

1 **The interplay between demography and neutral evolution at the expansion**
2 **front of a widespread conifer, *Picea sitchensis***

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8

9 **Abstract**

10 Tree species in the northern hemisphere have advanced and retreated with interglacial
11 and glacial periods, and are currently subject to rapid anthropogenic climate change. These
12 observations prompt questions about the mechanisms allowing tree populations to respond
13 quickly to selection pressures when establishing into new areas. Focusing on the northern
14 expanding range edge of *Picea sitchensis*, a widespread conifer of western North America, we
15 ask how genetic structure and diversity develop during colonization, and assess the role of
16 demographic history in shaping the evolutionary trajectory of a colonizing population. By
17 combining nearly 500 years of tree-ring and genetic data at the expansion front on the Kodiak
18 Archipelago, we show that allelic richness - but not expected heterozygosity - increased rapidly
19 during early stages of establishment in the 1600s, while genetic differentiation from populations
20 further from the front decreased. This trend ended in the 1700s, after an increase in population
21 growth rate. These findings highlight the major role of long-distance pollen dispersal in the
22 recovery of genetic diversity during initial stages of colonization, and suggest that demographic
23 dynamics including an initial lag in population growth are likely limiting factors in the
24 adaptation of tree populations tracking their niche in a changing climate.

25 **Introduction**

26 With an enhanced understanding of plant species migrations during past postglacial
27 cycles and numerous observations of current climate change effects on species distributions, we
28 are recognizing more than ever before the ubiquitous nature of range shifts. This awareness
29 comes with a substantial literature including simulation studies of genetic changes during range
30 expansions (Bialozyt et al., 2006; Hallatschek & Nelson, 2010; Peischl et al., 2013), empirical
31 studies of expanding species and associated evolutionary patterns (e.g. Darling et al., 2008; Pujol
32 & Pannell, 2008), and metaanalyses and reviews highlighting the general patterns common to -
33 or variable among - phylogenetic and functional biological groups (Excoffier et al., 2009).
34 Successive founder effects along colonization routes are a well-studied phenomenon causing an
35 erosion of diversity and enhancing genetic differentiation (Excoffier et al., 2009; Hewitt, 2000;
36 Slatkin & Excoffier, 2012). However, mechanisms related to species' dispersal and life history
37 traits have been shown to influence the genetic outcome of range expansions and give rise to
38 fundamentally different spatial patterns of genetic structure (Bialozyt et al., 2006; Waters et al.,
39 2013). It is therefore not surprising that among organisms with different life history and dispersal
40 traits, genetic effects of range expansions are not consistent (Eckert et al., 2008).

41 This heterogeneity is present across studies of tree species. Empirical studies at the scale
42 of species ranges have found both higher genetic diversity (Born et al., 2008; Pluess, 2011; Shi
43 & Chen, 2012) and lower genetic diversity (Johnson et al., 2017; Kitamura et al., 2015; Marsico
44 et al., 2009; Mimura & Aitken, 2007) in leading edge populations of tree species after range
45 expansion. Temperate forest tree species are generally associated with high gene flow via wind-
46 borne pollen across large geographic distances (Kremer et al., 2012), as well as a long lifespan
47 and juvenile phase. These characteristics can have a strong influence on the interplay between
48 genetic and demographic processes during range expansion. Founder effects may be buffered by
49 high levels of gene flow (Austerlitz et al., 1997). The longevity of trees allows for founders to
50 persist until other propagules colonize, and their long juvenile phase forces the reliance on gene
51 flow via foreign pollen, providing genetic diversity to the establishing population (Austerlitz et
52 al., 2000). In addition, long-distance dispersal can prevent the erosion of genetic diversity along
53 expansion routes (Le Corre & Kremer, 1998), promote genetic differentiation between demes
54 (Austerlitz & Garnier-Géré, 2003) or suppress local introgression (Amorim et al., 2017).

55 Recent empirical studies involving exhaustive sampling and pedigree reconstruction in
56 disjunct forest stands at range edges have greatly enhanced our understanding of demographic
57 mechanisms shaping the genetic composition of expanding populations at the local scale.
58 Founding individuals, often arriving via long distance dispersal of seeds, play a major role at the
59 start of establishment. Troupin et al. (2006) found that spatial genetic structure of a population
60 shortly after range expansion strongly reflected the genetics of founding trees in a *Pinus*
61 *halepensis* population. Lesser et al. (2013) identified Allee effects in a new *Pinus ponderosa*
62 stand, highlighting the importance of a certain level of long-distance dispersal of founders in the
63 establishment success of the new population. A general finding in these studies is the
64 predominance of high levels of pollen flow shortly after founding, leading to a quick recovery of
65 genetic diversity during recruitment (Hampe et al., 2013; Lesser et al., 2013; Pluess, 2011; Sezen
66 et al., 2007).

67 Here, we take a multi-scale approach to the study of expanding tree populations,
68 combining observations of spatial and temporal patterns at the regional and local scale. In
69 particular, we ask how demographic and spatial patterns of colonization affect genetic structure
70 along an expansion route in space and time, and interact with potential geographic barriers to
71 gene flow. To do so, we combine nearly five centuries worth of demographic and genetic data
72 from several forested sites along the recent colonization route of a widespread North-American
73 conifer, Sitka spruce (*Picea sitchensis* (Bong.) Carr.). With its ability to withstand salt spray and
74 thrive in hypermaritime environments, *P. sitchensis* is a major component of Pacific coastal
75 forests. Although it is rarely the most abundant species in the southern and central part of its
76 range, it dominates the forest cover together with mountain hemlock on the Kenai Peninsula and
77 is the only forest tree species on the Kodiak Archipelago. Historical human records report a rapid
78 advance of the monospecific *P. sitchensis* forest on the Kodiak Archipelago (Griggs, 1914;
79 Vincent, 1964). The westernmost and largest island of the group, Kodiak Island, is thought to
80 have been colonized no more than 500 years ago (Griggs, 1937). *P. sitchensis* is found in dense
81 stands on Afognak Island and the forest density tapers south-westward towards small groves of
82 young trees (Tae, 1997). The absence of spruce pollen in paleoecological records on Kodiak
83 Island (Bowman, 1934) strongly suggest that this is the first occurrence of the *P. sitchensis* forest
84 at this site since the last glacial period. This range expansion therefore seems to be part of the
85 long-term post-glacial colonization process of the species, with the most recent front advance

86 having likely been facilitated by a nearby volcanic eruption in 1912, which reduced interspecific
87 competition between *P. sitchensis* seedlings and herbaceous species (Tae, 1997). Southwestern
88 Kodiak Island features tundra grasses and scattered shrubby forms of *Alnus viridis*, *Populus*
89 *trichocarpa*, and *Betula nana*. Earlier studies focusing on *P. sitchensis* detected asymmetric gene
90 flow from core Alaskan populations to the Kodiak Archipelago (Holliday et al., 2012), as well as
91 a high self-fertilization rates (Gapare & Aitken, 2005; Mimura & Aitken, 2007) and a lack of
92 adaptive potential (Lobo, 2011) on Kodiak Island. Based on this knowledge, we propose to
93 characterize gene flow from populations on the Kenai Peninsula to the Kodiak Archipelago and
94 identify demographic or genetic mechanisms responsible for reduced levels of genetic diversity
95 at the expansion front.

96 Using dendrochronological methods, we first conduct a demographic analysis over island
97 and continental regions to determine the timing and spatial structure of dispersal patterns during
98 range expansion on the Kodiak Archipelago. To assess the current and past extent of
99 differentiation and genetic diversity at the regional level, we then quantify genetic population
100 structure between regions and genetic diversity within regions for different age classes at the
101 northern range of *P. sitchensis*. This direct monitoring of genetic diversity and structure allows
102 for the quantification of the extent and duration of potential founder effects, as well as the
103 relative importance of early colonizers and subsequent gene flow in the accumulation of genetic
104 diversity of the growing population. Finally, we take a closer look at sites at the expansion front,
105 to determine the short-term genetic consequences of fine-scale dispersal patterns and
106 demography.

107

108 **Materials and Methods**

109 Sampling design

110 We focused on the northern range of *P. sitchensis* in south-central Alaska. In 2013 and
111 2015, fifteen sampling sites in healthy forests with old-growth characteristics and with no
112 evidence of past outbreaks of spruce beetle (*Dendroctonus rufipennis*) were sampled on Kodiak
113 Island, Afognak Island, and on the Kenai Peninsula near Seward (Figure 1a). Sample sizes
114 within sites varied between 12 and 86 trees, depending on the size of the sampled site and its
115 accessibility (Table 1). We classified trees into four canopy structure levels (large canopy trees,
116 medium-sized canopy trees, sub-canopy trees, and immature saplings) and sampled sites to

117 maximize the range of tree ages and to obtain even sample sizes from each canopy structure
118 level. Large canopy trees were typically >70cm in diameter, and showed growth forms consistent
119 with earlier growth in an open environment (numerous large dead branches low on the trunk and
120 strongly tapered stems), especially on the Kodiak Archipelago. Medium-sized canopy trees were
121 generally <70cm in diameter and showed no signs of open growth. Sub-canopy trees were
122 mature trees that had not reached the main canopy, and immature saplings were generally no
123 more than 2m tall. All sampled trees were separated by at least 150 meters to avoid high
124 relatedness between individual samples. For DNA extraction, we sampled young needles
125 whenever possible; when foliage was out of the reach of a pole pruner we took two 1 cm-
126 diameter cambium disks with a leather punch. Sampled materials were stored in paper envelopes
127 in silica gel until DNA extraction. To estimate the age of individuals sampled, we used an
128 increment borer to core each tree up to 5 times as low as possible to obtain a wood sample that
129 included the pith or signature thereof. A detailed description of dendrochronological methods is
130 available in the supplemental information. The age of saplings was approximated by counting
131 major branch clusters on the stem. We used available samples of needles from 15 canopy trees in
132 two additional sites on Shuyak Island and Port Chatham for inclusion in population genetics
133 analyses but did not have tree ring data for these populations.

134

135 Dating population establishment

136 We used two methods to estimate timing of population establishment at the site level:
137 canopy age and date of canopy closure. Canopy age was obtained by averaging ages of all
138 canopy trees based on tree ring counts. This estimate has the advantage of being accurate for
139 canopy age but does not necessarily reflect initial forest establishment if tree longevity is shorter
140 than the duration of established forests since colonization or between major stand-replacing
141 disturbances. Canopy closure time is an attempt to overcome this limitation and relies on
142 signatures of growth during early life stages, based on the hypothesis that individuals growing in
143 an open environment will experience faster growth in early stages of life compared to individuals
144 competing under a closed canopy. Therefore we expect: (1) that trees on sites that were forested
145 long before the time encompassed by our sampling will have relatively narrow growth rings for
146 all samples at the juvenile stage; (2) that sites still in the process of forest colonization will show
147 wide growth rings for most samples at the juvenile stage; (3) that formerly forest-free sites will

148 show a shift from wide to narrow growth rings in juveniles during colonization as the canopy
149 closes.

150 For each tree core, we measured and averaged annual growth increment between years 10
151 and 20 (to avoid signals of competition with small-statured shrubby or herbaceous plants). We
152 modeled the relationship between individual estimated establishment date x and individual tree
153 average annual juvenile growth y at the site level using two different regression models: a linear
154 model $y \sim ax + b$ and a logistic model of the type $y \sim a / (1 + e^{-b(x-h)})$. We expect sites
155 following cases (1) and (2) above to show a better fit with a linear model with insignificant or
156 weak slope, and sites following case (3) to show a better fit with the logistic model. We retained
157 the model with the lowest AIC. When sites were best fitted by a logistic model, we checked that
158 the relationship between year of establishment and growth increment was negative ($b < 0$) and
159 recorded h as the estimated date of canopy closure. When the linear model was the best fit, we
160 tested the significance of the slope (p -value for coefficient b). Site K4 was removed from this
161 analysis due to the sub-canopy structure level being under-represented.

162

163 Genotyping

164 To obtain putatively neutral markers for 639 trees, we used genotyping-by-sequencing
165 (GBS) with a *sbf1-msp1* double-digest protocol (Elshire et al., 2011). Libraries were sequenced
166 with the HiSeq 2000 system, producing 100-bp single reads. We aligned the filtered reads to the
167 white spruce reference genome WS77111_V1 (Warren et al., 2015) using the *bwa mem*
168 alignment algorithm. Alignment files were then input into a variant calling pipeline using
169 functions from the program GATK (McKenna et al., 2010). A more detailed description of the
170 bioinformatics processing steps is provided in the supplementary materials. After SNP calling,
171 we removed all singletons across the 639 genotyped diploid individuals. Finally, when several
172 SNPs were present less than 100bp apart, we retained only one of them, resulting in a final
173 dataset with genotypes for 3244 biallelic SNPs. Different subsets of SNPs were used for different
174 population genetics analyses, depending on selected individuals and chosen missing data
175 threshold. Although the GBS approach outputs datasets with considerable missing data, it also
176 provides a cost-effective genome-wide picture of genetic diversity and structure.

177

178 Visualizing population structure

179 We visualized population structure among all regions sampled using 2 methods: principal
180 component analysis (PCA) and STRUCTURE clustering (Falush et al., 2003; Pritchard et al.,
181 2000). For the PCA, we retained all genotype calls and filtered sites for missing data with a 40%
182 cutoff value. The resulting dataset included 639 *P. sitchensis* individuals genotyped for 220
183 SNPs. We replaced all missing data by their mean over all individuals prior to PCA. The R
184 packages *adegenet* and *ade4* were used to convert data files and perform a centered PCA. To
185 characterize further population structure within the dataset, we used the program STRUCTURE,
186 which detects clusters of individuals based on Hardy-Weinberg equilibrium within clusters. We
187 first performed exploratory runs with run lengths from 10k to 100k after a 10k burnin and 3
188 replicate runs for each run length. For $K \leq 4$, a run length of 50k was sufficient, whereas for $K > 4$,
189 a run length of 100k was necessary. We used the independent allelic frequency model and the
190 admixture ancestry model for all runs, and performed 3 runs for each value of K between 1 and
191 6.

192

193 Temporal patterns of diversity and structure

194 To infer the role of founder individuals and subsequent migration in the development of
195 genetic diversity of the Kodiak-Afognak population, we selected all sites with less than 20%
196 missing genotypic data for trees with age estimates. This dataset (120 SNPs, 412 trees) was used
197 to estimate the year of first observation of each allele in the growing population. A 1000-
198 replicate randomization was applied to model the random distribution of allele accumulation
199 curves against which to test significance of the observed results. To reconstruct the changes in
200 gene flow patterns between continental and island populations, we assessed pairwise population
201 differentiation between regions by computing the Weir and Cockerham (WC) F_{ST} estimator with
202 R functions modified from the *adegenet* and *hierfstat* packages. Loci with less than 30% missing
203 data over the whole sample were used. As the WC estimator is sensitive to unbalanced sample
204 sizes (Bhatia et al., 2013), we randomly subsampled the larger population sample to the size of
205 the smallest population sample. Confidence intervals around F_{ST} estimates were assessed with
206 1000 bootstraps.

207

208 Site-level summary statistics

209 Using SNPs that were well represented in each region (< 60% missing data across the
210 sample), we calculated expected heterozygosity, F_{ST} and allelic richness at the site level using the
211 R packages *adegenet*, *hierfstat* and *PopGenReport*, respectively. The latter uses the methods of
212 El Mousadik and Petit (1996), which corrects for variable sample sizes through rarefaction.
213 Changes in dissimilarity between sites over time on the Kodiak Archipelago were estimated
214 using the dissimilarity calculations of Petkova et al. (2016). Estimates at the individual tree level
215 rather than allele frequencies (such as F_{ST}) better suited our temporal analysis at the local scale
216 due to low within-site sample sizes for each cohort. Briefly, we computed a matrix of genetic
217 distance between pairs of individuals using the average squared genetic difference across all
218 well-represented SNPs (<50% missing data). We then calculated D , the mean genetic distance
219 over all possible pairs of individuals from 2 distinct sites, as a measure of pairwise dissimilarity
220 between sites. To avoid confounding effects of within-site differences and better represent
221 genetic differences resulting from gene flow variations, we calculated between-site dissimilarity
222 (D_b) by subtracting the average within-site dissimilarity from D .

223

224 **Results**

225 Demographic patterns from tree rings

226 We successfully estimated tree ages for a total of 607 samples (N=412 on the Kodiak
227 Archipelago, N=195 in the Seward region on the Kenai Peninsula), evenly distributed among
228 four canopy levels. Estimated tree ages ranged from 5 to 552 years. Canopy trees were generally
229 younger on Kodiak Island (145 y.o. on average) than on Afognak Island and Seward (>200 y.o.)
230 and ages of large canopy trees differ considerably between regions: the largest canopy trees are
231 younger in regions closer to the range limit (Figure 1b). To obtain a finer resolution of the spatial
232 demographic patterns, we calculated the mean canopy age at sites within regions (Figure S1).
233 Canopy age at all Seward sites was around 250 to 300 years, with overlapping standard errors.
234 From these relatively consistent estimates, we deduced that canopy age will not correlate with
235 population establishment date on the Kodiak Archipelago beyond this time, as Seward sites were
236 colonized more than 1000 years ago (Jones, 2008; Mann & Hamilton, 1995). Within Kodiak
237 Island, two of the southernmost areas (K3 and K5) have no trees older than 200 and 135 years,
238 respectively, with mean canopy ages of 140 and 67 years. K5 is in the southernmost *P. sitchensis*
239 forest, located on the Southeast coast of Kodiak Island. At this site, tree ages within structure

240 levels are highly homogenous, with most canopy trees between 30 and 80 years old. The canopy
241 is close to the ground and there are no suppressed trees growing in the understory, suggesting
242 that this site was recently colonized. In general, canopy age is higher on Afognak Island than on
243 Kodiak Island. However, this pattern of decreasing canopy age towards the expansion front
244 breaks down at the local scale: some sites in the south have an older canopy than northern sites,
245 especially on Afognak Island (*i.e.*, A1 and A5, Figure S1). The large variability in canopy age
246 among areas at a similar latitude (*i.e.*, K3 and K4, Figure S1) suggests that colonization on the
247 Kodiak Archipelago occurred via patchy dispersal rather than a linear advancing wave.

248 We detected a signal of canopy closure using data from early-age annual growth
249 increment patterns at the site level (Figure 2). As expected, none of the five sites on the Kenai
250 Peninsula (S1 to S5) showed any significant relationship between growth increment and time for
251 either the linear or the logistic model, with growth rings around 1mm wide. This is consistent
252 with growth under a well-formed canopy with constant population density and no large-scale
253 disturbances over the time span sampled. Contrasting with this pattern, four sites on Kodiak
254 Island (K1, K2, K3, K5) show very large juvenile growth rings (3-7 mm) for older trees. Sites on
255 Afognak Island show moderately large growth rings (2-4 mm) for older trees (A1 to A5).
256 Another strikingly different pattern is that all sites but one on the Kodiak Archipelago present
257 best fit from a logistic curve or a linear model with significant negative slope, suggesting that
258 over time juvenile growth gradually decreased at all sites to values similar to current values in
259 the Seward population. K5 is the only site where ring width does not decrease, with current
260 values above 2mm. This is consistent with a young stand where all mature trees present
261 developed in the absence of substantial intraspecific competition. For sites where a logistic curve
262 was the best fit, estimated dates of canopy closure h varied little among sites. As growth rings
263 are narrower in old trees on Afognak Island than on Kodiak Island but we still observe a
264 decrease in radial growth over time, we suggest that stands with closed canopies on Afognak
265 Island earlier than the period for which we have data, and that the detected signal corresponds to
266 a slow increase in stand density.

267 Finally, we computed the cumulative distribution of establishment dates of canopy trees
268 in both the Kodiak Archipelago and Seward populations (Figure 3a). There was a sharp increase
269 in the cumulative number of established canopy trees on the Kodiak Archipelago around 1700.
270 The cumulative distribution of the Seward sample suggests that this shift is not due to intrinsic

271 mortality in trees established before 1700. Indeed, such old trees are present in the Seward
272 population (although few trees established before 1550 were sampled). Instead, the observed
273 shift in age distribution on the Kodiak archipelago compared to Seward might either indicate a
274 genuine increase in establishment rate around 1700 or an elevated extrinsic mortality of trees
275 established before that time. However we do not know of any catastrophic climatic or geological
276 event from this time, nor do we observe signals of it in annual tree rings of trees established
277 before 1700 on the archipelago.

278

279 Genetic structure and diversity in space and time

280 Both PCA plots (Figure S2) and STRUCTURE analyses (Figure S3) suggest that
281 population differentiation is moderate and mainly separates Seward from the other populations.
282 In particular, the mixed ancestry of Shuyak and Port Chatham displayed in the K=2 and K=3
283 STRUCTURE bar plots as well as their position on the PCA plot suggest that the strait
284 separating the archipelago from the mainland does not produce any marked differentiation
285 pattern, at least not compared to similar overland distance.

286 To determine how the present regional pattern of population structure evolved, we
287 analyzed the evolution of F_{ST} over 400 years between the Kodiak Archipelago and the Seward
288 region (Figure 3b). Despite large confidence intervals around estimates, we observe a decrease in
289 F_{ST} from 0.15 in 1610 to 0.12 in the mid-1700s, followed by a weak, statistically nonsignificant
290 increase to about 0.15, the current estimate. The early decrease in differentiation could indicate
291 relatively high gene flow from the mainland to the Kodiak Archipelago during early population
292 establishment. A shift to local recruitment likely happened in the 1700s, putting an end to the
293 decreasing trend in genetic differentiation. This shift is coincident with the upward shift in the
294 distribution of establishment time of canopy trees on the Kodiak archipelago (Figure 3a).

295 Genetic diversity decreased towards the expansion front for both allelic richness and
296 expected heterozygosity calculated over polymorphic loci (Figure 4). The Seward population had
297 the highest allelic richness, and Kodiak Island, Afognak Island, and Port Chatham had the
298 lowest. Interestingly, Shuyak Island has a higher allelic richness than Port Chatham suggesting
299 connectivity of the Shuyak population with other populations, possibly from *P. sitchensis* forests
300 outside of those sampled, or from *P. glauca* populations north of the archipelago. Heterozygosity

301 is high everywhere but on Kodiak and Afognak Islands, suggesting a deficit of some alleles
302 common elsewhere at the expansion front.

303 To determine how quickly the Kodiak-Afognak populations acquired their current allelic
304 diversity, we built an allele-accumulation curve (Figure 3c) and compared it to a null model of
305 comparable sample sizes. We found that most alleles present in the data were acquired between
306 1620 and the mid-1700s, a trend confirmed not to be an artefact of sampling effects.

307

308 Patterns of genetic structure and diversity at the colonization front

309 Expected heterozygosity calculated for each sampled site using all SNPs that are
310 polymorphic ranged from 0.11 to 0.28 across the Kodiak Archipelago (table 1). There is no
311 evidence for a latitudinal decrease within the archipelago towards the edge of the range: we
312 calculated a correlation coefficient of 0.04 between latitude and H_e (Pearson's correlation test, p
313 = 0.9004). We calculated a similar correlation coefficient value between expected heterozygosity
314 and canopy age ($r=0.08$, Pearson's correlation test, $p =0.8101$), and again failed to detect any
315 erosion of genetic diversity during successive colonization of demes at the expansion front.

316 To test the hypothesis that colonization leads to genetic sectors on the landscape, we
317 computed pairwise F_{ST} among sites (Figure 5). Larger F_{ST} values among areas on the Kodiak
318 Archipelago than among areas on Seward would suggest the presence of such colonization-
319 specific mechanisms at the front. However, we observe very low (<0.1) pairwise F_{ST} values
320 between sites on the archipelago, similar to those observed among Seward sites. This could be
321 due to high gene flow among sites after long-distance dispersal founding events, making genetic
322 sectors too transient to be observable in current datasets. Alternatively, it could be due to a
323 homogeneous pool of founding individuals across the archipelago, which could occur if all
324 propagules came from one, already depauperate source population. To test these alternative
325 hypotheses, we took a landscape genetics approach and calculated genetic dissimilarity among
326 sites at different distances within the Kodiak Archipelago and at four different times, and studied
327 the change in dissimilarity between sites over time (Figure 6). Dissimilarity between sites in
328 1710 was significantly higher than during subsequent centuries: We observe average
329 dissimilarity values an order of magnitude lower in 1810, 1910 and 2010 than in 1710. This
330 result brings support to the hypothesis that post-founding gene flow prevented initial genetic
331 sectors from persisting.

332

333 **Discussion**

334 Studying the evolution of long-lived organisms such as temperate tree species is
335 challenging because of their typically long generation times. This study shows that the
336 concomitant use of tree ring and genetic data can turn the inconvenience of these life history
337 characteristics into an opportunity to accurately reconstruct the demographic and genetic history
338 of colonization over five centuries. By applying this combination of methods to several regions
339 and sites within regions at the expansion front of *P. sitchensis*, we were able to describe
340 demographic and neutral genetic patterns of forest establishment at the regional and local scale.
341 We established a link between genetic diversity and spatial colonization patterns by showing that
342 both trends of decreasing diversity and decreasing time since forest establishment towards the
343 expansion front break down at the local scale. This provides insights into the effects of dispersal
344 patterns on neutral evolution during range expansion. It also highlights the importance of relating
345 geographic scale of study to the dispersal abilities of the studied organism when testing for
346 evolutionary trends commonly observed during range expansions. We also established a link
347 between temporal trends in demography and genetic structure of *P. sitchensis* populations over
348 the last five centuries at the expanding range limit: a shift from decreasing to stagnating
349 differentiation between the establishing Kodiak population and the Seward population on the
350 Kenai Peninsula coincides with a marked increase in successful establishment rate on the Kodiak
351 Archipelago, in the 1700s. This suggests that gene flow from continental populations was
352 predominant in early stages of establishment, until local recruitment became the major
353 mechanism of population growth. Most of the allelic richness on the Kodiak Archipelago was
354 acquired during initial stages of population establishment, and the high levels of local gene flow
355 in later stages homogenized the genetic structure of the Kodiak population, buffering founder
356 effects at the local scale and maintaining them at the regional scale.

357

358 Founder and Allee effects

359 Trees established as early as 1516 were sampled on the archipelago and local recruitment
360 only appears to have become significant in the 1700s, highlighting the existence of a lag of
361 several centuries in local recruitment. Although these results do not provide direct evidence of
362 density-dependent population success, they echo findings of Lesser et al. (2013), who identified

363 Allee effects in early stages of forest establishment in a *Pinus ponderosa* stand through reliance
364 on long-distance seed and pollen dispersal for the first few centuries of population growth. In *P.*
365 *sitchensis*, wind-borne pollen is likely to be the main vector of genetic material from distant
366 sources, although the abilities of seeds to travel by air and ocean surface currents are not well
367 understood. The shift we observe in differentiation trends in the mid-1700s coincides with the
368 start of a plateau in the allele accumulation curve for the Kodiak-Afognak region. This result can
369 also be related to Roques et al. (2012), who found through models of colonization waves that
370 Allee effects prevent the erosion of genetic diversity along colonization routes: populations at the
371 front accumulate genetic diversity during establishment through reliance on populations behind
372 the expansion front. If a lag in local recruitment through Allee effects is common in populations
373 at the edge of forest tree species, mechanisms described in Roques et al. (2012) could partly
374 explain why many studied forest expansions do not show a classic decrease in diversity at the
375 expansion front. In the case of *P. sitchensis*, when populations had a low density of
376 reproductively mature trees they produced a relatively small pollen cloud compared to external
377 sources, until large mature trees became the main producers of pollen locally present. It is
378 however worth noting that although the expansion process on the Kodiak Archipelago did not
379 result in local erosion of allelic richness, expected heterozygosity over polymorphic sites
380 remained low on Kodiak and Afognak Islands. This suggests that although allelic diversity was
381 recovered largely during colonization, many alleles remain at low frequencies in the newly
382 established population. The genotype of early colonizers might therefore have a long-lasting
383 influence in the establishing population.

384

385 Genetic structure at the expansion front

386 *P. sitchensis* started establishing at most sites on the Kodiak Archipelago before 1700.
387 Evidence for continental sources dominating gene flow prior to the mid-1700s indicates that
388 long-distance dispersal from the mainland played an important role in initial recruitment. Models
389 of colonization through patches from long-distance dispersal show that genetic sectors are
390 expected to arise (Hallatschek & Nelson, 2010). However, we found no evidence for spatial
391 genetic sectors in the current sample. We propose two explanations for this lack of spatial
392 genetic structure. First, it seems that most founders colonized Kodiak and Afognak Islands from
393 just a few source populations that were already somewhat depleted in alleles. Indeed, it seems

394 that the low allelic richness observed on a regional scale on the Kodiak Archipelago could be due
395 to the low levels of allelic richness of source populations at the tip of the Kenai Peninsula: we
396 observe similar levels of allelic richness on Kodiak and Afognak Islands as in Port Chatham, the
397 closest continental population sampled. Low levels of allelic richness in Port Chatham may be
398 explained by lower population sizes due to a fragmented landscape, as the region is highly
399 mountainous and suitable habitat is restricted to narrow valleys between ice-capped mountains
400 and numerous sinuous fjords. As we also observe higher allelic richness on Shuyak Island than in
401 Port Chatham, multiple source populations might contribute to the maintenance of genetic
402 diversity in regions at the expansion front. The second factor likely to explain the absence of
403 genetic sectors is high gene flow within the Kodiak Archipelago during the last 250 years. We
404 found a decrease in F_{ST} among sites at the expansion front between 1700 and subsequent
405 centuries, suggesting that initial spatial patterns of genetic structure from founding individuals
406 did not persist or develop further due to high levels of subsequent gene flow across the
407 archipelago.

408

409 Demographic estimates of establishment times: power and limitations

410 Estimates of establishment time, canopy age and time of canopy closure all detected a
411 clear demographic signal of population establishment on Kodiak Island, and a less clear signal
412 for Afognak Island. As these estimates were also calculated for the Seward population, known to
413 be several thousand years old, the power and limitations of these estimates can be established.
414 Mean canopy age is only informative for about 300 years, and estimated time of canopy closure
415 confirmed the recent nature of forests on Kodiak Island and – to a lesser extent – Afognak
416 Island. The complementarity of these two estimates is best illustrated with the Afognak Island
417 site A5: this site is similar to Seward sites in mean canopy age (Figure S1) but juvenile growth
418 rings show a signal of increasing canopy density throughout the 19th century, a pattern not
419 observed in Seward (Figure 2). Although time of canopy closure is useful for inferring the
420 absence of a closed canopy when the first trees established, the temporal change in juvenile
421 radial growth couldn't be modeled by a logistic curve, or was better fitted by a linear model. This
422 can be due to the initiation of intraspecific competition suppressing growth being too recent, or
423 to spatial heterogeneity within stands. In addition, we found little variability between sites in
424 estimates of time of canopy closure. The parameter h from the logistic curve modelling may not

425 be the most informative measure of establishment time. Visually inspecting juvenile ring width
426 over time (Figure 2) might provide more information about stand establishment than extracting a
427 single value from temporal ring width profiles.

428

429 Implications for long-lived wind-pollinated species

430 Our results suggest that the evolutionary potential of wind-pollinated tree species is more
431 likely to be limited by slow demographic growth than by slow accumulation of genetic diversity.
432 We showed that in spite of a slow initial population growth, allelic richness recovered during this
433 period up to levels comparable to nearby source populations. We also showed that geographic
434 barriers to gene flow are weak despite the studied population being isolated from the continent
435 by a 70 km-wide ocean strait. The demographic lag observed in this and other studies of tree
436 populations suggests an Allee effect, whereby the reproductive ability of establishing trees is
437 limited firstly by a long phase of juvenile growth, and secondly by a higher dependence on
438 foreign pollen fertilizing local mature trees when population densities are low. This potential
439 Allee effect could keep a colonizing tree population in a vulnerable state and contribute to the
440 migration lag of tree species tracking their suitable niche space, especially in the context of rapid
441 anthropogenic climate change. However, such a lag is also likely to be at the origin of an
442 efficient recovery of genetic diversity after a founding event, as several studies have shown a
443 predominance of pollen of foreign origin during early population establishment (Hampe et al.,
444 2013; Lesser et al., 2013; Pluess, 2011). In both cases, management through planting trees from
445 diverse carefully selected provenances could accelerate successful establishment and adaptation
446 in populations of conservation concern (Aitken & Whitlock, 2013). In general, understanding
447 demographic processes during range shifts and their effect on evolutionary potential is necessary
448 as climate change is shifting species' suitable niches nearly everywhere on the planet. We have
449 shown that dispersal potential and temporal patterns of population growth are important factors
450 influencing population expansion and adaptation, but the effects of other mechanisms such as
451 hybridization, competition, and natural selection also need to be assessed in order to predict or
452 help species movements in response to a rapidly changing world.

453

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468
469

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615 **Data accessibility**

616 Tree ring series will be made available on the NOAA website. Genetic data will be deposited on
617 Genbank (raw sequences) and Dryad (SNP dataset) upon acceptance of the manuscript.

618

619 **Author contributions**

620 J.S.E and S.N.A designed the study. J.S.E conducted analyses and J.S.E wrote the manuscript
621 with suggestions and modifications from S.N.A.

622

623 **Supporting information**

624 Additional supporting information including methods and figures can be found online.

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Tables

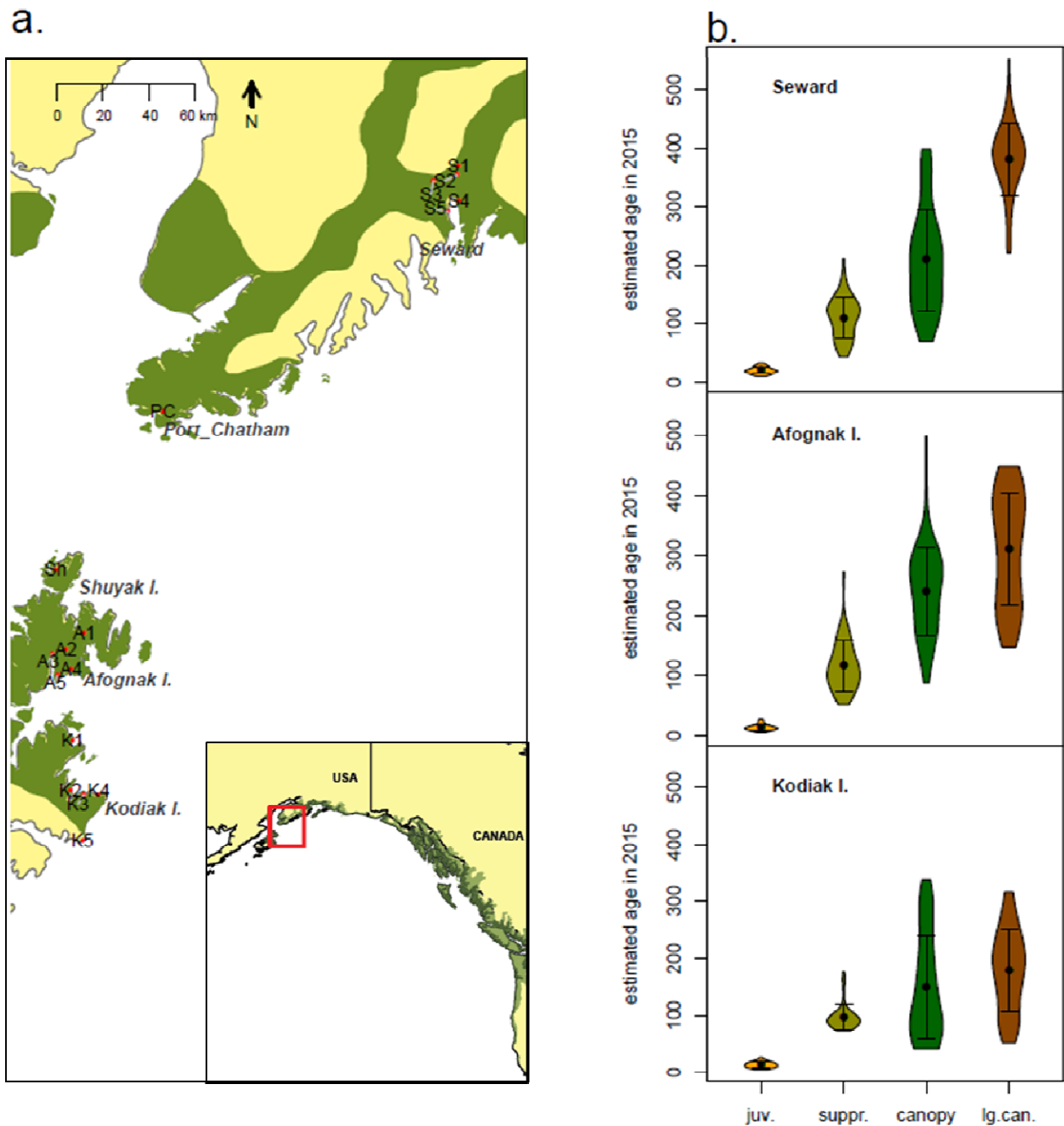
632 **Table 1.** Nomenclature, description, and diversity estimates of sampled sites (shown on Figure
633 1a). Size=sample size; H_e =population-level heterozygosity averaged across loci; mean canopy
634 age=average tree age across large canopy and medium-sized canopy trees, in years.
635

site	region	latitude	longitude	size	H_e	mean canopy age
S1	Seward	60.253	-149.357	37	0.283	294
S2	Seward	60.213	-149.369	36	0.29	288
S3	Seward	60.19	-149.558	48	0.268	285
S4	Seward	60.107	-149.354	48	0.251	319
S5	Seward	60.06	-149.444	26	0.202	266
PC	Port Chatham	59.224	-151.703	15	0.123	NA
Sh	Shuyak	58.563	-152.555	15	0.183	NA
A1	Afognak	58.298	-152.329	24	0.119	206
A2	Afognak	58.231	-152.475	37	0.155	223
A3	Afognak	58.209	-152.585	12	0.12	315
A4	Afognak	58.145	-152.433	25	0.121	239
A5	Afognak	58.118	-152.541	86	0.15	310
K1	Kodiak	57.845	-152.422	52	0.134	203
K2	Kodiak	57.638	-152.437	49	0.134	147
K3	Kodiak	57.619	-152.334	50	0.123	207
K4	Kodiak	57.617	-152.219	31	0.136	201
K5	Kodiak	57.428	-152.344	48	0.13	66

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639 **Figures**

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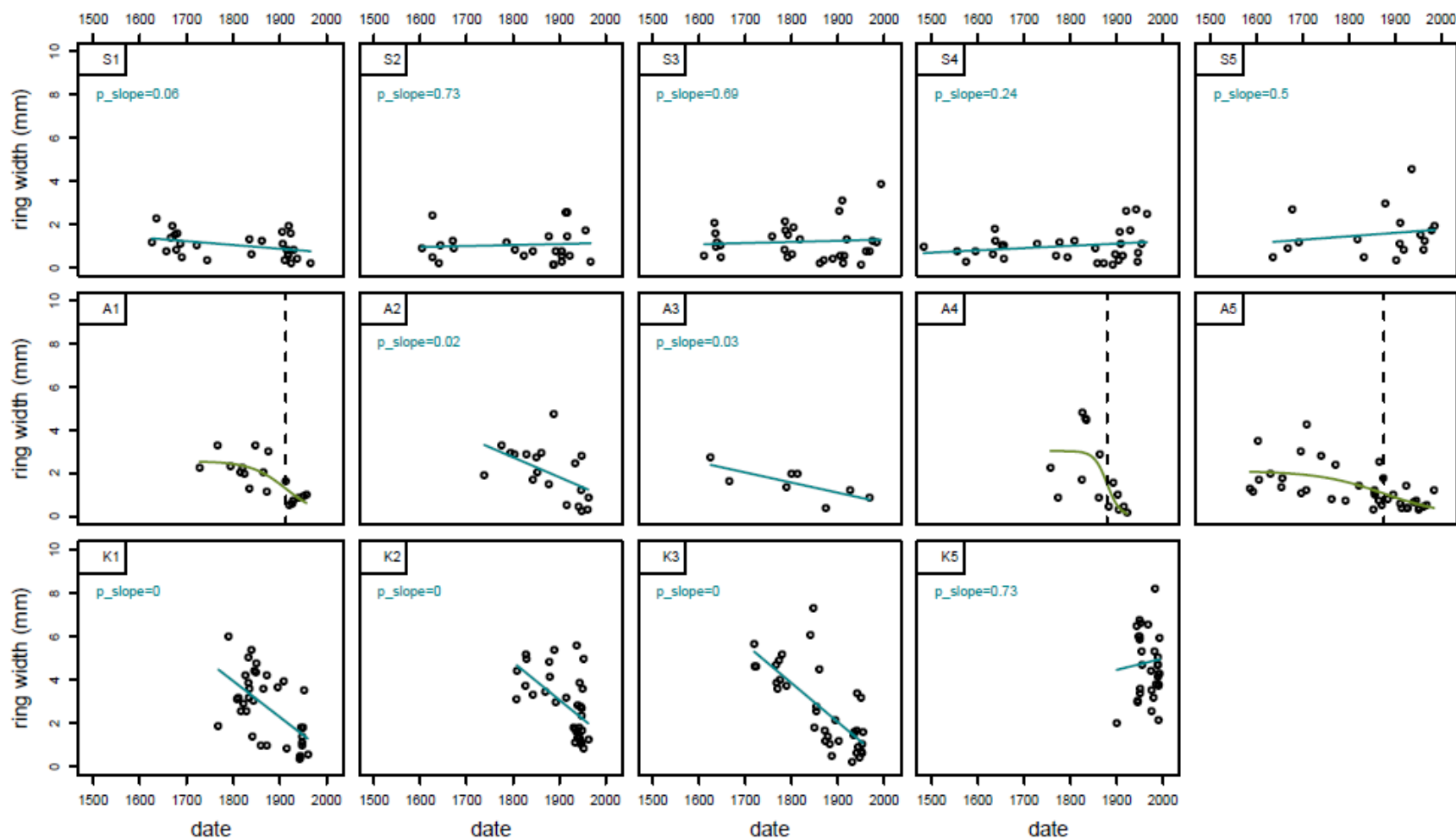
641

642 **Figure 1. a.** Sampled sites in south-central Alaska, with the whole range of *P. sitchensis* (green

643 area) in inset. **b.** Violin plots of individual tree ages for each canopy structure level within each

644 region sampled, with mean and standard deviation displayed in black.

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646
 647 **Figure 2.** Individual annual radial growth between years 10 and 20 vs. date of establishment. The best model among linear and
 648 logistic models is displayed in blue (linear model) or green (logistic model). In the latter case the estimated time of canopy closure h is
 649 represented by a dashed line.
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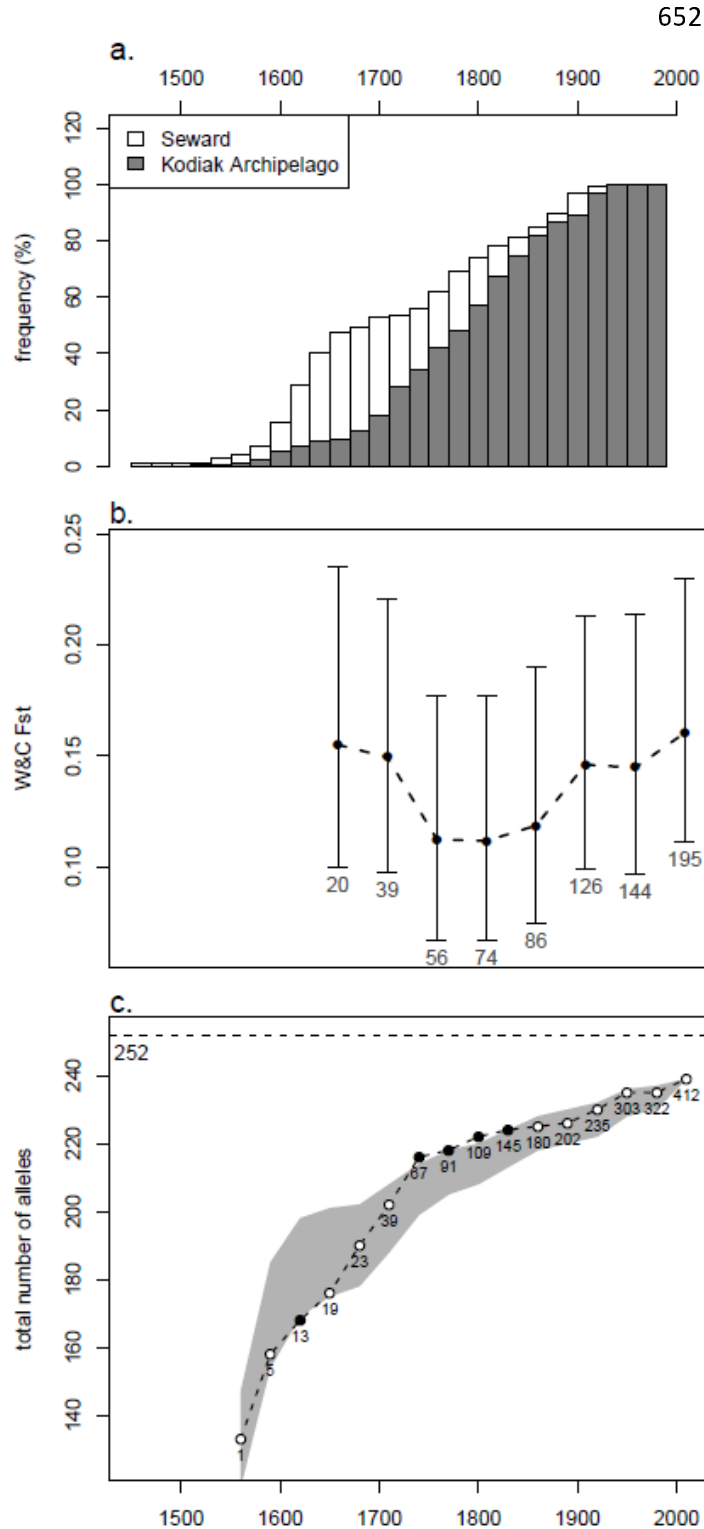
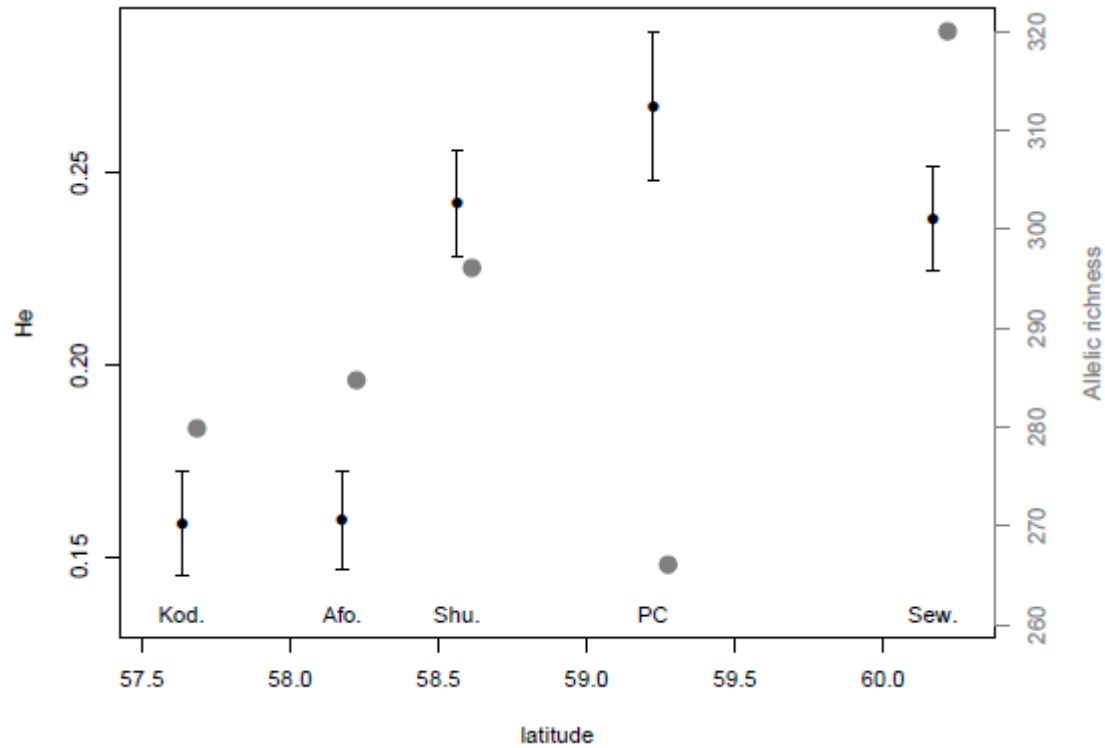
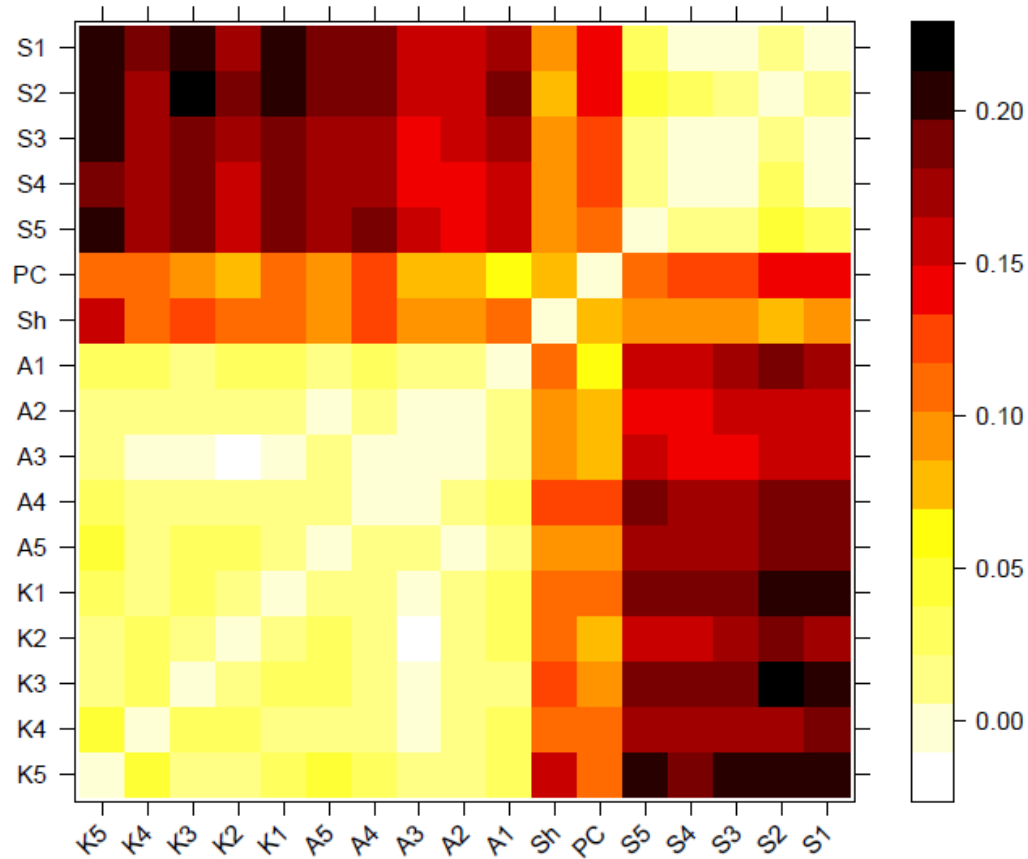


Figure 3. Demographic and genetic changes over time on the Kodiak Archipelago in relation to the Kenai Peninsula. **a.** Cumulative distribution of establishment dates for canopy trees for the Kodiak Archipelago and the Seward region. **b.** Temporal change in F_{ST} between the Kodiak Archipelago and Seward. F_{ST} Values are calculated for the cumulative sample (each sample associated with a date is made of all individuals alive at this date). Error bars represent confidence intervals from 1000 bootstraps. The number of individuals per population is indicated below error bars. **c.** Allele accumulation curve for the Kodiak Archipelago with 95% interval band from 1000 random permutations (grey). Numbers under datapoints correspond to cumulative sample sizes. Data points with values outside the 95% confidence band are represented with filled circles. The top dotted line correspond to the maximum number of alleles in the whole sample of 639 individuals.

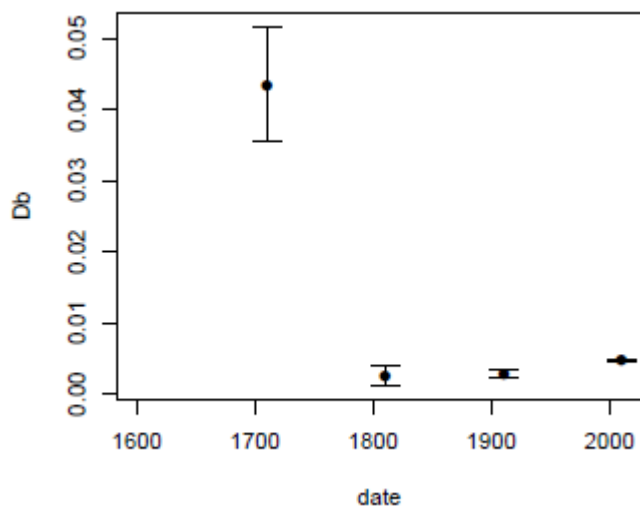


682
683 **Figure 4.** Regional expected heterozygosity over variable SNPs (black) and estimated allelic
684 richness (grey) vs. latitude or regions. Error bars on H_e are standard errors of the mean.
685 Kod.=Kodiak Island, Afo.=Afognak Island, Shu.=Shuyak Island, PC=Port Chatham,
686 Sew.=Seward.
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Figure 5. Heat map of pairwise F_{st} values between sampled sites.



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Figure 6. Temporal change in mean pairwise dissimilarity between sites on the Kodiak Archipelago. Error bars represent standard error of the mean.