

1 Full Title: Population extinctions driven by climate change, population size, and time since observation
2 may make rare species databases inaccurate

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4 Short Title: Population extinctions may make databases inaccurate

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22

23 **Abstract**

24 Loss of biological diversity through population extinctions is a global phenomenon that threatens many
25 ecosystems. Managers often rely on databases of rare species locations to plan land use actions and
26 conserve at-risk taxa, so it is crucial that the information they contain is accurate and dependable.
27 However, climate change, small population sizes, and long gaps between surveys may be leading to
28 undetected extinctions of many populations. We used repeated survey records for a rare but
29 widespread orchid, *Cypripedium fasciculatum* (clustered lady's slipper), to model population extinction
30 risk based on elevation, population size, and time between observations. Population size was negatively
31 associated with extinction, while elevation and time between observations interacted such that low
32 elevation populations were most vulnerable to extinction, but only over larger time spans. We interpret
33 population losses at low elevations as a potential signal of climate change impacts. We used this model
34 to estimate the probability of persistence of populations across California and Oregon, and found that
35 31%-56% of the 2415 populations reported in databases from this region are likely extinct. Managers
36 should be aware that the number of populations of rare species in their databases is potentially an
37 overestimate, and consider resurveying these populations to document their presence and condition,
38 with priority given to older reports of small populations, especially those at low elevations or in other
39 areas with high climate vulnerability.

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46 **Introduction**

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48 Population extinctions are a major threat to plants, leading to range contractions, fragmentation and
49 isolation [e.g., 1-4], which together reduce the abundance of species. As Darwin [5] pointed out, rarity is
50 a precursor of extinction. Orchids in particular face a global conservation risk with high species diversity
51 but also a high rate of species that are rare or threatened with extinction [6-12], and rare orchids are
52 likely to need aggressive conservation actions to prevent their extinction [13]. Nearly half of the genus
53 *Cypripedium* may be threatened and in need of protection if the species are to survive in the wild [14].
54 Therefore, accurate assessments of the number of populations of a rare species and its major threats
55 are crucial to conservation planning and resource allocation for recovery actions [15, 16].

56

57 Several processes can contribute to rare plant population extinctions, including habitat loss, interactions
58 with invasive species, changes in disturbance frequency, etc. [17]. Climate change in particular is
59 affecting species ranges globally [18], with organisms shifting toward higher latitudes [19] and
60 elevations [20]. For example, plant ranges in western Europe have moved upslope at 29 m/decade over
61 the last century [21] and in California at similar rates [22]. Climate change effects on temperature and
62 moisture may threaten plant diversity in Europe, especially in mountains [23]. Low-elevation
63 populations of organisms can be especially at risk of extirpation as climatic conditions change and force
64 upslope range shifts [24]. Any contraction in the range of a rare species can have significant effects on
65 its long term conservation and viability.

66

67 The number of individuals present can also affect the viability of plant populations, with small
68 populations having greater risk of extirpation. In general, the extinction probability of a population
69 increases as population size decreases [25, 26]. Small populations may be at greater risk of extinction

70 because of several factors, including losses in reproductive individuals [27], Allee effects [28], declines in
71 seed production [29] and viability [30], loss of genetic diversity [31] and accumulation of genetic load
72 [32], and demographic stochasticity [33]. In empirical studies that surveyed the same locations of
73 multiple plant species over several years in Germany [4] and the Swiss Jura Mountains [34], extinction
74 rates were found to be higher for small populations. And although population size may be a strong
75 predictor of population vulnerability, passage of time can compound the likelihood of extinction
76 because as more time passes in stochastic environments the chances that a population will fall to zero
77 increase [25, 26].

78
79 Taken together, climate change, population size, and time since observation create considerable
80 uncertainty regarding the current status of wild plant populations recorded in various rare species
81 databases. Several US agencies and organizations (e.g., US Bureau of Land Management, US Fish and
82 Wildlife Service, US Forest Service, NatureServe, state Natural Heritage Programs) maintain databases of
83 rare plant occurrences and many of these occurrences may not have been visited recently. Therefore,
84 the number of populations in the wild of some species could be smaller than the number listed in
85 databases due to extinctions that have not yet been detected. Increasing our ability to estimate the
86 number of populations that remain extant or have gone extinct in these data bases will improve
87 conservation planning for rare species. We used information on repeated surveys in California and
88 Oregon for a rare but widespread orchid, *Cypripedium fasciculatum* (clustered lady's slipper), to test the
89 hypothesis that extinction probability is affected by elevation, population size, and time since
90 observation. We applied the resulting model to populations in Oregon and California in the Geographic
91 Biotic Observations (GeoBOB) data base maintained by the US Bureau of Land Management and the US
92 Forest Service Natural Resource Information System (NRIS-Terra) to estimate the number of populations
93 that are still extant.

94

95 **Materials and methods**

96

97 Study species

98

99 *Cypripedium fasciculatum* (clustered ladies slipper; Figure 1) occurs in scattered population centers in
100 western North America in California, Oregon, Washington, Idaho, Montana, Utah, Wyoming and
101 Colorado. In California and Oregon, this taxon occurs predominantly in the Klamath-Siskiyou Mountains
102 and Sierra Nevada Mountains. The United States Forest Service (USFS) considers it to be a Sensitive
103 Species and the Bureau of Land Management (BLM) lists it as a Bureau Sensitive Species, and it is
104 considered globally secure because of its widespread geographic range and abundance in some states
105 [35]. In California and Oregon the species is most often found on north facing slopes in mixed
106 coniferous forests of >60% canopy closure [36]. *Pseudotsuga menziesii* is the most common associated
107 tree, but other frequently noted forest components include *Abies concolor*, *Cornus nuttallii*, *Pinus*
108 *lambertiana*, and *Calocedrus decurrens*. Clustered lady's slipper is known to occur in California and
109 Oregon at elevations from about 180 to nearly 2000 m. The species has a complex life-history and
110 depends on specific mycorrhizal fungi [37], which may affect its seed germination and growth.
111 Mycorrhizal fungi may determine where and in which specific habitats this orchid can grow and how it
112 responds to disturbance, but little information is available on the fungi, their requirements, associated
113 tree species, and their function in forest ecosystems [36].

114

115 **Figure 1. *Cypripedium fasciculatum* (clustered lady's slipper).**

116

117 Data sources

118

119 We compiled repeated-survey data from multiple sources to test for effects of elevation, time between
120 surveys, and population size on extinction probability. The sources of these resurvey data were from an
121 assessment of the conservation status of *C. fasciculatum* in California that reviewed available records
122 (78 sites) for the species throughout that state [36] and from repeated surveys in southwestern Oregon
123 (158 sites) conducted on federal lands. Both resurvey data sources (236 populations combined)
124 included sites revisited at least once and documented site location, elevation, population size, and time
125 between surveys. We used information on population size from the first survey, and time between
126 surveys was calculated as the number of years between the first and last (most recent) survey. The last
127 survey was used to score each population as either extant or extinct (no individual plants found at the
128 site). The time between surveys ranged from 1 to 29 years. While most observers censused
129 populations, some estimated population size, and when this occurred we used the highest integer
130 reported for a population during the first survey. For example, if 50-100 plants were reported, we used
131 100. If the number was vague (e.g., 75+, >30, or ca. 50) we used the actual integer listed (75, 30, or 50,
132 respectively). Populations used in the analysis varied in size from 1 to 1084 individuals. *C. fasciculatum*
133 plants that were single stems or clumps were considered individuals [following 40].

134

135 Population Viability Analysis

136

137 We used a generalized linear model with quasibinomial errors to estimate extinction probability. The
138 response variable was population status at the most recent visit (a binomial response, either extinct or
139 extant) and independent variables were size of the population at the first survey, elevation of the
140 population, and number of years between the first and last survey. All analyses were performed in R
141 3.3.2 [R Core Development Team, www.cran-r.org].

142

143 Estimating extant population number

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145 To estimate the number of populations of *C. fasciculatum* recorded as still extant in the GeoBOB and

146 NRIS-Terra databases for California and Oregon, we applied our statistical model for predicting

147 extinction probability to each of the 2896 populations recorded based on their elevation, size and years

148 since the last survey. To estimate uncertainty, we bootstrapped the parameters in the model from our

149 resurvey data set of 236 populations by randomly selecting 236 populations from this group, with

150 replacement, and estimating the generalized linear model parameters. For each bootstrapped set of

151 parameters, we calculated the extinction probability of each population in the GeoBOB and NRIS-Terra

152 databases, summed those probabilities to estimate the number of extant populations, and repeated this

153 bootstrap process 10,000 times to estimate 95% confidence limits. We performed this analysis in R

154 3.3.2.

155

156 **Results**

157

158 Population Viability Analysis

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160 Of the 236 populations in our data sets, we found 34% were no longer present when revisited.

161 Elevation, time between surveys, and population size were each significant factors for predicting

162 extinction probability of populations (Table 1). Probability of extinction was best explained by all of

163 these factors, including a significant ($p < 0.001$) interaction between elevation and years between

164 surveys. The general linear model suggested that populations at lower elevations were more likely to go

165 extinct than high elevation populations, but only as the length of time between surveys increased

166 (Figure 2, right). Small populations had a greater probability of extinction than large populations, and
167 extinction probability was near zero for populations with >100 individuals (Figure 2, left), regardless of
168 the length of time between samples. Further, extinction probability increased as the time between
169 surveys increased, most notably for smaller populations.

170

171 Table 1. Generalized linear model for factors affecting the probability of population survival for *C.*

172 *fasciculatum*.

173

Factor	Estimate	Standard Error	t value	<i>P</i>
(Intercept)	1.75	1.03	1.70	0.091
Starting population size	0.09	0.02	4.36	<0.001
Years between surveys	-0.38	0.1	-3.81	<0.001
Elevation	-0.0002	0.0003	-0.713	0.476
Years between surveys X Elevation	0.00008	0.00003	2.76	0.006

174

175

176

177 **Figure 2. Extinction probability as a function of population size (left) and the interaction between**
178 **elevation (m) and time (years) between surveys (right, with each line representing an example of a**
179 **specific time interval between surveys. Shadings around each line represent 95% confidence**
180 **intervals.**

181

182 Estimating extant populations

183

184 A total of 2415 populations with one or more plants were reported in the GeoBOB and NRIS-Terra
185 databases for Oregon and California. An additional 426 populations were reported as already extinct by
186 2016. Populations in that database ranged in size from 1 to 1859 individuals, with a mean population
187 size of 27 (95% CI \pm 1.6). We estimated that of the 2415 populations reported as extant, only 1,349
188 (95% bootstrapped quantiles: 1213-1486) were likely still present. This is equivalent to an overall
189 extinction rate of 44% (95% bootstrapped quantiles: 38%-50%). The predicted probability of population
190 survival varied widely across the landscape in California and Oregon, with some population centers
191 showing greater potential for population extinction than others (Figure 3). For example, populations in
192 southwestern Oregon had a predicted extinction rate of 60% (53% – 67%) of 1258 reports compared to
193 27% (19% - 35%) of 1157 records in California. This difference was driven in our model by the generally
194 lower population sizes in Oregon (mean: 12.7 95% CI: \pm 1.5) than California (37.9 \pm 6.6) and lower
195 elevations of populations in Oregon (757.2m \pm 13.4m) than California (1319.2m \pm 15.4m). Years
196 between observations did not differ between states, averaging 15.4 years overall (\pm 0.39).

197

198 **Figure 3. Distribution of *Cypripedium fasciculatum* in the western United States (inset), with map of**
199 **California and Oregon showing the probability of persistence estimated from elevation, population**
200 **size, and time since observation.**

201

202 Discussion

203

204 We found that elevation, population size, and time between surveys predicted extinction in *Cypripedium*
205 *fasciculatum*. When these factors were used to model the persistence of wild populations, we found
206 that only 56% of populations reported in the GeoBOB and NRIS-Terra databases for California and

207 Oregon are likely still present on the landscape. Extinction rates are predicted to be higher in Oregon
208 than in California, primarily due to the lower average population size and elevation there. Our results
209 suggest that negative impacts from climate change might already be apparent for *C. fasciculatum*
210 through extinction of low elevation populations. Loss of low elevation populations may be expected
211 when climates warm to the point that populations can no longer survive in the hotter portions of their
212 range. For example, loss of butterfly species at low elevations has been attributed to warming trends in
213 Spain [39]. Our findings with *C. fasciculatum* are generally consistent with orchid responses to climate
214 change in North America and elsewhere. Documented declines of species in the Orchidaceae in eastern
215 North America appear to be related, at least in part, to an inability of these species to alter their
216 phenology, particularly flowering time, as climate has warmed over the last century and a half [40].
217 Climate change appears to be a threat to orchids in Mexico [41], and orchids in general appear to be
218 highly vulnerable to climate change in China [42]. In contrast, orchids were more likely to increase
219 abundance in Mediterranean France from 1886-2001 compared to many other plant taxonomic groups
220 [43]. Precipitation appears to be a strong driver of plant survival in *C. reginae* [44], making the species
221 vulnerable to changes in regional climate. And it is clear that climate has changed recently and is
222 forecasted to change further in California and Oregon, in part due to warming and drying that, when
223 combined, exacerbate moisture deficits and increased evaporative demand [e.g., 45].
224
225 Many orchid species have populations with a wide range of sizes [46], and small average population
226 sizes are common. In the GeoBOB and NRIS databases of 2415 populations of *Cypripedium fasciculatum*
227 in California and Oregon that we reviewed, the average population size was 25 individuals. The average
228 population size of *C. kentuckiense* is 40 individuals, *C. calceolus* in Europe generally has populations with
229 fewer than 100 plants, and *C. dickensonianum* occurs as small colonies or individuals [47]. As population
230 size declines in orchid species, gene flow by pollen may decline [48], inbreeding may increase [49],

231 pollination, fruit set and seedling recruitment may decrease [50], genetic drift may increase [51], and
232 genetic diversity may decline [52]. Transition matrix models of *C. calceolus* [53] indicate extinction
233 probability over a 100 year period in populations with 10 plants is 37%, and in populations with 5 plants
234 it increases to 67% without disturbance. In populations where flowers are removed or plants are dug
235 up, extinction probability rapidly approaches 100%. The typically low population size in *C. fasciculatum*
236 was a major contributor to the high rate of predicted extinctions we have shown for the species.

237

238 Population extinction probability was associated with time between surveys in *C. fasciculatum*. In
239 stochastic environments, even populations with stable intrinsic population growth rates are vulnerable
240 to extinction, and this vulnerability increases with time [25, 26]. In populations with declining growth
241 rates, the rate of extinction will be even faster. Therefore, as time between surveys increases,
242 population extinction should also increase, especially for small populations. Surprisingly, time between
243 surveys had no significant effect on probability of extinction in eight rare plants in Germany [4], but the
244 study was conducted over a relatively short period (ten years).

245

246 Resurveys of plant populations and communities can provide substantial insights into the nature and
247 causes of changes that occur in the natural world over time [54-57]. Even so, there are some limitations
248 to our estimates of extinction probability of *C. fasciculatum* in this study. Repeated surveys may fail to
249 relocate previously documented populations even when they are still present [58-60] if the survey is not
250 sufficiently thorough. The datasets we used contained information on population resurveys that were
251 carefully conducted with precise location information, but the possibility remains that some extant
252 populations may have been missed. This could be aggravated by individual plant dormancy, which
253 would make plants very difficult to detect during surveys, and if all plants in a population were dormant
254 at the same time – a possibility that increases as population size declines – whole extant but dormant

255 populations could be falsely classified as extinct. Dormancy above ground is not uncommon in
256 terrestrial orchids [61], including *Cypripedium* [38, 62-66]. *Cypripedium reginae*, for example, may be
257 dormant for up to four years [44]. On the other hand, dormancy is associated with decreased orchid
258 reproduction [67] and survival [68], and if all individuals in a population were dormant, the population
259 might already be close to extinction. These factors suggest that although we could have overestimated
260 extinction probability [58] due to dormancy, this same dormancy could suggest increased plant
261 vulnerability. Either way, we are unable to quantify this potential bias in our results given the available
262 data.

263
264 Because orchids depend on fungi, at least in the early stages of plant development, the presence of
265 appropriate fungi and the environmental factors that affect them may in turn determine the growth and
266 survival of many orchids [69], including *C. fasciculatum* populations. Soil and topography, and especially
267 temperature and moisture are the most important factors that control orchid distribution and survival
268 [70], and this may be due to the influence of these factors on mycorrhizal fungi. *Cypripedium* spp. are
269 associated with fungi in the Sebacinaceae, Ceratobasidiaceae, and especially the Tulasnellaceae [37].
270 The degree of specificity of orchids with fungi is significant because orchids with highly specific
271 associations may be more sensitive to disturbance and environmental change than generalist species
272 [71]. Further, climate and fungal symbionts of orchids may interact to shape the evolutionary response
273 of specific vital rates to climate change, such as sprouting after dormancy [72].

274
275 Implications for conservation

276
277 This study demonstrates the need for additional and more frequent surveys of rare plant populations to
278 improve the reliability of information in databases used by land management agencies. Land managers

279 who make decisions on how best to conserve rare species often base their decisions in part on the
280 abundance and distribution of those organisms as reported in databases. However, many reported
281 populations may no longer be extant. Managers should be aware that the number of populations of
282 rare species in their databases is potentially an overestimate, and consider resurveying populations in
283 databases to document their presence and condition, with priority given to older reports of small
284 populations, especially those at low elevations or other areas with high climate vulnerability. Species
285 like *C. fasciculatum* may be candidates for assisted migration [73-75] as their low-elevation populations
286 experience extinction and if expansion or colonization at higher elevation locations does not occur
287 naturally. We suggest that development of propagation and planting techniques [e.g., 76-78] to allow
288 for intervention is warranted, and needs to consider the fungal dependency of this rare orchid [79].

289

290 **Acknowledgments**

291

292 The authors gratefully acknowledge the contributions and cooperation by the Medford District Bureau
293 of Land Management, especially Bryan Wender and Mark Mousseaux, who compiled database records
294 for the species regionally. Support was also provided the Rogue-Siskiyou National Forest and facilitated
295 by Wayne Rolle and Barb Mumblo. Staff of the Institute for Applied Ecology assisted with this project,
296 including Carolyn Menke who made the maps used in this paper, and Amanda Stanley and Heather Root
297 who provided statistical support.

298

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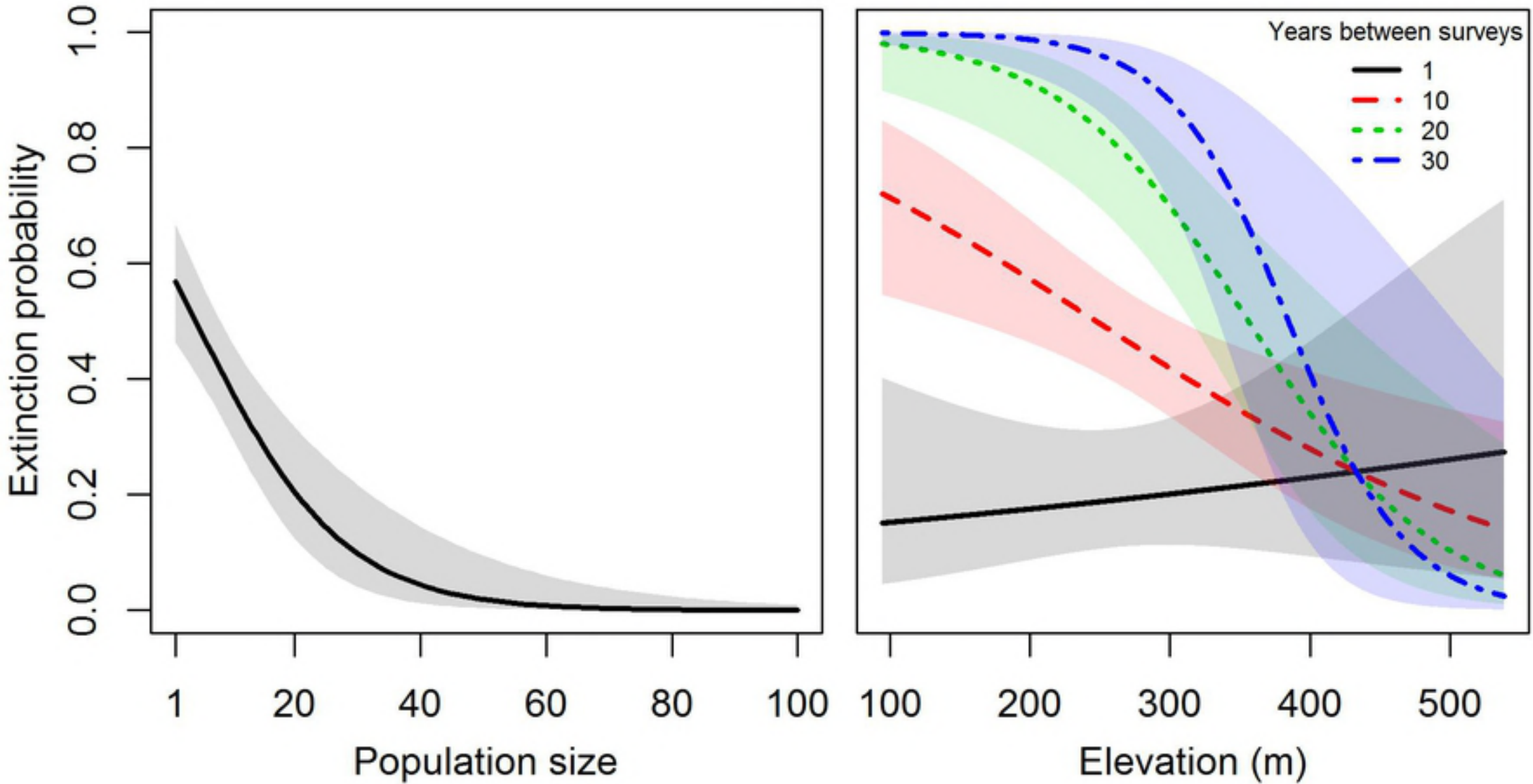


Figure 2

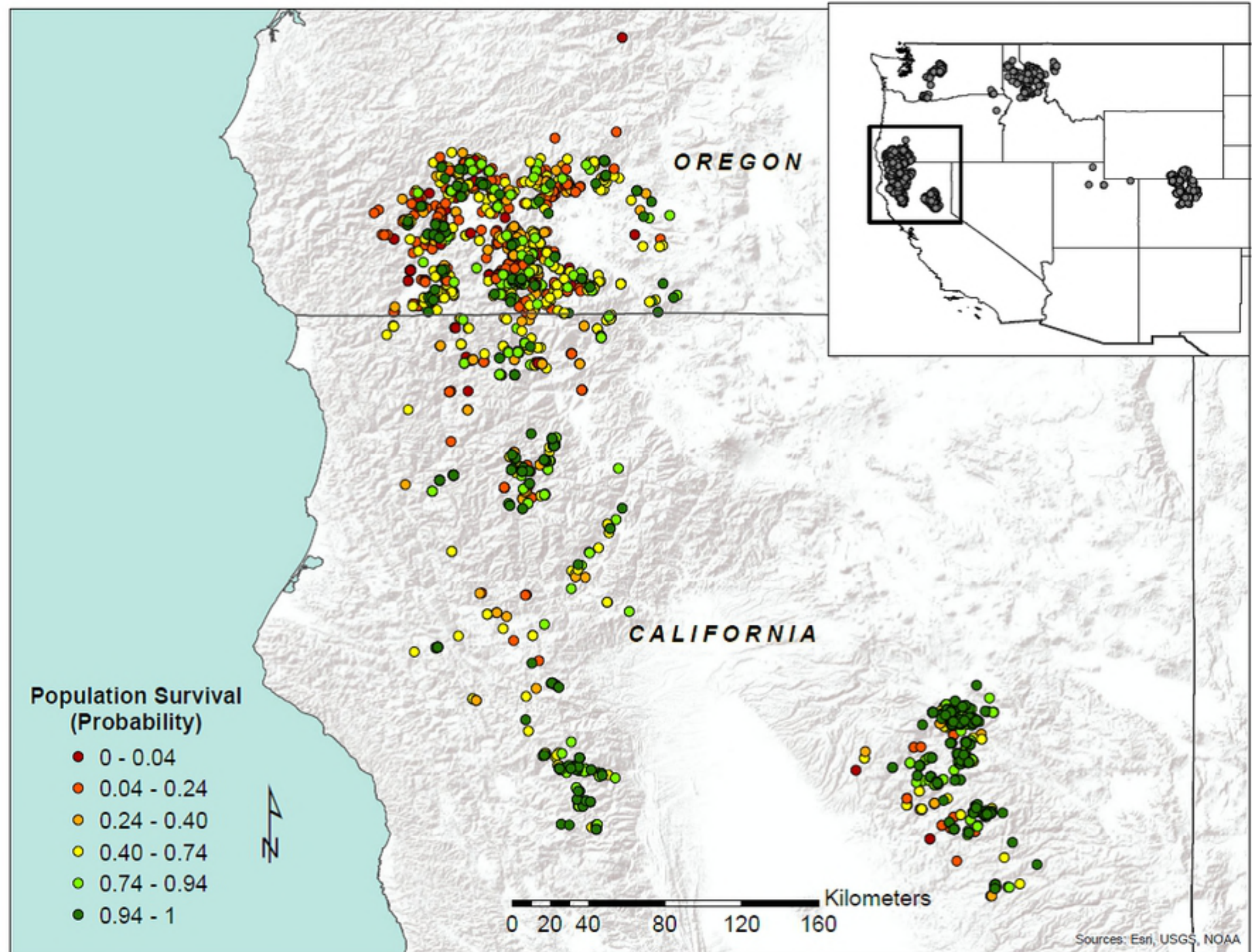


Figure 3



Figure 1