

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

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17 **Abstract**

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

36

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

39 **INTRODUCTION**

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

49 Climate change has already altered the timing of major life-history transitions, such as seed
50 germination timing (from seed to plant). Timing is directional and completely asymmetric and the
51 timing of seed germination is the earliest life-history trait that is expressed and sets the context for
52 the traits that follow (Donohue et al., 2010). It is controlled by the level of seed dormancy, whereby
53 dormant seeds await germination cues for dormancy release (Finch-Savage and Leubner-Metzger,
54 2006;Baskin and Baskin, 1998). Moreover, early developmental stages of plants are more sensitive
55 to environment perturbations than adult stages and represent a major bottleneck to regeneration
56 from seeds (Johnsen and Skrøppa, 1996;Hedhly et al., 2009). At the core of plant regeneration,
57 temperature and water availability (or precipitation) are critical drivers for a plant's distribution
58 (Woodward and Williams, 1987). Hence, climate-changed plant regeneration will be manipulated
59 in both temperature- and moisture-controlled ecosystems (Walter and Breckle, 2002) and much of
60 plant regeneration climate research has been directed at tundra and boreal forest, and treeline
61 ecotones (reviewed in (Walck et al., 2011)).

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

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

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

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

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

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

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

124

125 **METHODS**

126 *Plant materials, and current and future climate data*

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

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

135 Climate data (197 climatic variables) of the 83 studied sites for the reference normal period
136 1961-1990 were generated using ClimateWNA version 4.85 (a software package used for regional
137 climate predictions using historical weather station data and global circulation models) (Wang et
138 al., 2012). The same 197 climatic variables for the future period between 2041 and 2070 (or 2050s)
139 were also projected using ClimateWNA. The future climate data were downscaled to point
140 locations using a delta approach (Wang et al., 2012). We used three Representative Concentration
141 Pathways (RCP) 2.6, 4.5 and 8.5 from the CGCM4 model output of the phase 5 of the Coupled
142 Model Intercomparison Project (CMIP5), generated by the United States National Center for
143 Atmospheric Research. The CCSM4 model output was included in the Intergovernmental Panel
144 on Climate Change (IPCC) Fifth Assessment Report (AR5) (Stocker and Randall, 2013).
145 Moreover, CCSM4 is close to the average in both temperature and precipitation increases in the
146 study areas (B.C.). In the prediction of seed dormancy indicators across B.C. for the reference
147 period and 2050s, climate data were generated for each pixel at the spatial resolution of 800×800
148 m using ClimateWNA. The full list of climatic variables is given in Table S1 and the four most
149 relevant variables for the present study were *Eref07* and *_summer* (July and summer hargreaves
150 reference evaporation estimated based on temperature and solar radiation), *DD_0_summer*
151 (summer degree-days below 0°C), *PPT07* and *10* (July and October precipitation (mm)), and
152 *Tmax07* (July maximum mean temperature ($^{\circ}\text{C}$)).

153 *Life-history traits' measurement*

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

165 *Data analysis and visualization*

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

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

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

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

199 period and 2050s via CCSM4 RCP 4.5, *DI* values were estimated for each pixel across BC at the
200 resolution of 800×800 m and mapped across B.C for visualization.

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

$$207 \quad DI_{ij} = \mu + G_i + E_j + GE_{ij} + \varepsilon \quad [2]$$

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

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

222

223 **RESULTS**

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

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

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

245 In the hierarchical model for seed dormancy using climatic variables, the climatic variables
246 *Eref07*, *Eref_summer*, and *DD_0_summer* were significant (Table 3A). This indicates that summer
247 moisture and temperature, the period corresponding to the plant-to-seed transition, played an
248 important role in the development of seed dormancy. The intercept including error from ecosystem
249 zones was not significant (Table 3A). For seed weight, variables *PPT07* and *PPT10*, *Tmax07*, and
250 intercept were significant (Table 3B), indicating that July temperature and precipitation and
251 October precipitation were important to seed weight. Ecosystem zones, representing ecological
252 boundaries in geography, had a greater impact on the variation of seed weight than that of seed
253 dormancy. In the geographic variable-based hierarchical model for seed dormancy, only longitude
254 and intercept were significant (Table S4A and Fig. S6A). For seed weight, longitude, elevation
255 and intercept were significant (Table S4B and Fig. S6B), indicating that longitude was an
256 important geographic factor in life-history traits and geographic factors had greater influence on
257 the variation of seed weight than seed dormancy. Considering all these results collectively, life-
258 history traits were significantly influenced by precipitation as well as temperature in the plant-to-
259 seed chronology, and roughly distributed in a longitude pattern.

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

261 Using current climate data, seed dormancy predicted had a moderate linear relationship ($R^2 = 0.47$,
262 $P < 0.0001$) with that observed (Fig. 2), which was used for the correction of the climate scenario
263 predicted in 2050s. Seed dormancy predictions using three greenhouse gas emission scenarios
264 (RCP2.6, 4.5, and 8.5) showed that *DI* in 2050s would increase (Fig. 2). In general, the spatial
265 pattern of *DI* across the entire province showed that the seed dormancy in the south of B.C. would
266 pronouncedly increase and the territory previously not suitable for pines to establish (grey area in
267 1970s) is expected to shrink in 2050s, which are responses to climate change (Fig. 3). In addition,

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

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

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

279 AUC and phenotypic plasticity under chilling treatment had a moderate correlation ($R^2 =$
280 0.53 , $P < 0.0001$) (Fig. 4), indicating that populations that germinated after chilling treatment were
281 more plastic. However, when no treatment prior to germination was applied, they yielded a weak
282 and not statistically significant correlation ($R^2 = 0.04$, $P = 0.3479$) (Fig. 4). Therefore, germination
283 after the chilling treatment was able to increase the magnitude of phenotypic plasticity, which was
284 a response to subsequent predictable environments.

285 *Expression of bet-hedge under manipulated environmental uncertainty*

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

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

294

295 **DISCUSSION**

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

309 ***Environmental conditions in the plant-to-seed transition***

310 In the plant-to-seed chronology, the sexual reproduction of plants is vulnerable to climate change
311 as influenced by the maternal environment (Hedhly et al., 2009;Donohue, 2009;Schmitt et al.,
312 1992a), and temperature is involved in both genetically-based and environmentally-induced
313 parental effects (Lacey, 1996). Global warming has resulted in an upward shift in species optimum

314 elevation and latitude (Chen et al., 2011;Lenoir et al., 2008;Parmesan and Yohe, 2003), an
315 observation similar to that reported by Parmesan C. (2006) as she pointed out that the best places
316 to seek potential changes in species ranges is at their altitudinal and latitudinal treelines (Parmesan,
317 2006). This suggested that climatic variables are the real causes of species' responses to
318 environmental signals. Compared with last three decades, the Pacific Northwest is expected to
319 warm about 0.8-2.9°C by mid-century (Leung et al., 2004;Duffy et al., 2006;Mote et al., 2008),
320 and 1.5-5.4°C by the end of the century (Mote et al., 2008). Warming in this region will be
321 probably greater in summer (3.9°C on average) than in winter (2.7°C) (Mote et al., 2008).

322 In the hierarchical model for seed dormancy, the climatic variable, summer degree-days
323 below 0°C (*DD_0_summer*) was not equal to zero only for 16 out of the total 83 study populations
324 and was projected to be zero for 80 populations in 2050s. We performed approximation by
325 removing *DD_0_summer* from the model and the result of seed dormancy projection could be
326 interpreted as: given the current-future difference in July hargreaves reference evaporation (*Eref*)
327 is more than one third higher than that in summer *Eref* (Jun.-Aug. period), seed dormancy will
328 increase in 2050s, and if such a difference is less than one third higher, seed dormancy will
329 diminish. These results also suggest that the allocation of summer *Eref* in July (i.e., seed
330 development period) was critical in the development of seed dormancy.

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

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

342 A number of ecologically and evolutionary relevant genes have been identified in
343 Arabidopsis and some annuals, such as *FLC* (Flowering Locus C), *SCR/SP11* (S-locus Cysteine-
344 Rich protein/ S-locus Protein 11) (Shimizu et al., 2011;Amasino, 2010), as they provide genetic
345 diversity in adaptive evolution. Moreover, both seed dormancy (genes in ABA and GA signalling
346 circuit) and flowering (such as *FLC*) were modulated by epigenetic mechanisms (Müller et al.,
347 2012;Chinnusamy et al., 2008;Bossdorf et al., 2008). This indicates that epigenetic changes play
348 a significant role in evolution and ecology and the environment signals acting on genes by
349 epigenetic modification were crucial for life-history traits. In recent years, much progress has been
350 made in uncovering genes operating on different seed compartments i.e., embryo, endosperm, and
351 seed coat, which modulate seed development (Le et al., 2010). Processes that regulate seed size
352 and development are coordinated across several morphologically distinct sub-regions (Belmonte
353 et al., 2013) and the complex cross-talk and integration of signals from different components of
354 the seed together determine its final size (Garcia et al., 2005).

355 ***Temperature signals in winter-chilling***

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

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

365 With substantial climate warming ($>3^{\circ}\text{C}$), chilling may be insufficient in many woody
366 perennials, such as, poplar, western hemlock, and Sitka spruce, resulting in delayed bud burst and
367 poor growth (Cannell and Smith, 1986; Murray et al., 1989; Morin et al., 2009). Based on the three
368 different RCP scenarios, we predicted that winter-chilling days (*DD_0_winter*) would on average
369 decrease by 24% across the 83 study habitats in 2050s relative to present (Fig. S8, ranges also
370 provided), which may lead to insufficient dormancy alleviation through winter-chilling. However,
371 spring and annual heat sums (*DD5_spring* and *DD5*) would increase by 95 and 49%, respectively,
372 in 2050s (Fig. S8), resulting in earlier springs and advanced vegetative green-ups and an increase
373 in growing season length (Robeson, 2004; Schwartz et al., 2006). In 2050s, inadequate winter-
374 chilling may delay germination and an extended germination span leads to adverse conditions
375 during dry summers. As such, future climate will change the timing of conifer phenology and may
376 give rise to adverse consequences.

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

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

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

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

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

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

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

421

422 **AUTHOR'S CONTRIBUTION**

423 YL conceived of the study, carried out data analysis, and drafted the manuscript; TW participated
424 in selection of study populations, performed current and future climate predictions and mapping,
425 and commented the manuscript; and YAE coordinated the study and helped draft the manuscript.

426 All authors gave final approval for publication.

427

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436

437 **SUPPLEMENTARY MATERIAL**

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

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

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

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

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

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

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

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

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

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

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

458 **Figure S7** Linear relationship between 1,000-seed weight and ‘predicted’ 1,000-seed weight using
459 83 populations.

460 **Figure S8** The amount of changes for *DD_0_winter*, *DD5_spring*, and *DD5* in 2050s relative to
461 present.

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

464

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711 **FIGURE LEGENDS**

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

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

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

720 Note: ① model for seed dormancy prediction, $DI = (2.4819 + ecosystem\ zone) + 2.7079 \times Eref07$
721 $- 0.9284 \times Eref_summer + 6.6170 \times DD_0_summer$ [refer to Table S2 for intercept adjustment in
722 each ecosystem zone]; ② the population was ranked as per its current *DI* in ascending order and
723 95% confidence interval (CI) was plotted.

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

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

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

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

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

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

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

743 **Table 1 Canonical correlation analysis between individual variables and their own and opposite set**
 744 **of variables**

745 A)

Variables		Life-history traits	Climatic Ecology [†]	Geographic Ecology ^{††}
Life-history traits	Seed weight	0.7429	0.9021	0.5481
	<i>DI</i>	0.5909	0.6582	0.5327

746 Note:

747 [†]Based on the PLS analysis, 27 most correlated climatic variables for seed dormancy (*DI*) and weight were
 748 used as Climatic Ecology (three climatic variables were strongly correlated with both seed dormancy and
 749 weight).

750 ^{††}Geographic Ecology consists of latitude, longitude, and elevation.

751 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%

752

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

756 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		

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

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

759 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**	- [¶]	0.54
G × E	82	$\sigma_{\epsilon}^2 + 4\sigma_{G \times E}^2$	129.8935	25.09**	39.43%	
Error (ϵ)	498	σ_{ϵ}^2	5.1767		6.55%	

760 [¶]no variance components or percent of total variation were estimated for the fixed effect (E).

761 ** $P < 0.05$.

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

764 A) Seed dormancy model

Effect	Estimate	Standard Error	DF	Statistic	<i>P</i>
Intercept [¶] (β_0)	2.4819	7.9418	21	$t = 0.31$	0.7577
<i>Eref07</i> (β_1)	2.7076	0.8932	58	$F = 9.19$	0.0036
<i>Eref_summer</i> (β_2)	-0.9284	0.3354	58	$F = 7.66$	0.0076
<i>DD_0_summer</i> (β_3)	6.5170	1.8480	58	$F = 9.06$	0.0039

765 [¶]residual from the ecosystem zone (ϵ_j) is integrated into ‘intercept’ (Table S3).

766 B) Seed weight model

Effect	Estimate	Standard Error	DF	Statistic	<i>P</i>
Intercept [¶] (β_0)	1.3290	0.3799	21	$t = 3.50$	0.0021
<i>PPT07</i> (β_1)	0.0046	0.0019	58	$F = 5.66$	0.0207
<i>PPT10</i> (β_2)	-0.0014	0.0007	58	$F = 4.68$	0.0346
<i>Tmax07</i> (β_3)	0.0721	0.0150	58	$F = 23.11$	<0.0001

767 [¶]residual from the ecosystem zone (ϵ_j) is integrated into ‘intercept’ (Table S3).

Figure 1

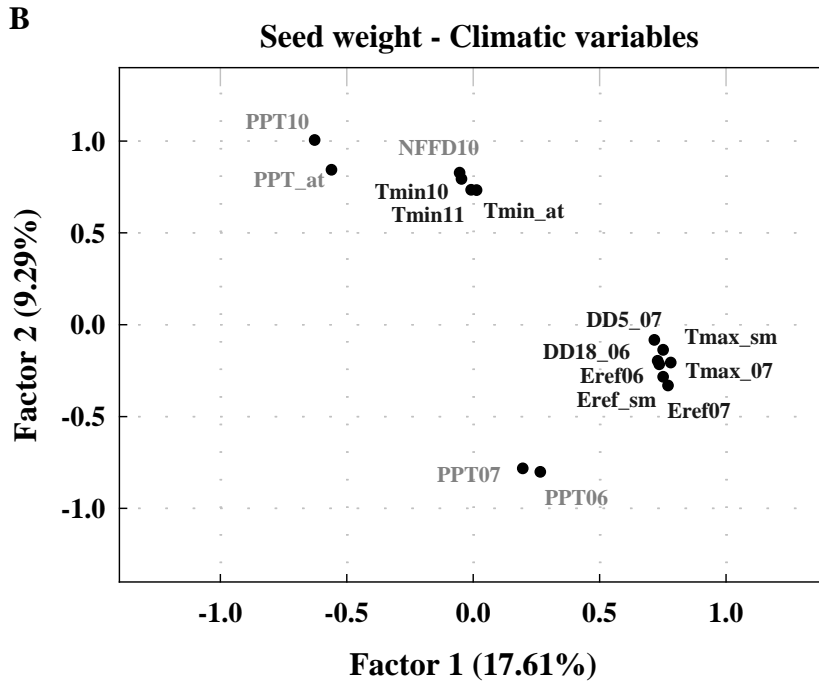
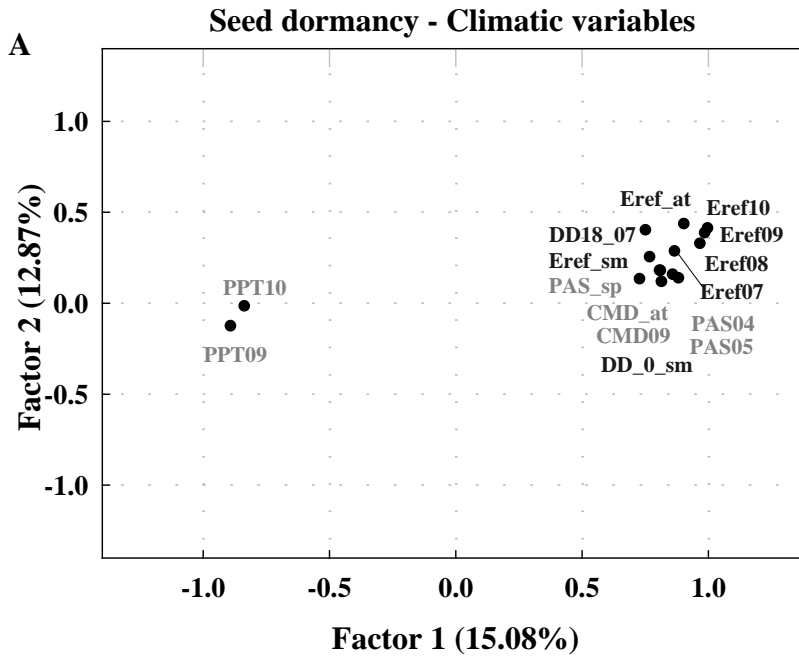


Figure 2

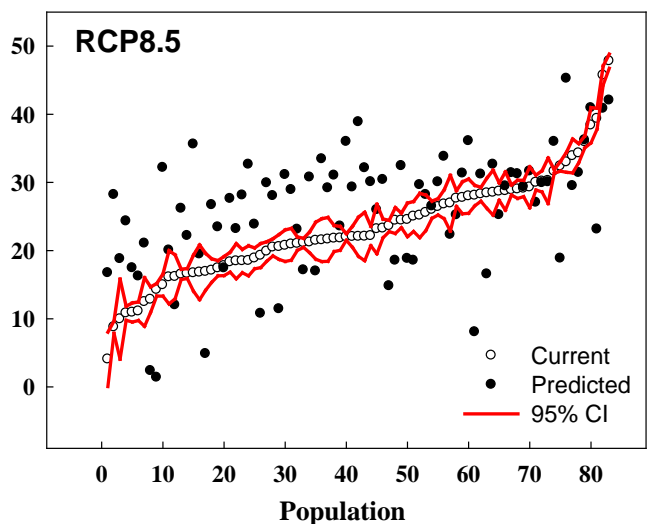
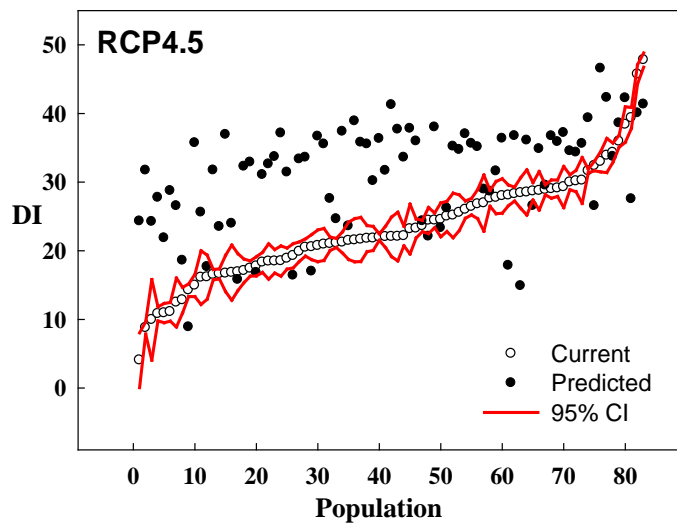
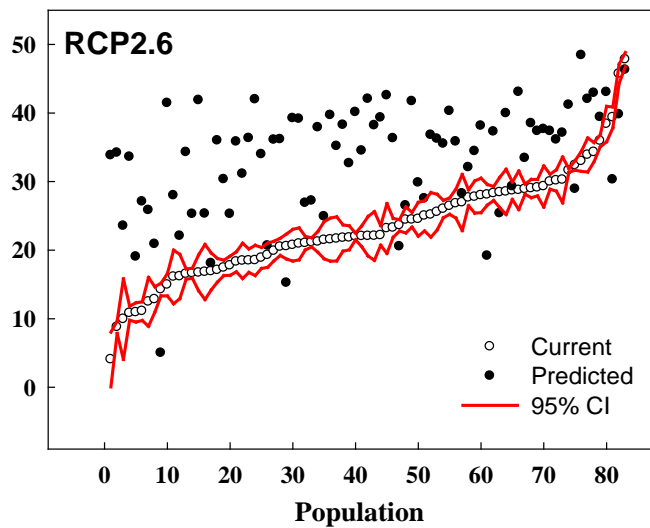
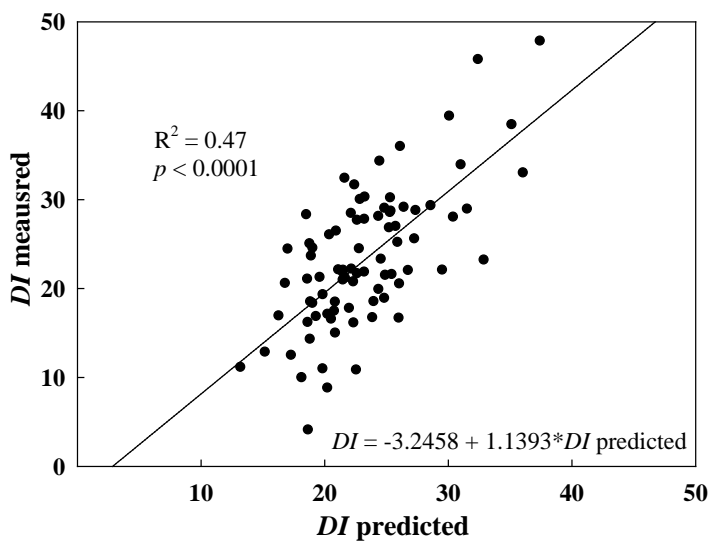


Figure 3

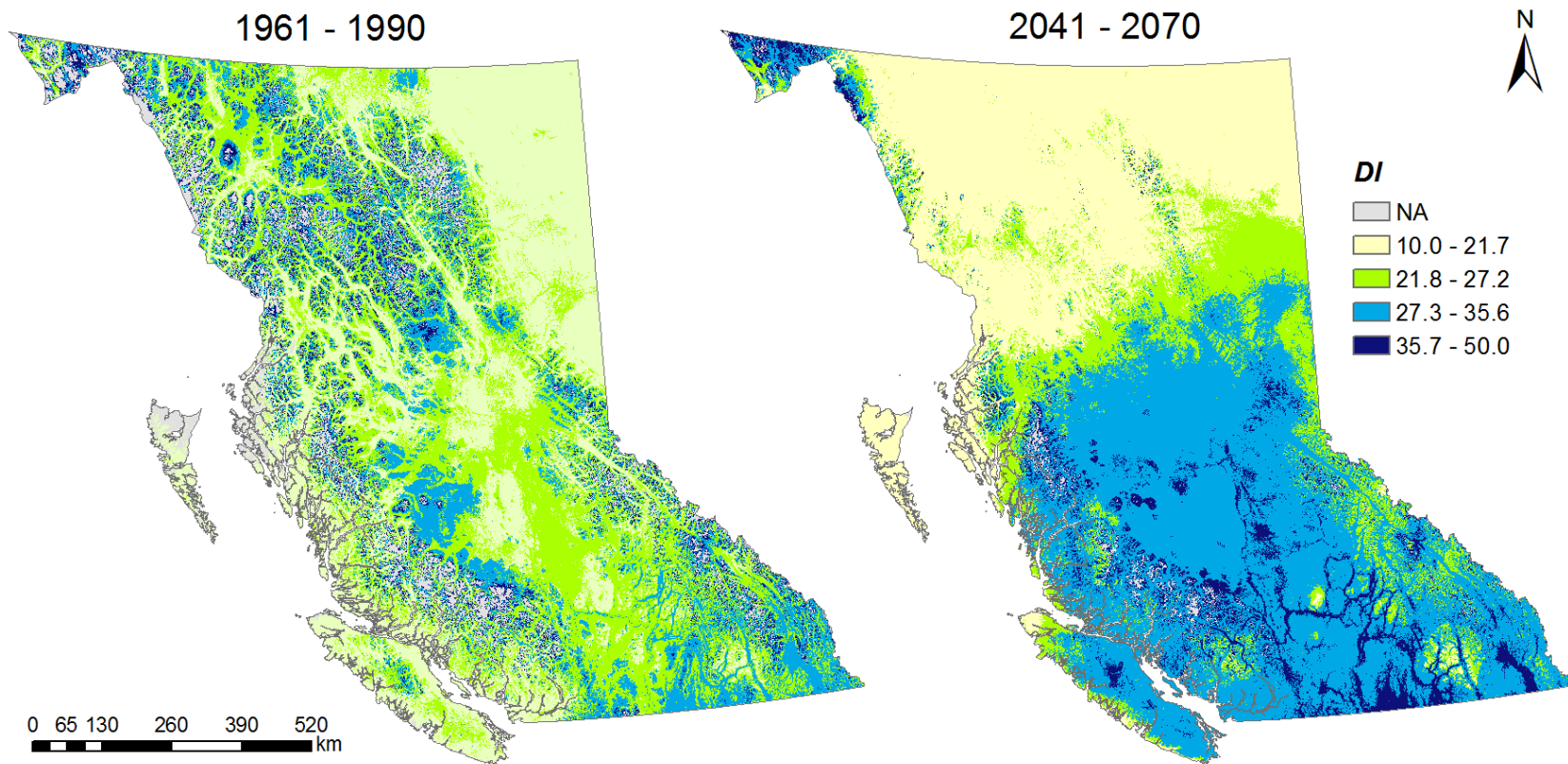


Figure 4

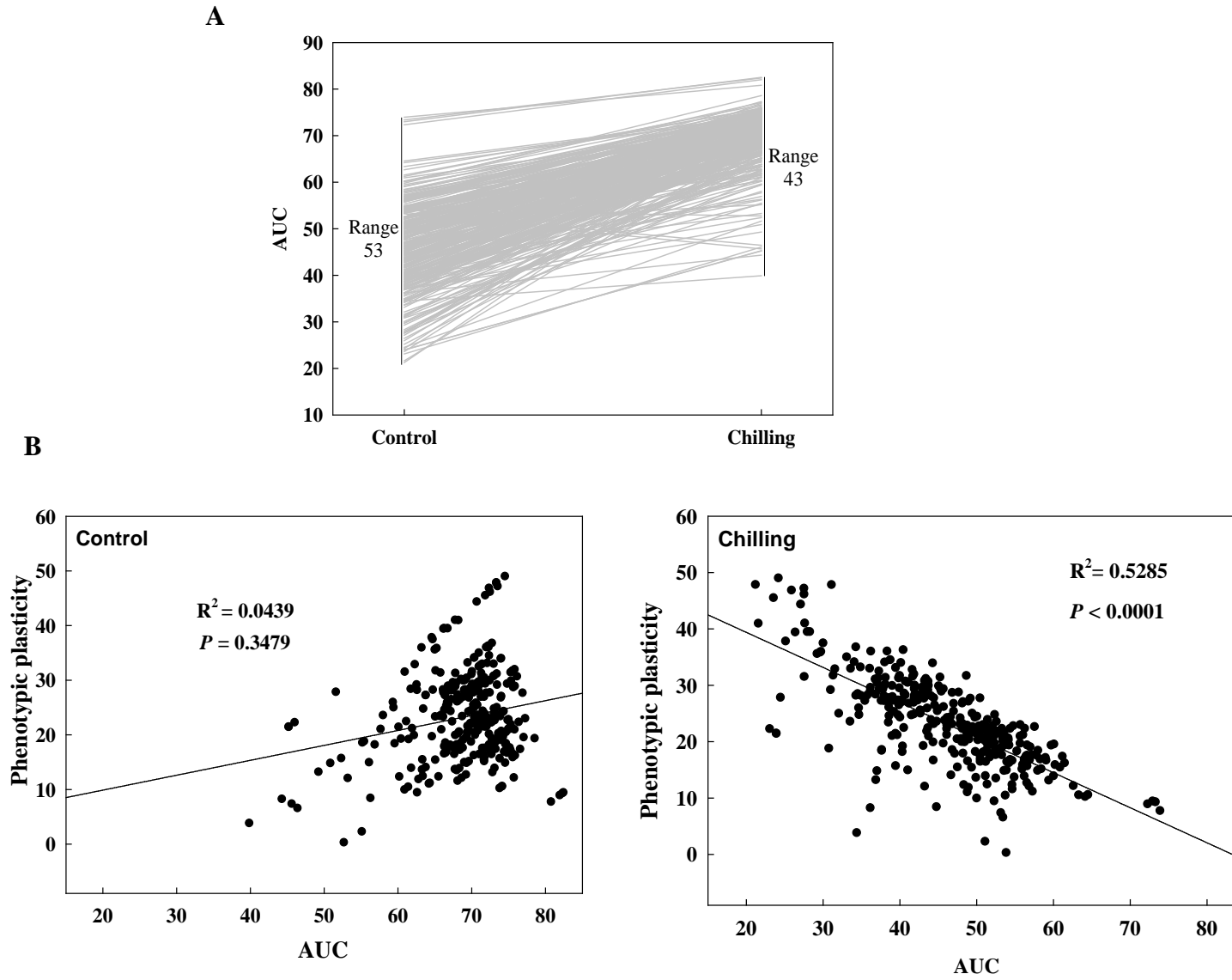


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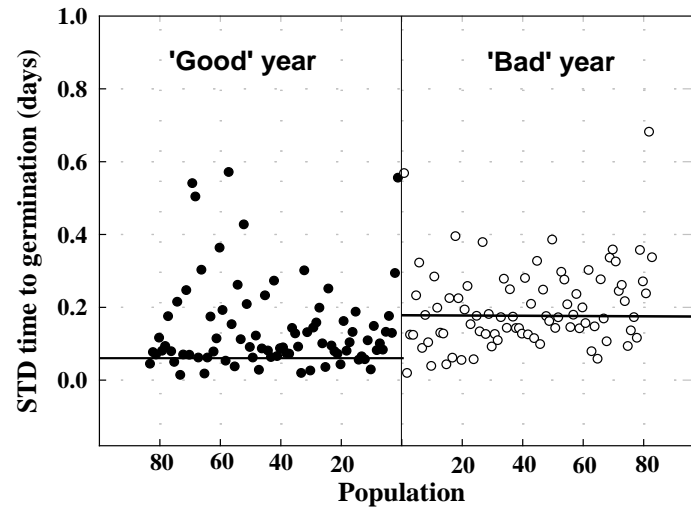
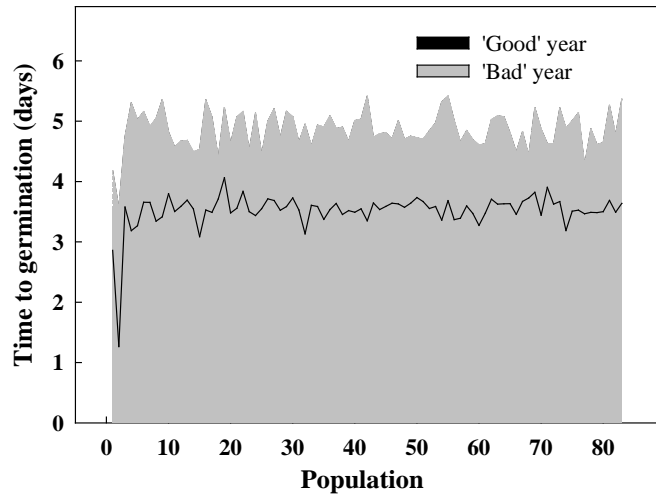
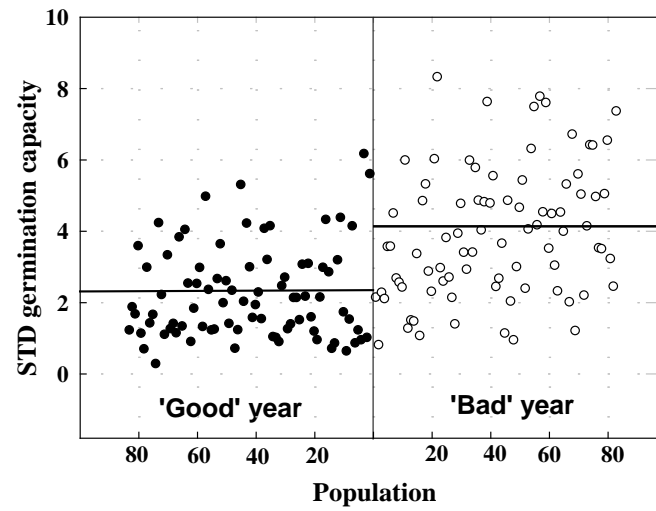
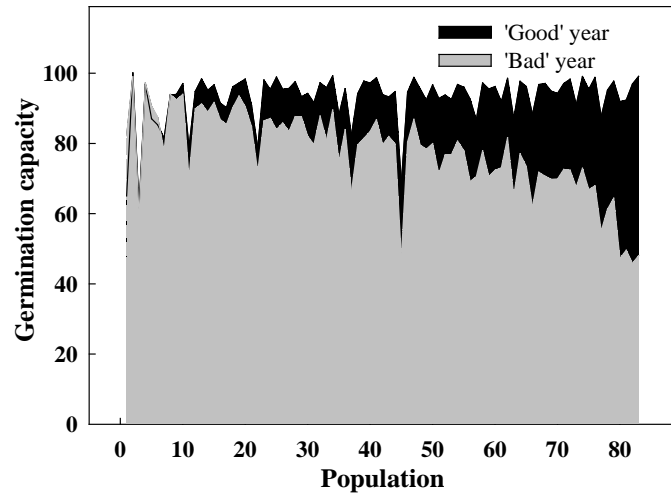


Figure 6

