An experimental test of a Bayesian method for inferring extinction with varying search efforts

Determining whether a species is extinct or extant is notoriously difficult, but is fundamental to both our understanding of biodiversity loss, and our ability to implement effective conservation measures. Many methods have been proposed in an attempt to infer quantitatively whether a species has gone extinct, with many seeking to do so by using sets of historic sighting events. Until recently, however, no methods have been proposed that explicitly take into account search effort (the proportion of a habitat searched when looking for a species), a key determinant of if/when historic sighting events have occurred. Here we present the first test of a recently proposed Bayesian approach for inferring the extinction status of a species from a set of historic sighting events where the search effort that has produced the sightings can be explicitly included in the calculation. We utilize data from a highly tractable experimental system, as well as simulated data, to test whether the method is robust to changing search efforts, and different levels of detectability of a species. We find that, whilst in general the method performs well, it is susceptible to both changes in search effort through time, as well as how detectable a species is. In addition, we show that the value of the prior expectation that the species is extant has a large impact on the accuracy of the methods, and that selecting correct priors is critical for accurate inference of extinction status.

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Abstract

Determining whether a species is extinct or extant is notoriously difficult, but is fundamental to both our understanding of biodiversity loss, and our ability to implement effective conservation measures. Many methods have been proposed in an attempt to infer quantitatively whether a species has gone extinct, with many seeking to do so by using sets of historic sighting events. Until recently, however, no methods have been proposed that explicitly take into account search effort (the proportion of a habitat searched when looking for a species), a key determinant of if/when historic sighting events have occurred. Here we present the first test of a recently proposed Bayesian approach for inferring the extinction status of a species from a set of historic sighting events where the search effort that has produced the sightings can be explicitly included in the calculation. We utilize data from a highly tractable experimental system, as well as simulated data, to test whether the method is robust to changing search efforts, and different levels of detectability of a species. We find that, whilst in general the method performs well, it is susceptible to both changes in search effort through time, as well as how detectable a species is. In addition, we show that the value of the prior expectation that the species is extant has a large impact on the accuracy of the methods, and that selecting correct priors is critical for accurate inference of extinction status.

Introduction

Accurately determining whether a species is extant or extinct is notoriously difficult (Keith & Burgman 2004), with many quantitative methods developed to infer extinction status (e.g. Solow 1993a, 2005; McCarthy 1998; Gotelli et al. 2011). Such methods have typically concentrated on inferring the extinction status of a species from sets of historic sighting events (i.e. a species has been observed as being extant

47   at a given point in time, e.g. Roberts & Solow (2003)), as these are often the only

48   records of a species prior to a possible extinction event. Such sighting events are a

49   product of the detectability of a species (how easy it is to observe), the amount of the

50   species' habitat you search, and the abundance of that species. For example, if a

51   species has a very high population size, and is very detectable, only a small fraction of

52   its habitat needs be searched for the species to be observed, whereas low population

53   sizes and low detectabilities mean that even searching a large proportion of the habitat

54   may not guarantee a sighting. Consequently, information on the search efforts that

55   produced a set of historic sighting events could provide important additional

56   information in determining whether species is extant or extinct. Whilst in the majority

57   of instances these data are unlikely to be available, in some circumstances active and

58   systematic searches for particular species are conducted to determine population size,

59   or to definitively classify a species as extant or extinct (e.g. Turvey et al. 2007). Such

60   scenarios can provide information in addition to simple presence/absence data. This

61   potentially important additional information is disregarded by many estimators of

62   extinction (Solow 1993b, 2005; Roberts & Solow 2003).

63   Recently, in an attempt to overcome this issue, a Bayesian approach has been

64   proposed that explicitly accounts for the effort invested in producing sighting events,

65   as well as implicitly taking into account the detectability of a species (Thompson et al.

66   2013). Such a method might significantly improve attempts to classify a species as

67   extant or extinct, if data are available to parameterize it. However, as with many

68   traditional parametric and non-parametric based methods, testing the performance of

69   these techniques for inferring extinction remains limited (Clements et al. 2013).

70   Here we tackle this problem by using data generated in highly controlled, small-

71   scale experimental systems (shown to provide realistic sets of historic sighting events

72 (Clements et al. 2014)), and simulated population declines, to test the reliability of a

73 proposed Bayesian method for estimating extinction status (Thompson et al. 2013).

74 We simulate a range of search efforts, and species detectabilities, to produce sets of

75 historic sighting events (as proposed in Clements *et al.* 2013). We then assess whether

76 the method of Thompson *et al*. (2013) performs better than a Bayesian method for

77 inferring extinction that does not incorporate search effort (Solow 1993a), and how

78 robust the method is to varying search efforts, and levels of detectability, and values

79 of the prior.

80

81 **Methods**

82 *Model details*

83   A common Bayesian method used to infer extinction is that of Solow (1993a).

84 Solow's method is straightforward to use, where the likelihoods are easily generated

85 from the time of the last sighting (T_N), the total number of time periods (T, usually in

86 years) and the total number of sightings (S). However, the method only considers one

87 record of certain sightings. Thompson et al. (2013) built upon Solow's method to

88 allow parallel sighting records that may include uncertain sightings (for example

89 sightings that cannot be verified, or poor quality photographs) or records of survey

90 effort. For simplicity, we use point estimates for the prior (and therefore a point

91 estimate of extinction generated by the model, rather than a distribution of

92 probabilities) and detectability, and no uncertain sightings. The model does, however,

93 allow for uncertainty around the prior and detectability estimates. The model requires

94 at least one sighting record, which is a vector of ones and zeros, with each element of

95 the vector corresponding to a particular time period. When at least one observation

96 occurred during a sighting period, the corresponding sighting record element is a one,

97 whereas zero denotes no observation. The model can include parallel sighting records

98   denoting uncertain sightings but this is not needed here. Similar methods which use

99   parallel sighting records to include uncertain records, such as those of Solow et al.

100   (2011) and Lee et al (2014), require the sighting record to comprise of zeros and ones

101   only. However, when including a sighting record for survey effort, there may be a

102   successful survey, an unsuccessful survey, or no survey. To include search effort,

103   Thompson et al. (2013) devised the first method that can allow a parallel sighting

104   record comprising of ones, zeros, and NAs (to represent years where no survey effort

105   occurred). Here we use two sighting records, one record to denote certain sightings,

106   and a second to denote whether a survey was conducted (Table 1). For this

107   experiment – sightings can only occur during a survey, but in reality a sighting could

108   occur without a survey (e.g. from a random event such as roadkill).

109   To account for (i) the detectability of the species and (ii) the proportion of area

110   surveyed, we define probabilities of observing the species at given point in time under

111   the two different records (Table 1). We infer detectability (d_i) as $d_i = d = S/T_N$,

112   where S is the total number of observations and T_N is the time of the last sighting (that

113   is, extinction could not have occurred before T_N), as suggested by Thompson et al.

114   (2013). Note that in cases of high detectability $d \approx 1$. The proportion of an area

115   surveyed at time interval t_i is $\tilde{d}_i$. Thompson et al. (2013) use the detectability d and

116   proportion surveyed $\tilde{d}_i$ to determine the likelihoods defined by Bayes theorem. For

117   simplicity we present only the results based on the microcosm data; the results from

118   simulations run with the modelled population declines are presented in the

119   supplementary information (appendix S1).

120

121   *Creating sighting events*

122   We simulated sighting data by sampling from the abundance time series from five

123 replicate populations of the ciliate *Paramecium caudatum* that went extinct in a

124 micrcocosm study (Fig. 1a; Clements *et al.* 2013), and 10 simulated populations that

125 declined at varying rates (Fig. 1b, Appendix S1). The experimental data were selected

126 as they provided a long (~100 generations) time series of abundance (and therefore

127 potential sighting events, whilst the simulated data provided very different population

128 decline trajectories (Fig. 1b). Details on the experimental setup and sampling method

129 can be found in Clements *et al.* (2013), whilst details on the modelled population

130 declines can be found in the supplementary information (appendix S1).

131   To create sighting events from the experimental abundance data (times at which

132 sightings of an extant individual occurred) we applied four different regimes of search

133 effort (the proportion of the habitat searched): (i) constant, (ii) increasing, (iii)

134 decreasing, (iv) random. The "constant" search regime was simulated with search

135 efforts (proportion of the habitat searched) from 0.05 to 0.95, in 0.01 steps. For

136 "increasing" search efforts, the initial effort was randomly assigned (between 0.05

137 and 0.95), and then the search effort increased by a random fraction at each

138 subsequent time step, until the search effort reached 0.95. "Decreasing" mirrored

139 "increasing", but the fraction of the habitat searched decreased over time. The

140 "random" search regime had the search effort at each time step drawn from a uniform

141 distribution between 0.05 and 0.95.

142   The number of individuals observed at each time interval was calculated from a

143 binomial distribution, where the probability of an observation is defined as the search

144 effort multiplied by detectability. For example with a population of 100 individuals, a

145 detectability of 0.1 and a search effort of 0.1, on average there would be one

146 individual observed.

147   We used the models proposed by Thompson *et al.* (2013) and Solow (1993b) to

148 estimate the probability that the species remained extant at each time step for 350

149 days after the last sighting event, which were then normalized by subtracting the

150 observed date of extinction. Normalized extinction times were calculated for each of

151 the scenarios with different search regimes and detection probabilities. We present

152 detailed results from simulations with a constant search regime. Results of increasing,

153 decreasing, and random search regimes, and results of simulations using the model's

154 population declines are in the supplementary information (Appendices S1, S2). All

155 simulations and analyses were carried out using the R statistical software (R

156 Development Core Team 2013).

157

158 **Results**

159 *Constant search regime*

160   The estimated probability that a species was extant produced by both models was

161 altered by the amount of the habitat searched (search effort), and also the detectability

162 of the species (Fig. 2). At high search efforts, Thompson et al.'s model tended to be

163 pessimistic, and in the majority of cases predicted the species to have a very low

164 probability of persisting prior to the actual extinction event occurring, a pattern

165 enhanced when detectability was low (Fig. 2, 3). When search efforts were low

166 Thompson et al.'s model suggested that the species was likely to still be extant, even

167 after extinction had occurred (Fig. 2). The detectability of the species shifted the

168 distribution of probabilities that that species was extant, with lower detectabilities

169 producing lower probabilities, and higher detectabilities producing higher

170 probabilities (Fig. 3). However, regardless of detectability the model produced low

171 estimates of probability after the species went extinct (Fig. 3).

172   Solow's model showed the opposite pattern; high search efforts produce

173 optimistic estimates of the species surviving, and low search efforts suggested

174 extinction had occurred before it had (Fig. 2). Overall, the model tended to be overly

175 optimistic about a species persisting (Fig. 3).

176   Altering the value of the prior expectation that this species was extant had a large

177 impact on the distribution of inferred probabilities that the species was still extant

178 (Fig. 4). The Thomson et al. model was overly pessimistic when the prior was set at

179 0.1, and overly optimistic when the prior was 0.9. A prior of 0.5 provided a balance

180 between optimism and pessimism, and thus the most reasonable inferences of a

181 species persisting (Fig. 4). The value of the prior had less of an effect on the Solow

182 model, with, in general, the model providing overly optimistic estimates of a species

183 persisting regardless of the prior (Fig. 4). The most accurate estimates produced by

184 the Solow model were made with a prior of 0.1 (Fig. 4).

185   Results produced using the simulated population declines showed almost

186 identical results to those produced using data from the microcosm experiments

187 (appendix S1).

188

189 *Other search regimes*

190   As well as the constant search regime, the model was tested with decreasing,

191 increasing, and random search regimes (Appendix S2). At high detectabilities the

192 model performed well across the different search regimes, although with a decreasing

193 search regime the estimates were often overly optimistic, but low detectability

194 typically meant that the method suggested the species was extinct significantly earlier

195 than observed (Appendix S2).

196

197 **Discussion**

198   Accurately inferring extinction status, and consequently the current rates of

199 biodiversity loss, has been a key goal for conservation biology for many years. Many

200 methods have been proposed to tackle this issue, but until recently these have not

201 explicitly incorporated search effort (Thompson *et al.* 2013). Our results suggest that

202 this recently proposed method for inferring extinction status generally performs better

203 than a similar Bayesian based method that does not incorporate search effort (Solow

204 1993a), although the accuracy of the method depends on both historic survey effort

205 and the detectability of a species, as well as the value of the prior belief that the

206 species is still extant.

207   The amount of a habitat searched to produce historic sighting events, as well as

208 how this search effort has changed through time, are both known to significantly alter

209 how accurately we can infer the extinction status of a species (Clements *et al.* 2013).

210 Thompson *et al.* noted that Solow's method is a specific case of their method: the case

211 when search effort is constant and perfect; our observations for regular sampling

212 demonstrated this statement. That is, as the proportion searched tends to 100%, the

213 method of Thompson *et al.* converges to the method of Solow (which does not

214 incorporate different search efforts). We show that explicitly taking into account

215 historic search efforts reduces the uncertainty in declaring a species as extinct (Fig. 3),

216 producing more reasonable estimates of whether a species persists compared with not

217 incorporating search effort (Fig. 2, 3). However, changes to historic search effort can

218 still drive significant error (Appendix S2). Ideally, once search effort has been

219 explicitly incorporated into a model, search regime should have no effect on the

220 probability of the inferred date of extinction, but this is clearly not the case (Fig. 2,

221 Appendix S2). As with other methods for inferring extinction status (e.g. Clements *et*

222 *al.* 2013), search effort (particularly when it has declined through time) drives

223 significant error. However, the model performs well when search efforts are high

224 (Fig. 2).

225   Two other factors significantly affect the accuracy of this method: the

226   detectability of the species and the value of the prior used (Fig. 2, 3, 4). Of these two

227   factors only the value of the prior can be controlled. Consequently, choosing an

228   informative value for the prior is a prime concern when applying Thompson et al.'s

229   model (Fig. 4). In reality, determining a reliable value for the prior will be difficult.

230   Thompson et al.'s method does allow for uncertainty surrounding the prior probability

231   of persistence, which, instead of a point estimate of extinction (as generated in this

232   paper), would produce a probability distribution around the date of extinction. Whilst

233   the results presented here serve to test how well this model performs, using a

234   distribution of priors is likely to be more suitable in real-world scenarios where the

235   value of the prior is unknown. For inferring extinction in real-world instances, an

236   expert may provide a prior based on information such as available habitat and food

237   source. Nonetheless, in our analyses, a prior of approximately 0.5 appeared suitable.

238   Whilst the value of the prior given to the model is controllable, the inherent

239   detectability of species is not. Detectability has been shown, for example in birds, to

240   vary with habitat, species, survey quality, and observer ability (Boulinier et al. 1998).

241   Detectability can also change as a function of population size (McCarthy et al. 2013).

242   2013), which can be compounded by behavioral changes as a population gets smaller

243   (e.g. conspecific attraction may increase as population's numbers decline (Stephens &

244   Sutherland 1999)). Thompson et al.'s method tends to underestimate the probability

245   of persistence, which is exacerbated when the species' detectability is low (Fig. 3).

246   After the species has gone extinct the model is robust to various levels of

247   detectability, in almost all cases predicting the species has a low chance of persisting

248   (Fig. 3). Consequently, we suggest future models should seek to concentrate on

249   reliably incorporating the detectability of species, to produce less pessimistic

250   estimates of the probability of a species persisting prior to extinction.

251   In conclusion, we present the first test of a newly proposed method for inferring

252   extinction when historic search effort is known (Thompson *et al.* 2013). We

253   demonstrate that, while this method in general produces reasonable predictions of

254   whether a population is extant or extinct, other factors (specifically the value of the

255   prior and the detectability of the species, but also search regime) may drive significant

256   errors. However, this method is a marked improvement on similar methods that do not

257   explicitly incorporate historic search efforts, and in scenarios where such data are

258   available, the method proposed by Thompson et al. (2013) should be employed.

259

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References

266 Boulinier, T., J. D. Nichols, J. E. Hines, J. R. Sauer, and K. H. Pollock. 1998. Estimating species
267   richness: The importance of heterogeneity in species detectability. Ecology **79**:1018–1028.
268 Clements, C. F., B. Collen, T. M. Blackburn, and O. L. Petchey. 2014. Effects of Recent environmental
269   change on accuracy of inferences of extinction status. Conservation Biology **28**:971–981.
270 Clements, C. F., N. Worsfold, P. Warren, B. Collen, T. Blackburn, N. Clark, and O. L. Petchey. 2013.
271   Experimentally testing an extinction estimator: Solow's Optimal Linear Estimation model.
272   Journal of Animal Ecology **82**:345–354.
273 Gotelli, N. J., A. Chao, R. K. Colwell, W.-H. Hwang, and G. R. Graves. 2011. Specimen-based
274   modeling, stopping rules, and the extinction of the Ivory-Billed Woodpecker. Conservation
275   Biology **26**:47–56.
276 Keith, D. A., and M. A. Burgman. 2004. The Lazarus effect: can the dynamics of extinct species lists
277   tell us anything about the status of biodiversity? Biological Conservation **117**:41–48.
278 Lee, T. E., M. a. McCarthy, B. a. Wintle, M. Bode, D. L. Roberts, and M. a. Burgman. 2014. Inferring
279   extinctions from sighting records of variable reliability. Journal of Applied Ecology **51**:251–258.
280 McCarthy, M. A. 1998. Identifying declining and threatened species with museum data. Biological
281   Conservation **83**:9–17. Elsevier.
282 McCarthy, M. A. et al. 2013. The influence of abundance on detectability. Oikos **122**:717–726.
283 Roberts, D. L., and A. R. Solow. 2003. Flightless birds: When did the dodo become extinct? Nature
284   **426**:245.
285 Solow. 1993a. Inferring extinction from sighting data. Ecology **74**:962–964. JSTOR.
286 Solow. 2005. Inferring extinction from a sighting record. Mathematical Biosciences **195**:47–55.

287   Solow, A. R. 1993b. Inferring extinction in a declining population. Journal of Mathematical Biology
288   **32**:79–82. Springer.
289   Solow, A., W. Smith, M. Burgman, T. Rout, B. Wintle, and D. Roberts. 2011. Uncertain Sightings and
290   the Extinction of the Ivory-Billed Woodpecker. Conservation Biology **26**:180–184.
291   Thompson, C. J., T. E. Lee, L. Stone, M. a McCarthy, and M. a Burgman. 2013. Inferring extinction
292   risks from sighting records. Journal of theoretical biology **338C**:16–22. Elsevier.
293   Turvey, S. T. et al. 2007. First human-caused extinction of a cetacean species? Biology Letters **3**:537–
294   540. The Royal Society.
295

Table 1: An example of the sighting records, where one denotes an observation and zero denotes no observation. In reality, sightings can occur during a non-surveyed time period.

Time	Certain sighting $\underline{s}$	Survey $\underline{\tilde{s}}$	Detectability	Search effort
1	1	1	0.1	0.1
2	0	1	0.1	0.3
3	0	0	0.1	0
$\vdots$	$\vdots$	$\vdots$	$\vdots$	$\vdots$
t_i	s_i	$\tilde{s}_i$	$P(s_i = \|X_i)$	$P(\widetilde{s_i} = \|X_i)$
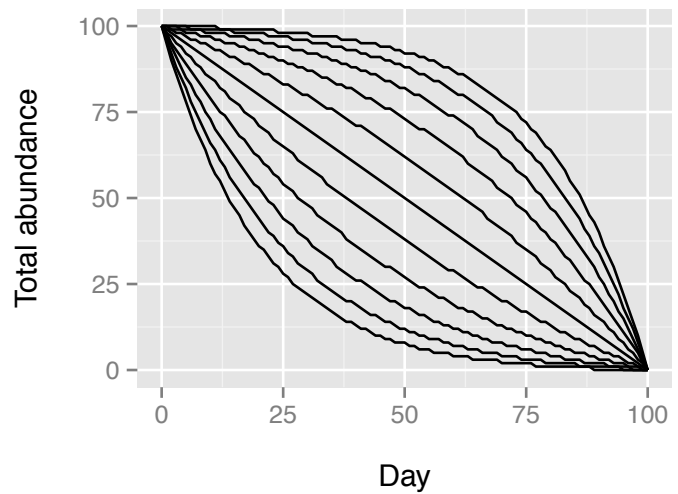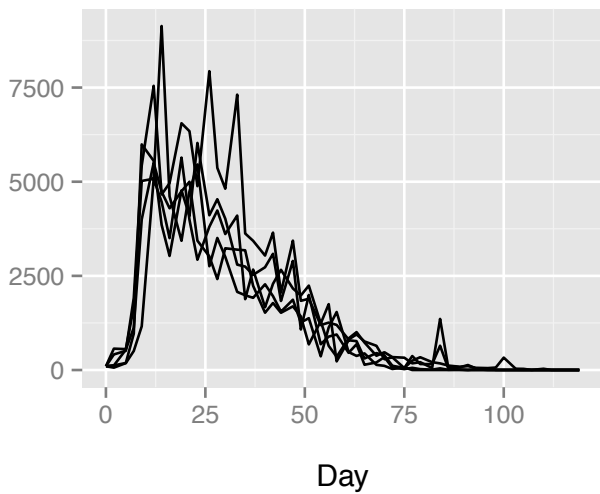
Figure 1. Population dynamics of the five replicate of *Paramecium caudatum*, and turn simulated population declines, to which the search effort and detectability simulations were applied.
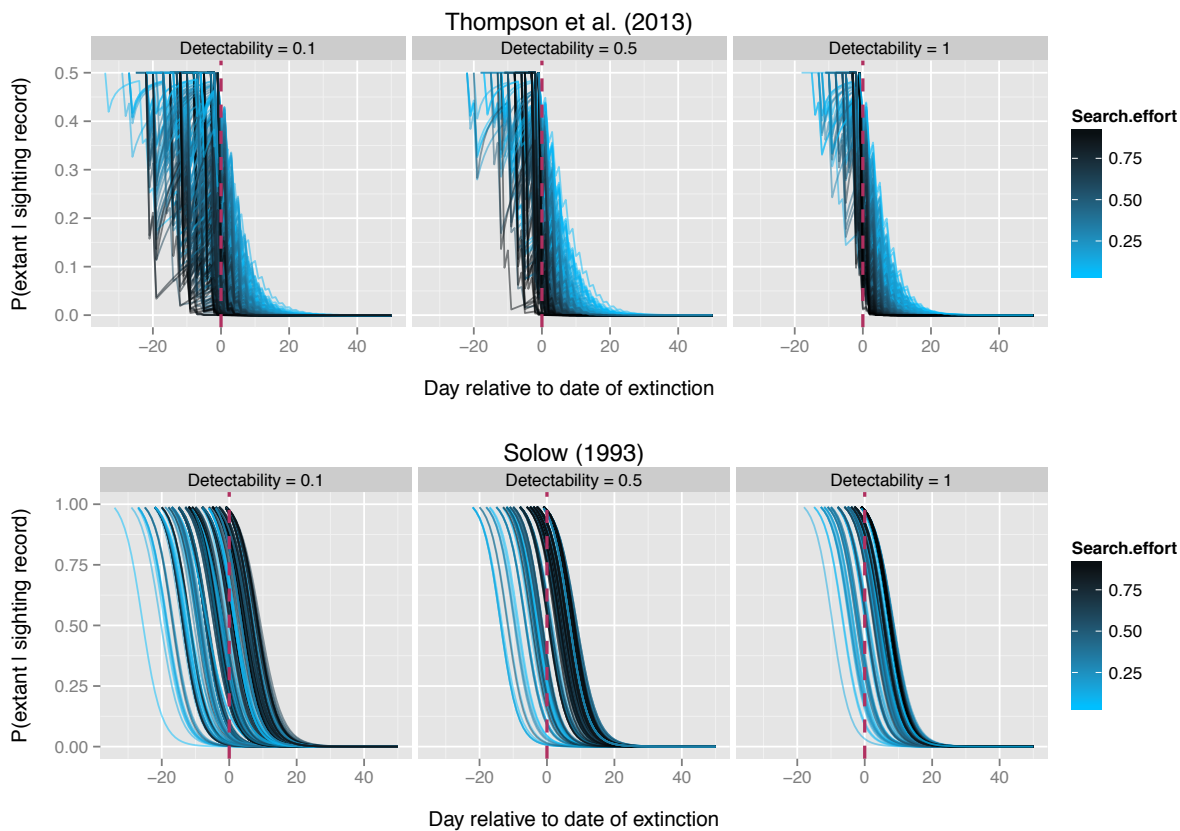
Figure 2. Probability of persistence at each time point when search effort is constant, and across 3 levels of detectability, with the prior set at 0.5. Probabilities of persistence are only calculated after the final sighting event. Because the different replicates went extinct at different points in time, days are normalised by subtracting the observed date of extinction of each of the replicates from the time steps at which probability of extinction was estimated. Red vertical line highlights the observed date of extinction. P values may increase because when there is no searching at a given time point, the model assumes the probability of persistence returns to the prior assumption that a species is extant (1-prior).
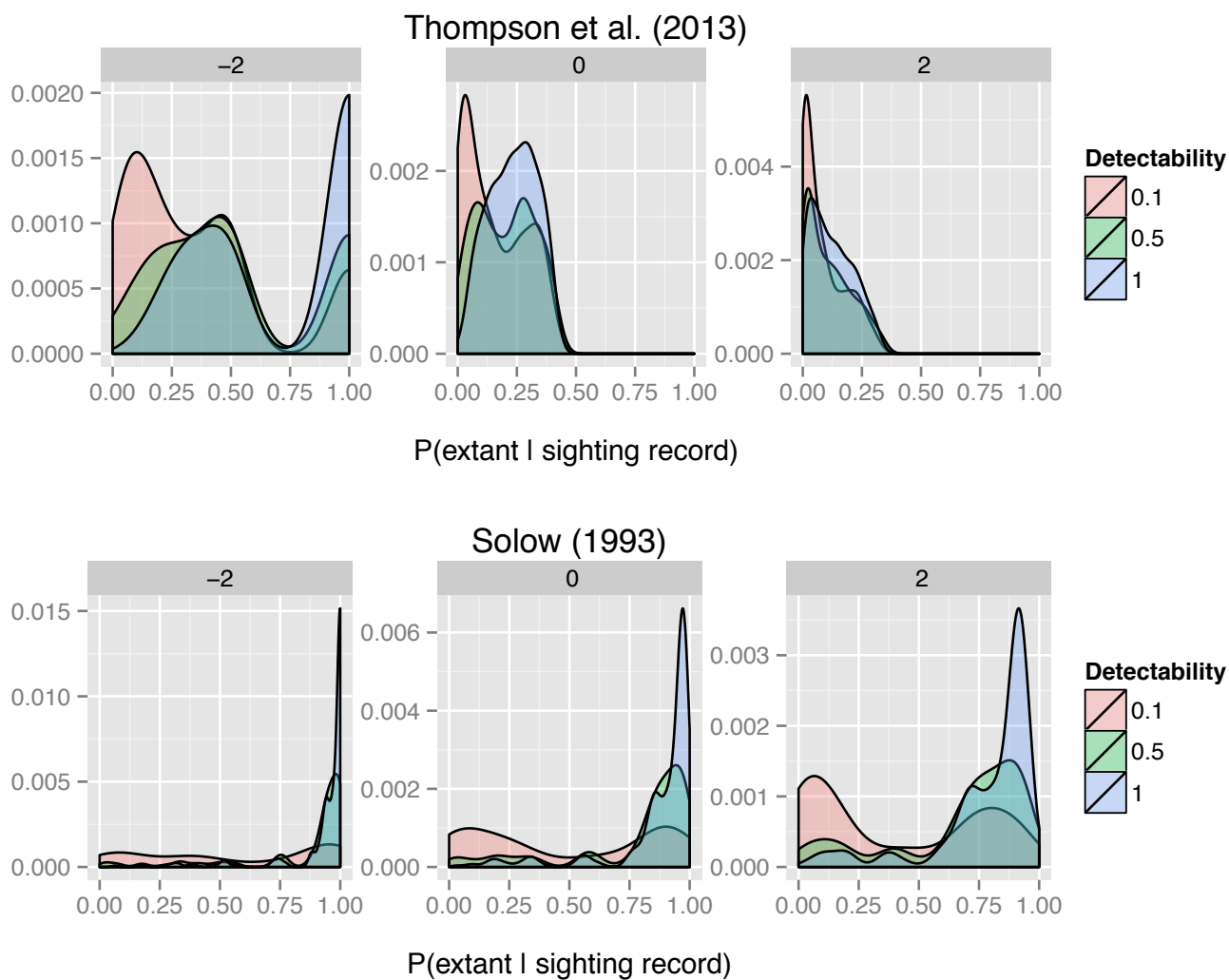
Figure 3. Distribution of probabilities of persistence produced by Thompson et al. (2013)'s method and Solow (1993)'s across the three detectability levels at two days prior to extinction (day -2, the last day the microcosms were sampled), the day of extinction (day 0, the first day the species was observed as extinct), and two days after extinction (day 2). Data shown is for constant search efforts with a prior of 0.5. P values of 1 indicate a species has been observed as extant.
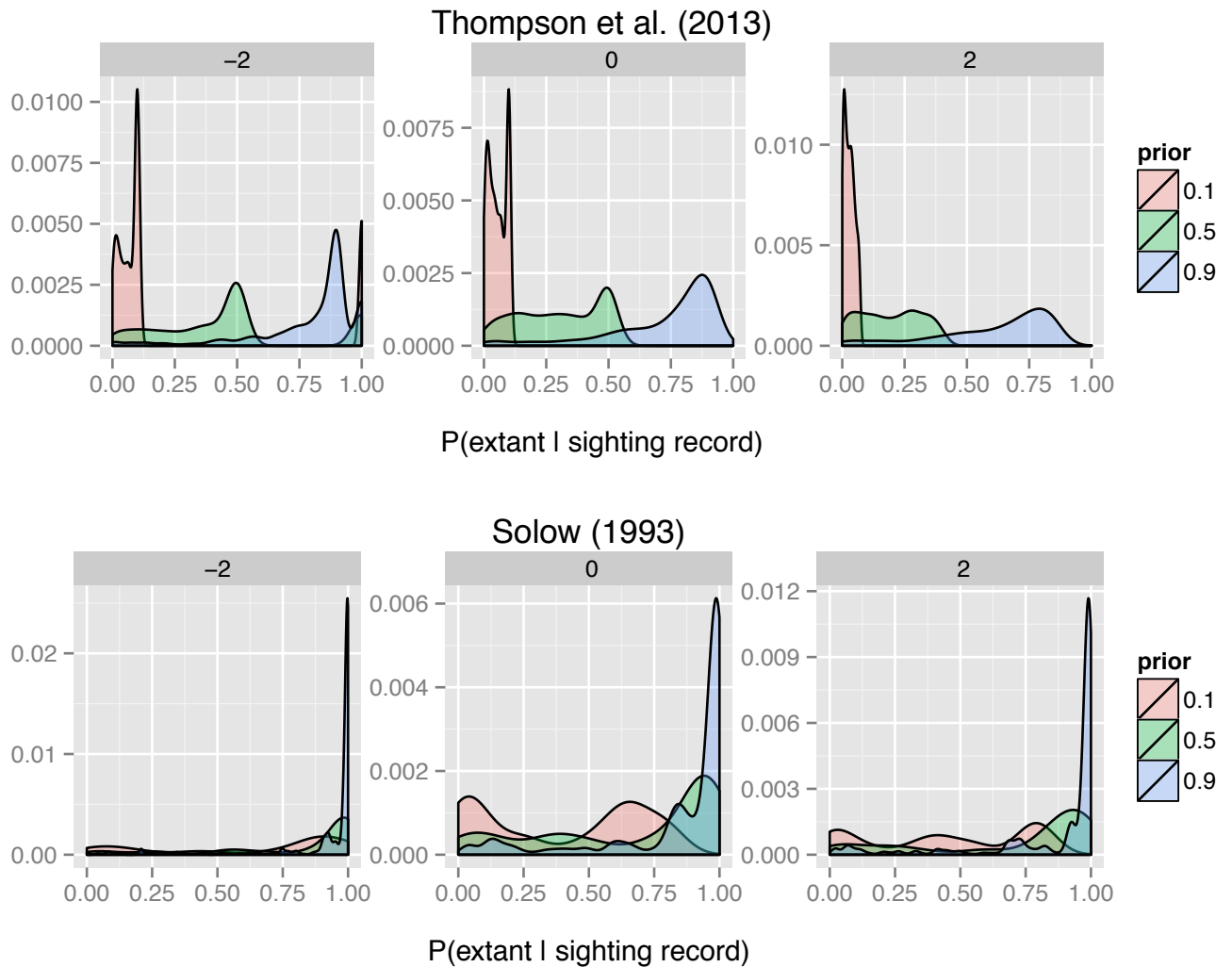
Figure 4. Distribution of probabilities of persistence produced by Thompson et al. (2013)'s method and Solow (1993)'s across the three prior values at two days prior to extinction (day -2, the last day the microcosms were sampled), the day of extinction (day 0, the first day the species was observed as extinct), and two days after extinction (day 2). Data shown is for constant search effort with all three levels of detectability Included (0.1, 0.5, 1). P values of 1 indicate a species has been observed as extant.