilling***

362 Winter dormancy is an important adaptive strategy, as it prevents plants from flushing during short  
363 warm periods in the winter. Winter chilling is an important environmental signal for plant life  
364 histories, which accelerates flowering through vernalization in winter annuals and alleviates both  
365 bud and seed dormancy, allowing the onset of growth in springs (Penfield, 2008;Penfield and



366 Springthorpe, 2012). Seeds take advantage of environmental temperature as a key signal to  
367 coordinate timing of seed germination, allowing plants to synchronize their life histories with the  
368 seasons. Low temperature can promote dormancy at the inception of seed maturation, but promotes  
369 dormancy alleviation in mature seeds after imbibition. It is therefore assumed that chilling plays a  
370 dual role in regulating dormancy (Batlla and Banech-Arnold, 2010).

371         With substantial climate warming ( $>3^{\circ}\text{C}$ ), chilling may be insufficient in many woody  
372 perennials, such as, poplar, western hemlock, and Sitka spruce, resulting in delayed bud burst and  
373 poor growth (Cannell and Smith, 1986; Murray et al., 1989; Morin et al., 2009). Based on the three  
374 different RCP scenarios, we predicted that winter-chilling days (*DD\_0\_winter*) would on average  
375 decrease by 24% across the 83 study habitats in 2050s relative to present (Fig. S8, ranges also  
376 provided), which may lead to insufficient dormancy alleviation through winter-chilling. However,  
377 spring and annual heat sums (*DD5\_spring* and *DD5*) would increase by 95 and 49%, respectively,  
378 in 2050s (Fig. S8), resulting in earlier springs and advanced vegetative green-ups and an increase  
379 in growing season length (Robeson, 2004; Schwartz et al., 2006). In 2050s, inadequate winter-  
380 chilling may delay germination and an extended germination span leads to adverse conditions  
381 during dry summers. As such, future climate will change the timing of conifer phenology and may  
382 give rise to adverse consequences.

383         In terms of molecular mechanisms in alleviation of seed dormancy via winter-chilling,  
384 several studies demonstrated that moist-chilling involves changes in levels of ABA, GAs, and  
385 auxin, and transcripts in respective signaling cascades, GA3 oxidase 1, for example (Yamauchi et  
386 al., 2004; Ali-Rachedi et al., 2004; Liu et al., 2013a; Liu et al., 2015).

387 ***Germination cues in the seed-to-plant transition***

388 Changes in climate alter patterns of phenology and thus multiple life-history traits. In response to  
389 climate change, phenotypic plasticity associated with life-history traits (Pigliucci, 2001;Chevin et  
390 al., 2010;Franks et al., 2014;Liu and El-Kassaby, 2015) and genetically based trait responses  
391 (Bradshaw and Holzapfel, 2001, 2008;Thompson et al., 2013) were well documented. In the long  
392 run, only the species that can respond by phenotypic plasticity and/ or genetically-based local  
393 adaptation can persist (Jump and Penuelas, 2005). However, the evolutionary response to climate  
394 change may be attenuated due to constraints causing a time lag between the environmental change  
395 and an observed evolutionary response (Etterson and Shaw, 2001;Davis et al., 2005). In tree  
396 populations, the extent of the constraints will hinge on phenotypic variation, strength of selection,  
397 fecundity, interspecific competition, and biotic interaction (Aitken et al., 2008).

398 Differences in plasticity exist among populations, but plasticity presumed to be adaptive  
399 may often be neutral or maladaptive (Caruso et al., 2006). An optimal balance between adaptive  
400 and non-adaptive (bet-hedging) plasticity may exist and possibly vary among populations.  
401 Moreover, germination characters are expected to exhibit phenotypic plasticity to environmental  
402 variables experienced not only by seed following dispersal but also by seed parents prior to  
403 dispersal (Schmitt et al., 1992).

404 It is noteworthy that seed dormancy and germination is a quantitative trait that interacts  
405 with environment factors (Bentsink et al., 2007). Some QTLs associated with germination  
406 phenology in *Arabidopsis* can attain allele frequencies approaching fixation within a single  
407 generation even though they started with frequencies below 50% (Huang et al., 2010), indicating  
408 strong directional selection. Seed dormancy in *Arabidopsis* was associated with a cohort of genes  
409 controlled by seasonally distinct hormone-signalling pathways in the seed soil bank, such as *DOG1*  
410 (Delay Of Germination 1), *MFT* (Mother of Flowering Timing), *DELLAs* (repressors of

411 germination potential and GA signalling), and *PIFs* (Phytochrome Interacting Factors) (Footitt et  
412 al., 2014;Footitt et al., 2011). In addition, photoperiod can affect seed dormancy and germination  
413 and phytochromes were the most investigated photoreceptors. Phytochromes are temperature- and  
414 light-dependent in association with GA pathway via the bHLH transcription factor SPATULA  
415 (SPT) (Heschel et al., 2007). SPT is a light-stable repressor of seed germination and mediates the  
416 germination response to temperature through temperature-sensitive changes in its transcription  
417 (Penfield et al., 2005).

418         In summary, we reinforced the importance of climatic signals during seed set to the  
419 formation of early life-history traits (i.e., seed dormancy and size). Variations of life-history traits  
420 may be acquired through signal transduction cascades and/ or gene/ protein imprintings triggered  
421 by specific environmental variables, such as, evapotranspiration and precipitation. The period of  
422 winter chilling exerts a pronounced influence on the range of life-history plasticity and the  
423 variation of bet-hedge strategy when the life-history trait expressed (i.e., seed emergence). In  
424 response to previous memory during seed development and different genetic architectures that  
425 every individual harbours, germination behaviour (e.g., timing of seed germination) varies even  
426 given same optimal germination cues.

427

#### 428 **AUTHOR'S CONTRIBUTION**

429 YL conceived of the study, carried out data analysis, and drafted the manuscript; TW participated  
430 in selection of study populations, performed current and future climate predictions and mapping,  
431 and commented the manuscript; and YAE coordinated the study and helped draft the manuscript.  
432 All authors gave final approval for publication.

433

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442

443 **SUPPLEMENTARY MATERIAL**

444 **Table S1** A list of important climatic variables

445 **Table S2** Canonical correlation analysis (CCA) and MANOVA statistical test criteria

446 **Table S3** Errors from ecosystem zones in life-history traits' models

447 **Table S4** Parameter estimates and statistical tests for the geographic variables-based hierarchical  
448 models regarding life-history traits

449 **Figure S1** Geographical distribution of the 83 populations (green triangles) on the map regarding  
450 AMT value (A) and ecosystem zones (B) of British Columbia, Canada.

451 **Figure S2** The distribution of the samples based on mean annual temperature (MAT) against  
452 annual heat moisture index (AHM).

453 **Figure S3** Schematic representation of the cumulative germination curve parameters used to  
454 characterize seed dormancy.

455 *DI* (dormancy index): the gray shaded area, the difference of area under germination curves (*AUC*)  
456 of control and any other treatment; *GS* (germination speed): the number of days to reach 50% of  
457 final germination; *GC* (germination capacity): the final germination percentage.

458 **Figure S4** PLS biplot of 194 climatic variables (green), 83 populations (red), and 21 (above) 20  
459 (below) categories for 83 population habitats (blue).

460 **Figure S5** PCA for 194 climatic variables. The 15 most correlated climatic variables were marked  
461 in red.

462 **Figure S6** Seed dormancy (*DI*, above) and weight (*SW*, below) distribution for the 83 populations  
463 labeled on the map of British Columbia, Canada.

464 **Figure S7** Linear relationship between 1,000-seed weight and ‘predicted’ 1,000-seed weight using  
465 83 populations.

466 **Figure S8** The amount of changes for *DD\_0\_winter*, *DD5\_spring*, and *DD5* in 2050s relative to  
467 present.

468 Note: The population was ranked as per its current *DI* in ascending order. Each data point is the  
469 average of predictions using three methods (RCP2.6, 4.5, and 8.5). Bars indicate the SEM.

470

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714 **FIGURE LEGENDS**

715 **Figure 1** The 15 most correlated climatic variables with seed dormancy (A) and size (B) after  
716 partial least squares (PLS) regression.

717 Note: ① three variables (*Eref07* and *\_summer*, and *PPT10*) were highly correlated with both seed  
718 dormancy and size; ② fonts in black and grey represent the temperature-and precipitation-based  
719 climatic variables, respectively; ③ see Table S1 for full names of abbreviated variables.

720 **Figure 2** Seed dormancy (*DI*) prediction in 2050s. (A) Linear relationship between predicted *DI*  
721 and *DI* used for the correction of predicted seed dormancy; (B) Corrected seed dormancy  
722 prediction using Representative Concentration Pathways (RCP) 2.6, 4.5 and 8.5, respectively.

723 Note: ① model for seed dormancy prediction,  $DI = (2.4819 + ecosystem\ zone) + 2.7079 \times Eref07$   
724  $- 0.9284 \times Eref\_summer + 6.6170 \times DD\_0\_summer$  [refer to Table S2 for intercept adjustment in  
725 each ecosystem zone]; ② the population was ranked as per its current *DI* in ascending order and  
726 95% confidence interval (CI) was plotted.

727 **Figure 3** Map of predicted seed dormancy using climatic model for the reference period and 2050s  
728 in lodgepole pine across British Columbia.

729 Note: *DIs* (i.e., dormancy indexes) are classified into five categories and represented by different  
730 colours on the map. The higher the value, the more dormant the seeds.

731 **Figure 4** Studies of phenotypic plasticity. (A) Reaction norms for *AUC* with or without moist-  
732 chilling treatment across the 83 populations; (B) Relationship between phenotypic plasticity and  
733 *AUC* with or without moist-chilling treatment. Best fit lines based on linear models are provided.

734 **Figure 5** Studies of bet-hedge strategy. Bet-hedge dormancy involving germination capacity and  
735 time to germination (left) and their STD (right) in response to ‘good-year’ and ‘bad-year’  
736 treatments.

737 Note: the population was ranked as per its current *DI* in ascending order.

738 **Figure 6** Important environment stages and intrinsic mechanisms in the life cycle of lodgepole  
739 pine for life-history traits.

740 Note: ① \*, seed dispersal may not occur in the following season and it may take years until the  
741 cone drops and seeds release in nature; ② the reproduction cycle of (lodgepole) pine undergoes  
742 three years, that is, seed/pollen cone initiation (A S O) → dormant (N D J F M) → pollen  
743 development (A M) → pollination (J) → female gametophyte development (J A) → dormant (S O  
744 N D J F M A) → female gametophyte development (M J). (Initial letters in the bracket represent  
745 months.)



746 **Table 1 Canonical correlation analysis between individual variables and their own and opposite set**  
 747 **of variables**

748 A)

Variables		Life-history traits	Climatic Ecology <sup>†</sup>	Geographic Ecology <sup>††</sup>
Life-history traits	Seed weight	0.7429	0.9021	0.5481
	<i>DI</i>	0.5909	0.6582	0.5327

749 Note:

750 <sup>†</sup>Based on the PLS analysis, 27 most correlated climatic variables for seed dormancy (*DI*) and weight were  
 751 used as Climatic Ecology (three climatic variables were strongly correlated with both seed dormancy and  
 752 weight).

753 <sup>††</sup>Geographic Ecology consists of latitude, longitude, and elevation.

754 B)

Canonical variate	% explained variance by	
	Their own	The opposite
Life-history traits	62.35%	47.11%
Climatic Ecology	62.85%	45.06%
Geographic Ecology	14.80%	6.82%

755

756 **Table 2 Multi- and uni-variate analyses for life-history traits. (A) MANOVA table reporting the**  
 757 **correlation of seed dormancy (*DI*) and weight with ecosystems; (B) ANOVA table reporting**  
 758 **significant effect of the genotype on phenotypic variance and associating broad-sense heritability ( $H^2$ ).**

759 A)

SOV	Parameters						
	DF	<i>DI</i>			Seed weight		
		Mean squares	<i>F</i> -value	$R^2$	Mean squares	<i>F</i> -value	$R^2$
Ecosystem zones	21	130.3132	3.50**	0.55	0.3011	3.63**	0.56
corrected error	61	37.1821			0.0829		

760 SOV, source of variation; DF, degrees of freedom; EMS, expected mean squares.

761 \*\*  $P < 0.025$  (= 0.05/2 dependent variables).

762 B)

SOV	DF	EMS	Mean squares	<i>F</i> -value	Variance components	$H^2$
Genotype (G)	82	$\sigma_{\epsilon}^2 + 8\sigma_G^2$	346.8691	67.01**	54.02%	
Environment (E)	1	$\sigma_{\epsilon}^2 + 4\sigma_{G \times E}^2 + 332\varphi_E$	89393.0625	17268.20**	- <sup>¶</sup>	0.54
G × E	82	$\sigma_{\epsilon}^2 + 4\sigma_{G \times E}^2$	129.8935	25.09**	39.43%	
Error ( $\epsilon$ )	498	$\sigma_{\epsilon}^2$	5.1767		6.55%	

763 <sup>¶</sup>no variance components or percent of total variation were estimated for the fixed effect (E).

764 \*\*  $P < 0.05$ .

765 **Table 3 Parameter estimates and statistical tests for the climatic variables-based hierarchical models**  
 766 **regarding seed dormancy and weight**

767 A) Seed dormancy model

Effect	Estimate	Standard Error	DF	Statistic	<i>P</i>
Intercept <sup>¶</sup> ( $\beta_0$ )	2.4819	7.9418	21	$t = 0.31$	0.7577
<i>Eref07</i> ( $\beta_1$ )	2.7076	0.8932	58	$F = 9.19$	<b>0.0036</b>
<i>Eref_summer</i> ( $\beta_2$ )	-0.9284	0.3354	58	$F = 7.66$	<b>0.0076</b>
<i>DD_0_summer</i> ( $\beta_3$ )	6.5170	1.8480	58	$F = 9.06$	<b>0.0039</b>

768 <sup>¶</sup> residual from the ecosystem zone ( $\epsilon_j$ ) is integrated into ‘intercept’ (Table S3).

769 B) Seed weight model

Effect	Estimate	Standard Error	DF	Statistic	<i>P</i>
Intercept <sup>¶</sup> ( $\beta_0$ )	1.3290	0.3799	21	$t = 3.50$	<b>0.0021</b>
<i>PPT07</i> ( $\beta_1$ )	0.0046	0.0019	58	$F = 5.66$	<b>0.0207</b>
<i>PPT10</i> ( $\beta_2$ )	-0.0014	0.0007	58	$F = 4.68$	<b>0.0346</b>
<i>Tmax07</i> ( $\beta_3$ )	0.0721	0.0150	58	$F = 23.11$	<b>&lt;0.0001</b>

770 <sup>¶</sup> residual from the ecosystem zone ( $\epsilon_j$ ) is integrated into ‘intercept’ (Table S3).

Figure 1

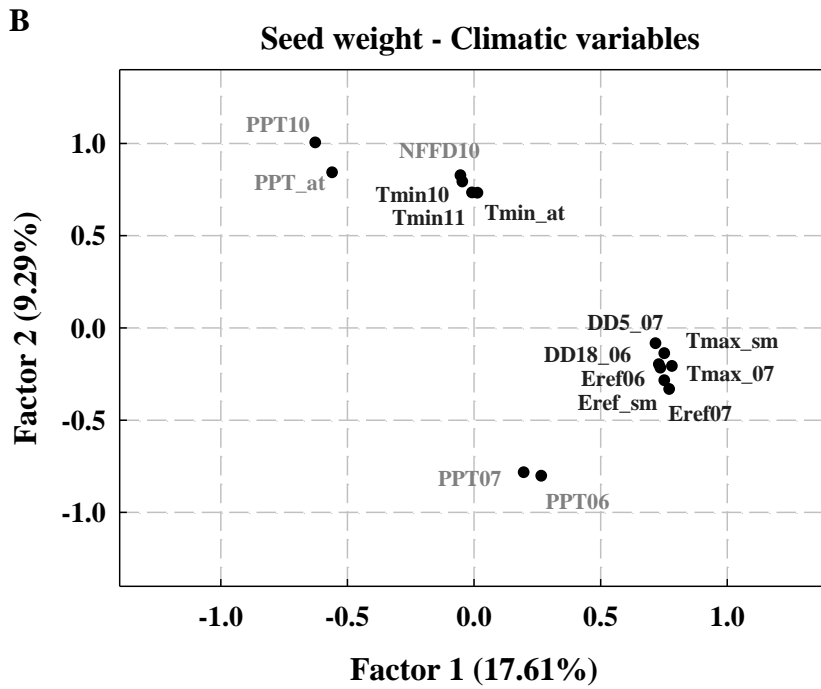
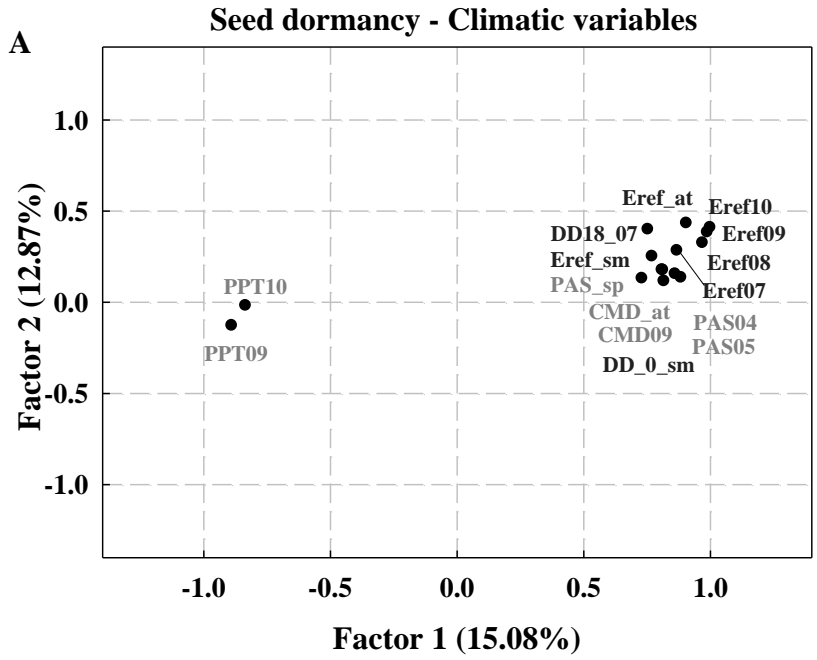


Figure 2

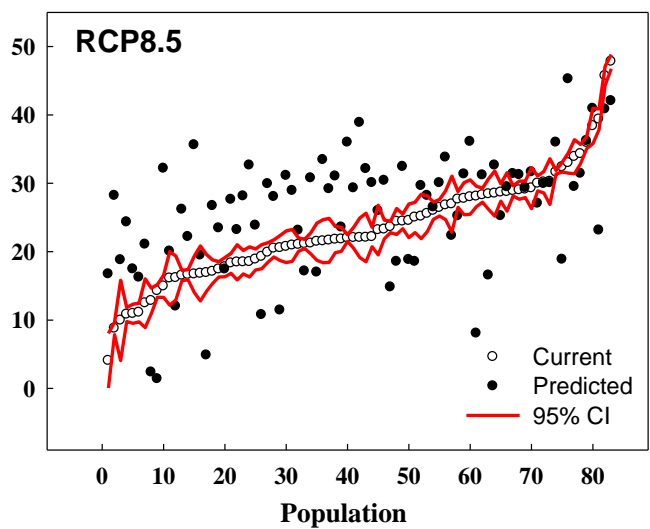
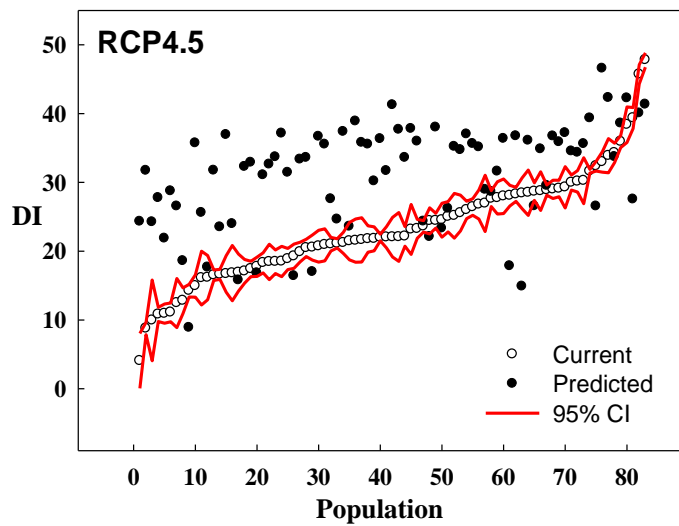
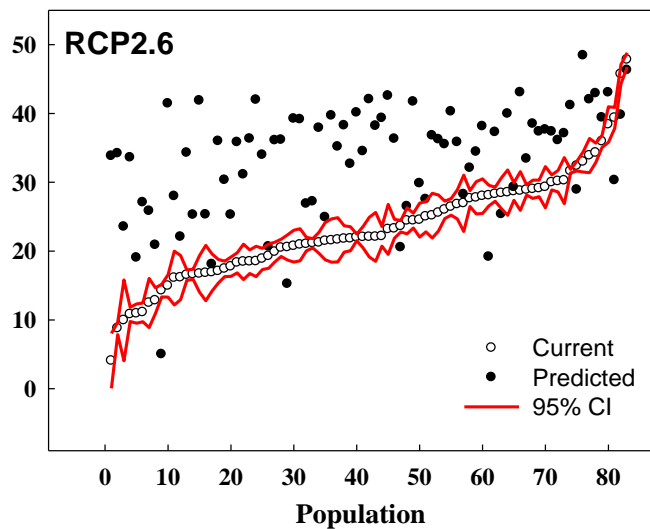
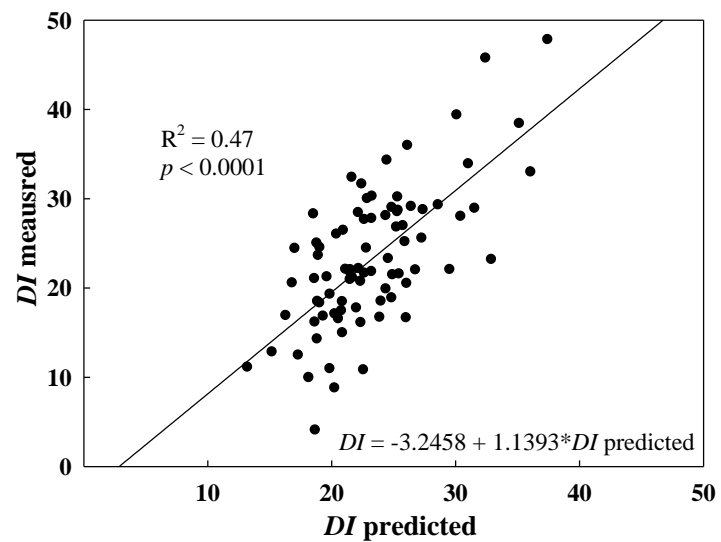
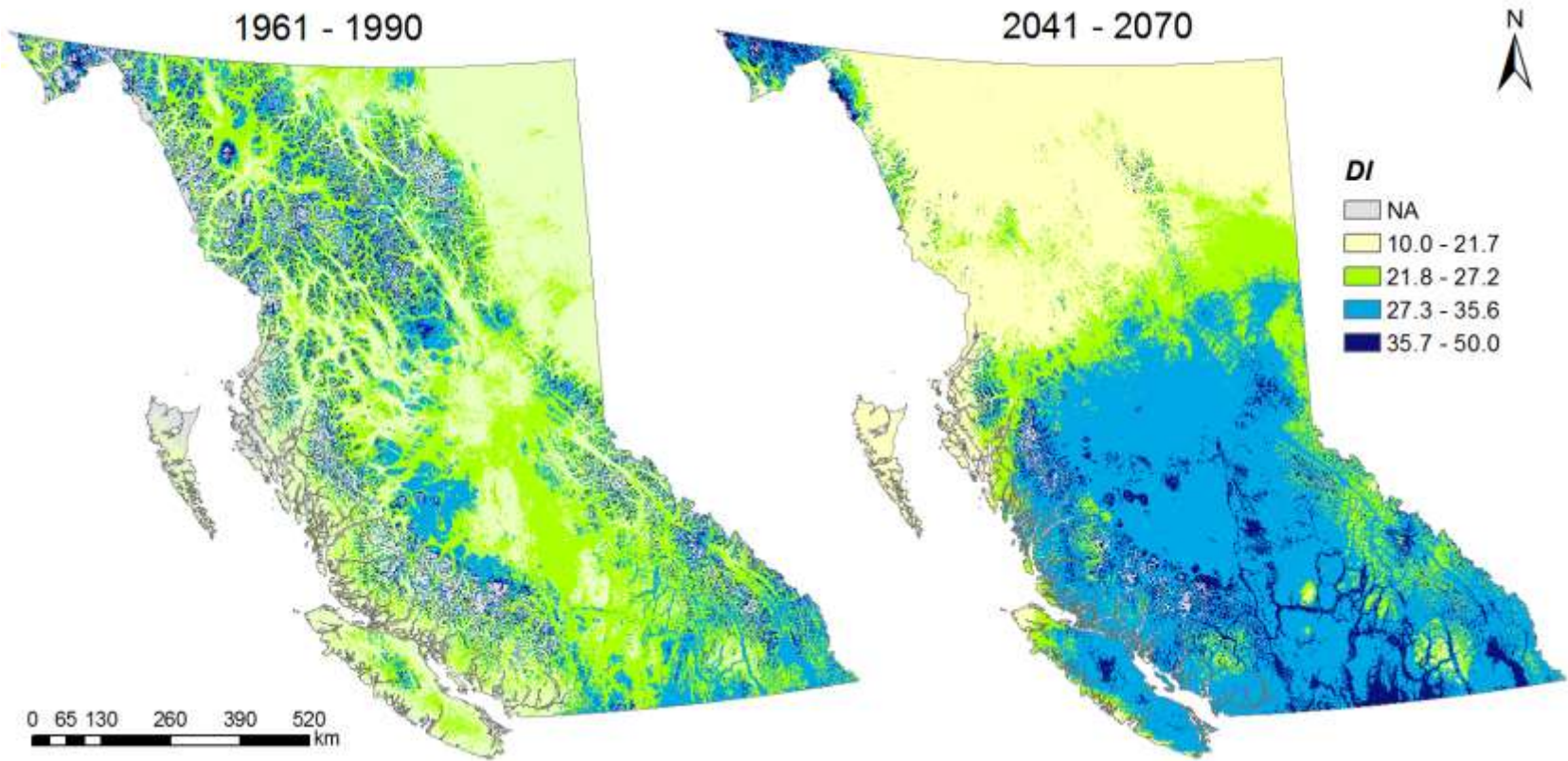


Figure 3



**Figure 4**

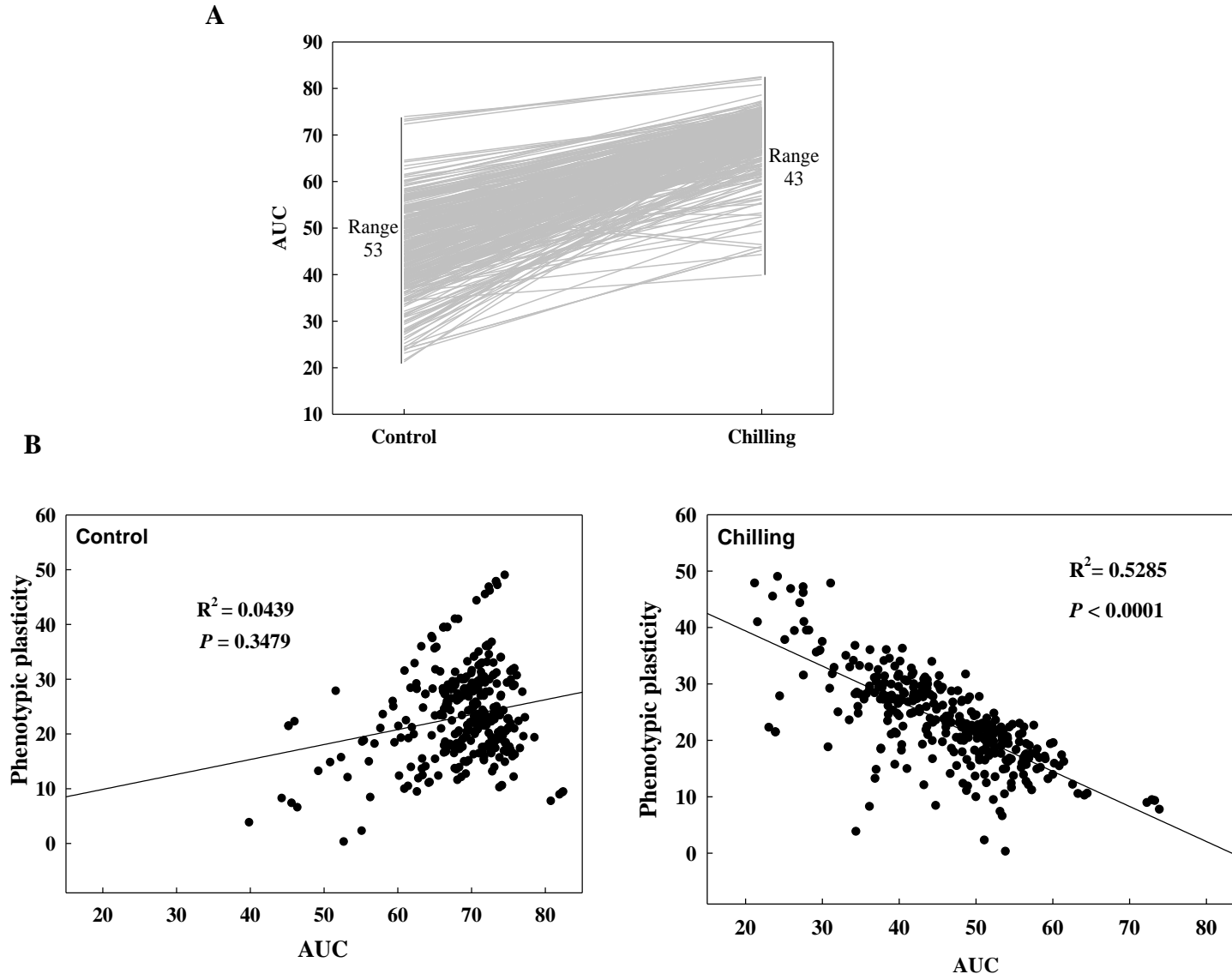


Figure 5

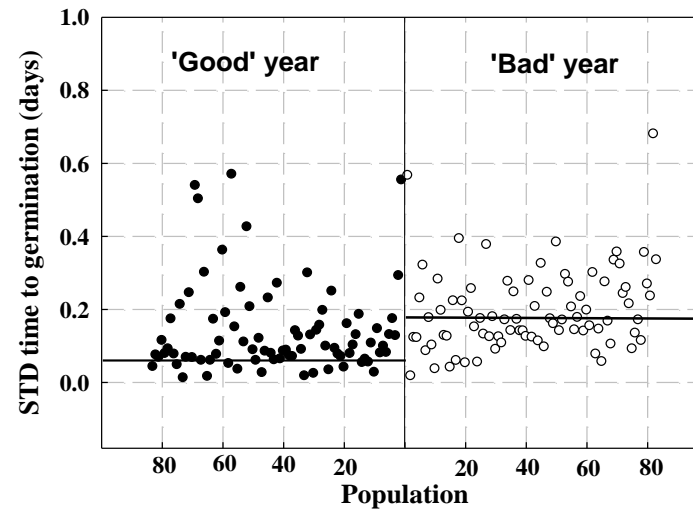
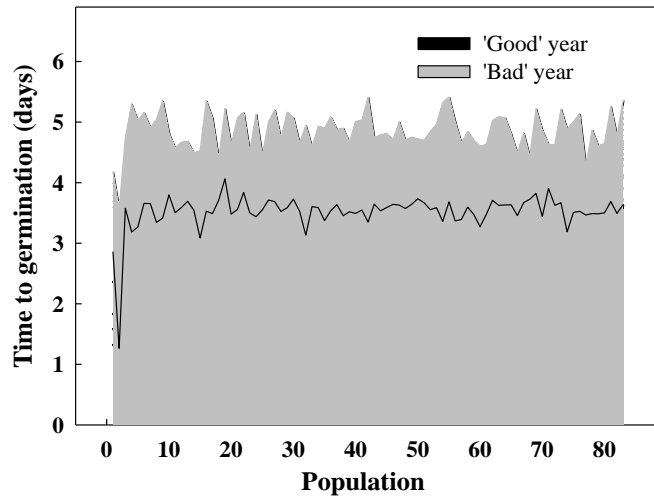
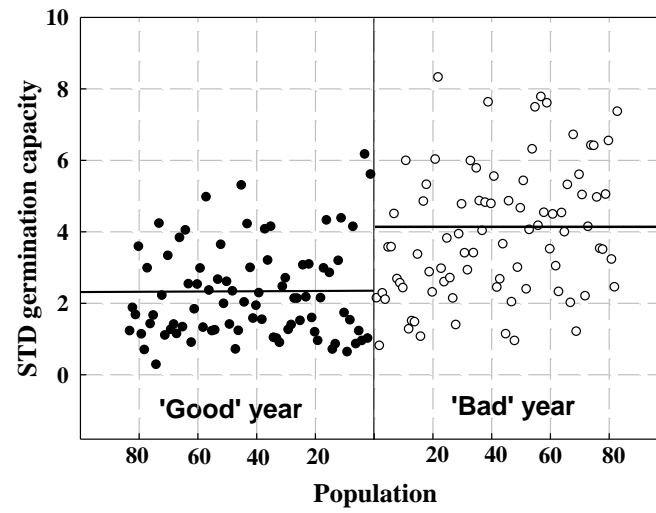
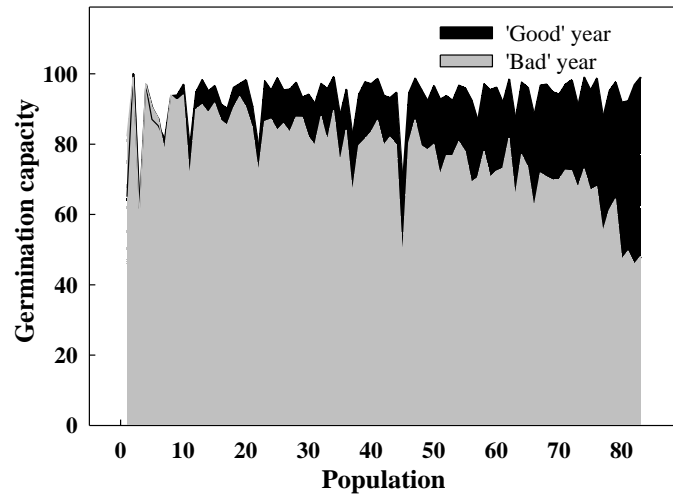




Figure 6

