1 **Title (a maximum of 20 words)**

2 Examining the bias of pitfall traps with enclosure experiments and removal sampling

3

4 **Running title (a maximum of 40 characters including spaces)**

5 Bias of pitfall traps

6

7 **Abstract (249/250 words)**

8 1. Pitfall trapping is among the most widely used sampling methods for ground-

9   dwelling beetles. However, the sampled ground-dwelling beetle abundance in

10   pitfall traps may be biased, which can lead to difficulties when comparing the

11   sampled abundance between different habitats.

12 2. To better understand the comparability of the sampled abundance, we focused on

13   two sampling processes: a temporary migration process (referring to the individual

14   movements into and out of the effective trap area) and a removal process

15   (determining the number of individuals collected given the number of individuals

16   within the trap area).

17 3. To examine the effects of the temporary migration process, we compared the

18   sampled abundance of ten ground-dwelling beetle species inside and outside

19   enclosures in two habitats (clear-cut and forested sites) and found that installing the

20   enclosure decreased the sampled abundance in both habitats, but the effects did not

21   differ among habitats.

22 4. To examine the effects of the removal process, we examined the effects of daily soil

23   temperature on the daily sampled abundance (removal probability) of *Pterostichus*

24   *thunbergi* using removal sampling within enclosures. We found that soil

25   temperature increased the removal probability, but this effect was limited and not

26   consistent across survey periods.

27   5.   The results suggest that the effects of the temporary migration process may not be

28   habitat dependent and that the effects of the removal process may be small.

29   Therefore, the traditional use of pitfall traps is, to some extent, a robust and

30   comparable measure of the sampled abundance of ground-dwelling beetles among

31   different habitats.

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36

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52   5551 Words (abstract: 249, references: 1345)

53   (Max 7000 words without Abstract and References - Insect Conservation and Diversity)

54

Introduction

55

56   Pitfall trapping is one of the most widely used techniques for ground

57 invertebrate sampling (Woodcock 2005; Henderson & Southwood 2016). As such,

58 pitfall trap sampling has been used in various studies of ground-dwelling beetles,

59 including the examination of their regional community and habitat preferences (e.g.,

60 Niemela & Halme 1992; Jouveau *et al.* 2019) and the anthropogenic impact on this

61 group (e.g., Koivula *et al.* 2019; Yamanaka *et al.* 2021). However, the abundance

62 sampled using pitfall traps is determined through the sampling process, which is

63 influenced by several factors, including the sampling design and targeted site- and

64 species-specific characteristics. Sampled abundance, therefore, does not equal the "true"

65 abundance existing in a certain area during an arbitrary time period (hereafter, initial

66 abundance; see Table 1 for glossary), and it should be interpreted with caution when

67 comparing sampled abundance among different sampling designs and sites and periods

68 with different environmental conditions (Adis 1979; Lang 2000; Woodcock 2005). For

69 example, if the catchability of pitfall traps differs greatly between sampling designs,

70 sites, or periods, the sampled abundance will be determined by the differences in the

71 catchability rather than differences in the initial abundance, making it difficult to infer

72 differences in the initial abundance between sites and periods.

73   The factors influencing the catchability of pitfall traps can be divided into two

74 groups: (1) sampling design and (2) site- and species-specific characteristics that affect

75 the movement activity of target species. There have been many studies on the effects of

76 sampling design on catchability, for example, trap design (Luff 1975; Koivula *et al.*

77 2003), preservation liquid types (Koivula *et al.* 2003), the number and arrangement of

78 traps installed (Lövei & Magura 2011; Engel *et al.* 2017), and the sampling period

79 (Schirmel *et al.* 2010; Lövei & Magura 2011). The differences in the sampling design

80 can lead to differences in the sampled abundance even if the initial abundance is the

81 same between sites. However, this problem can be addressed by using the same

82 sampling method across target sites, that is, by disseminating a standard design (Brown

83 & Matthews 2016).

84   For factors influencing catchability through changes in the movement activity

85 of ground-dwelling beetles, there are extrinsic factors, such as temperature (Honek

86 1988; Engel *et al.* 2017), vegetation complexity (Honek 1988; Lang 2000; Koivula *et*

87 *al.* 2003), and soil disturbances (e.g., digging-in effects; Schirmel *et al.* 2010). In

88 addition, there are intrinsic factors, such as body size (Lang 2000; Engel *et al.* 2017),

89 habitat preferences (Koivula *et al.* 2003; Růžičková *et al.* 2021), seasonal

90 abundance/behavior changes (Baars 1979), and the hunger level of individuals (Raworth

91 & Choi 2001). The influence of these factors can be expected to vary widely among

92 target sites and species. Therefore, it is difficult to control differences in sampled

93 abundance caused by changes in movement activity, which can become a serious

94 problem, particularly when comparing the sampled abundance between different sites

95 and/or periods. For example, even if the initial abundance is the same in two habitats,

96 such as forest and grassland, the sampled abundance may be different between the

97 habitats if the movement activity is higher in one habitat than the other. Similarly,

98 differences in the movement activity may mask differences in the initial abundance even

99 if the abundance truly differs between the two habitats.

100   In this study, to better understand the influence of differences in the movement

101 activity of ground-dwelling beetles on the comparability of the sampled abundance, we

102 deconstruct the pitfall trap sampling process into two subprocesses, namely, (i)

103   temporary migration and (ii) removal processes (Iknayan *et al.* 2014; Yamaura & Royle

104   2017). The temporary migration process is defined as individual movement into and out

105   of the effective trap area. In this process, the movement activity increases/decreases the

106   number of individuals moving into/out of the trap area. Differences in the movement

107   activity between sites can lead to differences in the potential number of individuals who

108   can be caught by traps between sites. The removal process determines the number of

109   individuals collected based on the removal probability (Table 1) of the traps given the

110   number of individuals exposed to the sampling within the trapping area. In this process,

111   the movement activity increases/decreases the removal probability, and differences in

112   the movement activity between sites can change the sampled abundance of each site.

113   The purpose of this study is to address the two sampling processes (temporary

114   emigration and removal process) separately and examine whether sampled abundance

115   can be compared among different habitats. First, to examine the effect of the temporary

116   migration process on the sampled abundance, we installed enclosure fences (hereafter,

117   fences) preventing the emigration of ground-dwelling beetles into/out of the trapping

118   area and compared their sampled abundance among areas with and without fences and

119   different habitats (clear-cut and forested areas). We hypothesized that the fences prevent

120   individuals from moving into the effective trap areas, and thus, the sampled abundance

121   within fences decreases more than that without fences. We also examined whether the

122   fence effect differed between habitats. If the effect differs between habitats, the

123   comparison of sampled abundance may be difficult because initial abundances are likely

124   to differ between sites, even if the sampled abundances are the same. In fact, the

125   movement activity of ground-dwelling beetles can change depending on its habitat (e.g.,

126   Niemela & Halme 1992; Allema *et al.* 2015; Růžičková *et al.* 2021).

127   Second, to examine the effect of the removal sampling process on sampled

128   abundance, we conducted removal sampling within fences and examined the

129   relationships between daily removal probability and sampled abundance. By installing

130   fences, we excluded the effects of the temporary migration process on the sampled

131   abundance and focused on the removal process. In this study, we focused on the effect

132   of soil temperature on removal probability because temperature is one of the

133   fundamental factors determining insect activity (e.g., Messenger 1959). High

134   temperature can increase movement activity and sampled abundance of ground-

135   dwelling beetles (Honek 1988; Honek 1997; Raworth & Choi 2001; Saska *et al.* 2013),

136   and temperature is highly variable on a short time scale and is easy to monitor. If soil

137   temperature affects removal probability, it may be problematic because sampled

138   abundances would differ between sites and/or periods with different soil temperatures

139   even if initial abundances are the same. We hypothesized that a high daily soil

140   temperature increases the daily removal probability and indirectly increases the sampled

141   abundance on each sampling day.

142

143   **Materials and methods**

144   Study area and experimental design

145   The study area is in the Irumukeppu Mountain area of Hokkaido in northern

146   Japan (43°34'37" to 39'26"N, 142°05'27" to 09'33"E). The mean annual temperature

147   and precipitation in this area are 7.4°C and 1141.6 mm, respectively, according to the

148   data obtained from 1991 to 2020 by the Ashibetsu Observatory, which is the closest to

149   the study area (Japan Meteorological Agency 2021). This area is dominated by conifer

150   plantations, which mostly consist of Sakhalin fir (*Abies sachalinensis* [F. Schmidt]

151   Mast.). Harvesting significantly changes forest structure, including forest floor

152   vegetation and soil conditions, and these changes can affect the initial abundance of

153   each species and may change their movement activity. Therefore, we surveyed two

154   forest stands, a clear-cut plantation site and an unharvested plantation site (Figure 1a;

155   Appendix 1), to examine the effects of the two sampling processes on sampled

156   abundance. At the clear-cut site, a mature plantation of Sakhalin fir was last harvested in

157   2015; hence, three to four years had passed by the time of the survey. The unharvested

158   plantation site mainly consisted of mature Sakhalin fir, and its forest age is

159   approximately 55 years (Akashi *et al.* 2017).

160   We installed three fences with galvanized iron panels on each site (clear-cut

161   site: C1, C2, and C3; plantation site: P1, P2, and P3). The fences were established as a 5

162    $\times$ 5 m square with a height of 0.8 m above ground level, and their footings were buried

163   0.1 m deep under the surface (Figure 1b). We installed a grid of nine pitfall traps (3×3

164   traps) within each fence. Each pitfall trap consisted of a plastic cup with a diameter of

165   95 mm and a depth of 124 mm and contained 100% propylene glycol for preservation.

166   The distances among traps and between traps and the nearest fence were 1 m and 1.5 m,

167   respectively (Figure 1c). We also installed the same trap grid outside of the fences at

168   least 5 m away from each fence. In all, we set 12 grids (2 sites $\times$ 3 fences $\times$ 2 grids;

169   Figure 1a). Fences were installed in May 2018, and sampling was conducted four times

170   during the following 14 months (period 1 [from June 28 or 29 to July 5 or 6, 2018],

171   period 2 [from July 25 or 26 to August 1 or 2, 2018], period 3 [from June 21 to July 10,

172   2019], and period 4 [from July 31 to August 21, 2019]: Appendix 5). In each period, we

173   collected ground-dwelling beetles each day for seven days. In periods 3 and 4, we

174   conducted additional sampling after day seven. We collected samples on days 10, 12,

175 and 19 in period 3 and on days 14 and 21 in period 4 to examine the number of

176 individuals who could be collected beyond the formal 7-day sampling period. Before

177 each sampling period, we removed two of the panels, each 1.5 m in length, from two

178 sides of each fence and allowed ground-dwelling beetles to move in and out of the

179 fences to eliminate the effects of the fences on the initial abundance in each grid. In

180 2018 (periods 1 and 2) and 2019 (periods 3 and 4), there were 18 and 20 days between

181 the two sampling periods, respectively (Appendix 5).

182   To examine the soil temperature across sites and periods, we installed a

183 temperature data logger (Onset, HOBO UA-001-64) 1 cm underground at the center of

184 each fenced area. Then, to examine whether soil temperature is correlated with air

185 temperature, another type of temperature data logger (Onset, HOBO U23-004) with a

186 solar radiation shield (Onset, HOBO, RS3-B) was set to observe air temperature. The

187 logger was set in the corner of the fences 1 m above the ground surface to avoid the

188 lower airflow caused by fences. The loggers were set at fences C1, C2, P2, and P3 in

189 periods 1 and 2; C2, C3, P1, P2, and P3 in period 3; and C2, C3, P1, and P2 in period 4.

190   We identified the species in the collected samples based on the work of Ueno *et*

191 *al.* (1985) and counted the number of individuals of each species collected on each

192 sampling day and at each grid. In this study, we categorized each species as a

193 macropterous, apterous, or brachypterous species by checking their wing types

194 according to Shibuya *et al.* (2018) and used only apterous and brachypterous species

195 (species having no, very short, or rudimentary wings) in the analysis. This is because

196 our fences had no roof, and we could not exclude the possibility of movement of

197 individuals in species that can fly over fences.

198

199   Data Analysis

200   Effects of the temporary migration process on sampled abundance

201   To examine the effects of the temporary migration process (i.e., installing

202   fences) on the sampled abundance of pitfall traps, we examined whether the sampled

203   abundance of ground-dwelling beetle species differed between areas with and without

204   fences and whether the effect of fences differed between the two habitats. Here, we

205   constructed abundance-based hierarchical community models (HCMs) according to the

206   method of Yamaura *et al.* (2016). HCMs can be used to estimate multiple hierarchical

207   parameters, allowing for simultaneous estimation of both community-level responses

208   (common responses of targeted species) and species-level responses.

209   In this analysis, we focused on ten ground-dwelling beetles (nine carabid

210   species and one carrion species: see Results section). For the HCMs, we pooled the

211   sampled abundance for each species from the whole period (7 sampling days $\times$ 4

212   periods) and used the total sampled abundance of each species as response variables

213   following a negative binomial distribution. As explanatory variables for the species-

214   level response variables, we used habitat type (binary variable where 0 denotes clear-cut

215   and 1 denotes plantation), installed fence (binary variable where 0 denotes absent and 1

216   denotes present), and the interaction of the habitat type and installed fence variables. We

217   also considered the log-transformed number of valid traps as an offset term because

218   several traps without fences were disturbed by mammals. In addition, for the intercept

219   and coefficients of each species, we set hyperparameters that were shared by species

220   parameters to estimate species- and community-level responses (see details in Appendix

221   2).

222   To build the HCMs, we used R version 4.0.5 (R Core Team 2021) and the R

package "RStan" version 2.21.2 (Stan Development Team 2020). For the model, we used four chains that had 20,000 iterations following 5,000 burn-in with 20 thinning rate. We used the "R-hat" and "N_eff/N" statistics (R-hat < 1.1 and N_eff/N > 0.1) to assess the convergence of the model according to Gabry and Modrák (2019).

Effects of the removal process on sampled abundance

Removal sampling is a method in which individuals are sequentially removed from a population to estimate population size, assuming that if the population is closed and the removal probability remains at a certain level, the number of individuals removed during each sampling event will gradually decrease. While classic removal sampling models assume that the probability is constant over a given period and/or across different sampling sites (Rodriguez de Rivera & McCrea 2021), recently, several models have been presented that can take into account the changes in removal probability with site-dependent factors (Kéry & Royle 2015; Kellner *et al.* 2022).

To examine the effects of the removal process (i.e., the changes in the removal probability) on the sampled abundance, we examined whether the daily soil temperature increases the daily removal probability using "unmarked" removal sampling models (Fiske & Chandler 2011). In the analysis, we focused on the most dominant species, *Pterostichus thunbergi*. We used the daily number of individuals collected within the fences during the four survey periods consisting of seven continuous sampling days. We used two types of data: (1) the whole period data, which covered the four survey periods, and (2) each period data, which included data from each survey period because the effects of soil temperature may differ across survey periods, i.e., we built four separate models for the four periods.

247   In the `unmarked` models, we used the daily number of individuals collected

248   as the response variable, assuming a negative binomial distribution, and categorical

249   habitat type (clear-cut vs. unharvested plantation) and standardized daily mean soil

250   temperature as explanatory variables for initial abundance and removal probability,

251   respectively. That is, the models assumed that the initial abundance of each grid was

252   determined by habitat type and that the daily removal probability (and the daily number

253   of individuals collected) depended on daily soil temperature. For the construction of the

254   models, we used the "`gmultmix`" function in the R package "`unmarked`" (Fiske &

255   Chandler 2011). We compared (1) the effects of soil temperature on removal probability

256   across survey periods, (2) the estimated removal probability across survey periods, and

257   (3) the initial abundance across survey periods and between habitat types.

258   Several removal sampling models have been presented in addition to the

259   `unmarked` models, including `ubms` models (Kellner *et al.* 2022). Therefore, we

260   additionally constructed several models, including the classic models that assume the

261   removal probability remains constant across survey sites and periods, with different

262   model-fitting methods and/or different distributions that were followed by response

263   variables (`unmarked` Poisson, `ubms`, and `Rstan` models; Appendix 3). We compared

264   the results with those of the abovementioned `unmarked` models.

265   Moreover, we constructed generalized linear models (GLMs) that assumed that

266   the response variables follow a negative binomial distribution. In the models, we used

267   the total sampled abundance of *P. thunbergi* in each period and at each grid as response

268   variables and habitat type as explanatory variables. Unlike the abovementioned

269   `unmarked` models, the GLMs do not account for the removal process, and therefore,

270   the abundance estimates would include the bias caused by the removal process. We

271 compared the effects of habitat type on the abundance estimates between GLMs and the

272 `unmarked` models to examine whether potential bias can impede the comparison of

273 abundance estimates between different habitats. If the effects of habitat type on the

274 abundance estimates were consistent between the GLMs and `unmarked` models, we

275 would interpret this as evidence that models that do not account for the removal process

276 could be used to obtain differences in the initial abundance between habitat types. For

277 the GLMs, the "`glm.nb`" function of the R package MASS was used.

278   To build the removal sampling models and GLMs, we used R version 4.0.5 (R

279 Core Team 2021). In all analyses, we used the 95% confidence interval or credible

280 interval (which is used in the Bayesian approach instead of a confidence interval) to

281 judge whether each variable was significant (hereafter, 95% CI). When the 95% CI of

282 the coefficient of each variable or estimated value did not contain 0, we considered the

283 variables to be significant.

284

Results

285
286   We collected a total of 606 individuals, consisting of ten apterous and

287   brachypterous ground-dwelling beetle species (nine forest species and one nonforest

288   species; Table 2), in four survey periods composed of seven continuous sampling days

289   (not including extended surveys in periods 3 and 4). We collected 203 individuals of the

290   most dominant species, *Pterostichus thunbergi*, within fences in four survey periods

291   composed of seven continuous sampling days. We collected 111, 25, 33, and 34

292   individuals of *P. thunbergi* in period 1, period 2, period 3, and period 4, respectively

293   (Appendix 4). Extension sampling in periods 3 and 4 collected an additional 5 and 42

294   individuals of *P. thunbergi*, respectively (Appendix 4). The daily mean values of soil

295   temperature were relatively higher in the clear-cut site than in the unharvested

296   plantation site, and the daily air temperature of each grid exhibited a trend similar to that

297   of soil temperature (Appendix 5).

298

299   Effects of the temporary migration process on sampled abundance

300   We constructed HCMs using the sampled abundance of ten species (Table 2).

301   For community-level hyperparameters, the coefficient of fence was significantly

302   negative, and the 95% CI of the coefficients of habitat type and the interaction between

303   habitat type and fences included zero (Figure 2). This suggested that, as the average

304   response, the sampled abundance did not differ between habitat types but decreased

305   within fences and that the fence effect did not differ between habitat types. At the

306   species level, the coefficients of habitat type and fences varied among species. The

307   sampled abundance of four species significantly differed between habitat types.

308   Specifically, the abundance of *Carabus blaptoides rugipennis* (SP2) and *Xestagonum*

309   *daisetsuzanus* (SP10) was higher in the unharvested plantation site, while the abundance

310   of *Carabus arcensis hokkaidoensis* (SP1) and *Pterostichus microcephalus* (SP6) was

311   higher in the clear-cut site (Figure 2). The coefficients of fences were significantly

312   negative for four species (*C. arcensis hokkaidoensi* [SP1], *Cychrus morawitzi morawitzi*

313   [SP5], *Pterostichus orientalis antiquus* [SP7], and *Silpha perforata* [SP9]; Figure 2).

314   Similar to the hyperparameter, the interaction term for habitat type and fences was not

315   significant for any species (Figure 2). In addition, there was no apparent relationship

316   between the coefficients of fences and the body size of each species (Appendix 6).

317

318   Effects of the removal process on sampled abundance

319   The estimated coefficients of removal sampling models were similar among the

320   different model-fitting methods and the model with a different distribution (Appendix

321   7). In addition, in periods 3 and 4, the mean values and ranges of most coefficients were

322   overly high and wide, respectively (Figure 3c and Appendix 7), indicating that the

323   models in these periods could not estimate the removal probability and initial

324   abundance precisely.

325   In `unmarked` models, positive effects of soil temperature on removal

326   probability were found only in period 1; that is, such positive effects were not observed

327   in other periods (Figure 3a). In addition, the estimated daily removal probability

328   differed among the survey periods (Figure 3b). During the whole period and during

329   periods 1 and 2, the daily removal probability was relatively high, and the range of

330   mean values was from 10 to 50% (Figure 3b). Conversely, the estimated probability was

331   overly low for periods 3 and 4, and the mean values were close to zero (Figure 3b). The

332   95% CI of the estimated initial abundance of *P. thunbergi* at clear-cut and plantation

333   sites overlapped in all periods (Figure 3c), suggesting that the initial abundance did not

334   differ between habitat types.

335   Comparing the effects of habitat types on the abundance estimate between

336   `unmarked` models and GLMs, in most cases, the effects were constant, that is, the

337   abundance estimates of *P. thunbergi* were slightly higher at the plantation site than at the

338   clear-cut site (Figure 3c). Thus, we concluded that the GLMs that do not account for the

339   removal process could also show the differences in the initial abundance between

340   habitat types. In addition, for the classic removal sampling models that do not account

341   for the daily changes in removal probability, the estimated coefficients did not largely

342   differ from those of `unmarked` models with the whole period data (Appendix 7). This

343   also suggests that the effect of the removal process (effect of soil temperature on

344   removal probability) was not substantial, especially when considered over the entire

345   survey period.

346

Discussion

Effects of the temporary migration process on sampled abundance

We found that the sampled abundance of ground-dwelling beetles in pitfall traps decreased within fences. This result is consistent with those of previous studies demonstrating that the movement of carabids into and out of effective trap areas (i.e., the temporary migration process) can increase their sampled abundance (Desender & Maelfait 1986; Andersen 1995; Holland & Smith 1999). Furthermore, we did not find that the effects were dependent on habitat type. Therefore, it could be argued that the temporary migration process did not impede the comparison of the sampled abundance among different habitats.

In addition, the results presented above also suggest that the movement activity of each species did not differ between clear-cut and unharvested forests, although previous studies demonstrated that the movement activity of forest carabids was generally larger in open land than in woodland (Allema *et al.* 2015; Růžičková *et al.* 2021). At our clear-cut site, there was a high degree of logging residue (slash) (Appendix 1). Slash increases the microhabitat complexity of harvested areas, which potentially provides a hiding site for forest ground-dwelling beetles and thus could maintain the community composition (e.g., Gunnarsson *et al.* 2004; Nittérus *et al.* 2007). Therefore, harvested areas with plenty of slash could be a suitable habitat for forest ground-dwelling beetles compared to other open lands, such as arable lands, and this may result in the small difference in the movement activity between the two habitats.

Previous studies suggested or assumed that large species have higher movement activity and are likely to be captured more than small species (Lang 2000;

371 Engel *et al.* 2017). However, our results also revealed that installing fences decreased

372 the sampled abundance of each species, but the degree of the decrease was not

373 correlated with the body size of the species (Appendix 5). Therefore, the negative fence

374 effects were not explained by differences in body size. This was inconsistent with the

375 findings of previous studies that pitfall trap bias can be corrected by using the body size

376 of each species (Hancock & Legg 2012; Engel *et al.* 2017). This may be because our

377 targeted species were relatively large (mean size: 9.75-34.5 mm), and most of the

378 species had high movement activity rates.

379

380 Effects of daily soil temperature on the removal probability

381   Saska *et al.* (2013) conducted a meta-analysis on the effect of weather on the

382 sampled abundance of carabids in several regions and demonstrated that while

383 temperature generally increased the sampled abundance, the effects varied among

384 species. We found that soil temperature increased the removal probability of pitfall traps

385 and indirectly increased the sampled abundance of *Pterostichus thunbergi* but that

386 positive effects were found in only one survey period (period 1: June 2018). With

387 respect to *P. thunbergi*, therefore, it could be argued that the effects of soil temperature

388 on the removal probability were not consistent throughout the survey periods. In period

389 1, the daily mean values of soil temperature and their ranges were not substantially

390 different from those of the other periods (Appendix 5), but the precipitation was higher

391 than that in the other periods (Appendix 5). Although other weather factors, such as

392 precipitation and soil humidity, can affect the removal probability (Mitchell 1963; Saska

393 *et al.* 2013), the effect of soil temperature appeared to be small at least in our study,

394 which focused on a restricted area and season (i.e., hot summer season). In fact, Saska *et*

395   *al.* (2013) suggested that temperature bias may be small on a short time scale and/or in

396   the absence of distinct temporal trends in temperature.

397   In addition, because we did not examine differences in vegetation structure

398   among sites, which can affect soil temperature, we could not clearly distinguish between

399   the effects of soil temperature and vegetation structures on the removal probability.

400   However, we dealt with daily changes in soil temperature, which can change greatly on

401   a short time scale compared to vegetation structure; therefore, we concluded that our

402   analysis mainly examined the effects of soil temperature changes on sampled abundance

403   rather than those of vegetation.

404   We could not estimate the removal probability and initial abundance precisely

405   for periods 3 and 4 (June and July 2019; Figure 3bc). In these periods, the total number

406   of collected individuals of *P. thunbergi* was relatively small (Appendix 4). Moreover,

407   the number of collected individuals was highest on the third day of periods 3 and 4

408   (Appendix 4), despite the general expectation that the daily number of collected

409   individuals would be high on the first day and decrease on subsequent days. It is

410   possible that the small total number and irregular patterns of collected individuals in

411   these periods made estimating the coefficients imprecise. Comparing the results of

412   several removal sampling models, we did not find substantial differences in the

413   coefficients among the models. Developing customized complex models, such as the

414   `RStan` models (Appendix 3), required additional skill, knowledge, and effort to write

415   code. Thus, `unmarked` and `ubms` models are recommended for estimating the initial

416   abundance and removal probability, at least in our case.

417

418   Comparing abundance estimates among different habitats

419   Comparing the abundance estimates between the GLMs and `unmarked`

420   models, we found that the habitat type effects on the abundance of *P. thunbergi* were

421   consistent (Figure 3c), suggesting that the effects of the removal process on sampled

422   abundance were small. In addition, we found that the temporary migration process did

423   not depend on habitat differences (Figure 2). Therefore, we could compare the sampled

424   abundance without considering the removal process to represent the difference in the

425   initial abundance of *P. thunbergi*.

426   Furthermore, our results infer abundance changes in ground-dwelling beetles

427   after harvest. Studies reported that the sampled abundance of some forest carabids did

428   not decrease for several years after harvest (e.g., Work *et al.* 2010; Yamanaka *et al.*

429   2021). There are two possible hypotheses for this finding. One, the changes in the

430   movement activity of carabids in harvested areas masked the decreased initial

431   abundance, and two, the initial abundance did not decrease immediately after the

432   harvest. Our results support the latter hypothesis, suggesting that the initial abundance

433   of these forest carabids did not change after harvest and that the beetles could survive in

434   clear-cut areas for at least a few years.

435

436   Conclusion

437   We focused on two processes potentially affecting pitfall trap sampling and

438   found that the sampled abundance of each species tended to increase in the temporary

439   migration process, but its effect did not differ among habitat types. We also found that

440   in the removal process, soil temperature could affect the removal probability and

441   sampled abundance, but its effect was inconsistent and relatively small over the entire

442   survey period. Therefore, we concluded that the traditional use of pitfall traps is, to

443   some extent, a robust measure, particularly when comparing the sampled abundance of

444   each species among neighboring habitats, such as in the case of our study.

445   Our study also has several limitations. First, in our removal sampling models,

446   we only examined one species' response and the effect of soil temperature. Removal

447   probability and its influencing factors can vary among species (Saska *et al.* 2013;

448   Růžičková *et al.* 2021) and may depend on individual and habitat conditions, such as

449   starvation and prey density distribution (Raworth & Choi 2001). Second, we could not

450   account for the possibility that vegetation density could hamper the movement of

451   ground-dwelling beetles and decrease the removal probability (Melbourne 1999;

452   Thomas *et al.* 2006). Third, we could not examine the reason that the removal

453   probability and effect of soil temperature changed across the survey periods. Future

454   studies should focus on multispecies responses, the effects of structural complexity, and

455   different spatial-temporal ranges to compensate for our study's limitations and to gain a

456   full understanding of the limitations and effective usage of pitfall traps.

457 **Author contributions**

458 Conceptualization: SY, KO; Methodology: SY; Investigation: SY; Formal analysis: SY,

459 YY; Writing - original draft: SY, YY; Writing - review & editing: SY, YY, KO; Funding

460 acquisition: SY, KO.

461

468

469 **Conflict of Interest**

470 The authors declare that they have no known competing financial interests or personal

471 relationships that could have appeared to influence the work reported in this paper.

472

473   **Figure captions**

474

475   Figure 1 Study sites and enclosure experiment

476   (a) Location of study sites and sampling grids. C1-3 and P1-3 indicate sampling

477   grids in clear-cut and unharvested plantation sites, respectively. (b) Enclosure fences

478   installed. (c) Spatial arrangement of a sampling grid.

479

480   Figure 2 Coefficients of hyperparameters and species parameters of the HCMs

481   Black circles and horizontal bars indicate mean values and 95% CIs of

482   coefficients, respectively. Dashed lines indicate zero values. Intercept: coefficient

483   indicating log-scale sampled abundance at clear-cut site; Habitat type: changes in

484   sampled abundance at unharvested plantation compared to clear-cut site; Fence: the

485   changes in sampled abundance due to installing fences; Habitat type × Fence: the

486   interaction between habitat type and fences. When the 95% CIs of the coefficients of

487   Habitat types, Fence, and Habitat × Fence were above (below) zero, we considered that

488   the abundance significantly increased (decreased) in the plantation site, within fences,

489   and within fences in the plantation site, respectively. Hyperparameter: the community-

490   level response, SP01 CAAR: *Carabus arcensis hokkaidoensis*, SP02 CABL: *Carabus*

491   *blaptoides rugipennis*, SP03 CAGE: *Carabus gehinii gehinii*, SP04 CAOP: *Carabus*

492   *opaculus opaculus*, SP05 CYMO: *Cychrus morawitzi morawitzi*, SP06 PTMI:

493   *Pterostichus microcephalus*, SP07 PTOR: *Pterostichus orientalis antiquus*, SP08

494   PTTH: *Pterostichus thunbergi*, SP09 SIPE: *Silpha perforata*, SP10 XEDA: *Xestagonum*

495   *daisetsuzanus*.

496

497   Figure 3 Results of removal sampling models (`unmarked` model) with the whole

498   period data (Whole period) and each period data (Periods 1, 2, 3, and 4) in the analysis

499   of *P. thunbergi*

500   The mean values of estimates are denoted by circles or triangles, and their 95%

501   CIs are denoted by vertical bars. (a) Effects of daily soil temperature on removal

502   probability, (b) estimated per-day removal probability (given the mean soil

503   temperature), and (c) abundance estimates are shown separately for different survey

504   periods. In (c), we compared the abundance estimates between `unmarked` models

505   (unmarked) and generalized linear models that do not consider the removal process

506   (GLM).

507

508   **Table captions**

509   Table 1 Glossary of terms used in this study

510

511   Table 2 Mean value of the sampled abundance of each species per day at clear-cut and

512   unharvested plantation sites

513   Values indicate the mean value of sampled abundance per day and per 1 pitfall

514   trap. Values with parentheses indicate the standard deviations. These values show the

515   sampled abundance of 7 continuous days in four survey periods (not including extended

516   sampling in periods 3 and 4). Mean values were calculated with the data of whole

517   periods (each 7-sampling day in June and July 2018 and 2019). The scientific name of

518   each species was in accordance with Suzuki (2022). Carabid species are categorized

519   into forest and nonforest species according to the literature (Hori 2001; Hori 2003; Hori

520   2012; Yamanaka *et al.* 2021). Silphid species (*Silpha perforata*) are categorized as

521   forest species according to Katakura *et al.* (1986). *Pterostichus microcephalus* is a wing

522   polymorphic species (Shibuya *et al.* 2018), but most of the individuals we captured

523   were brachypterous (only 2 of 18 individuals were macropterous). Thus, *P.*

524   *microcephalus* was included in the analysis.

525

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669

(a)

C3
C2
C1

Sampling grid
□ within fence
× without fence
Forest stand
▨ Sakhalin fir
■ Broadleaved forest
□ Openland

P3
P2
P1

0   75   150 m

(b)
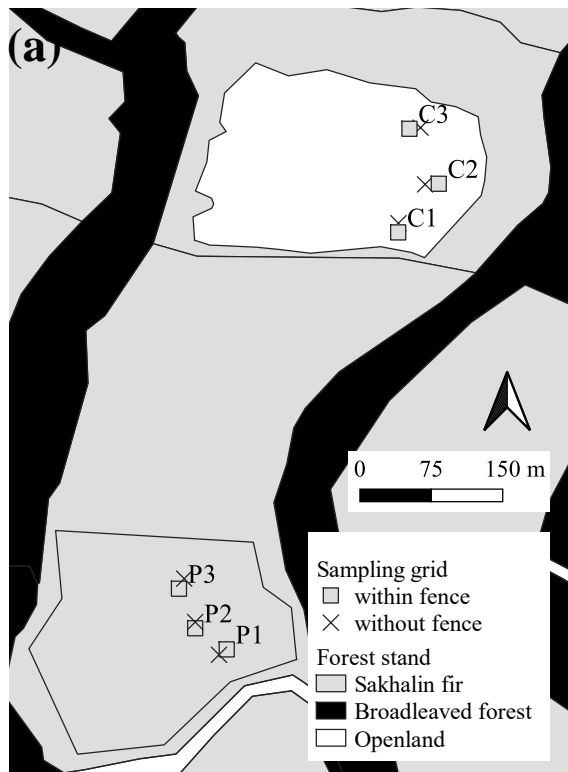
(c)

Sampling grid within fence
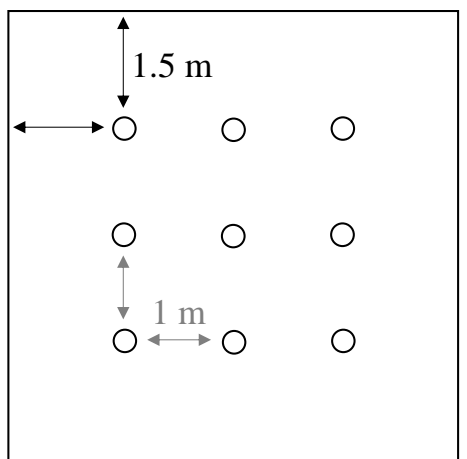
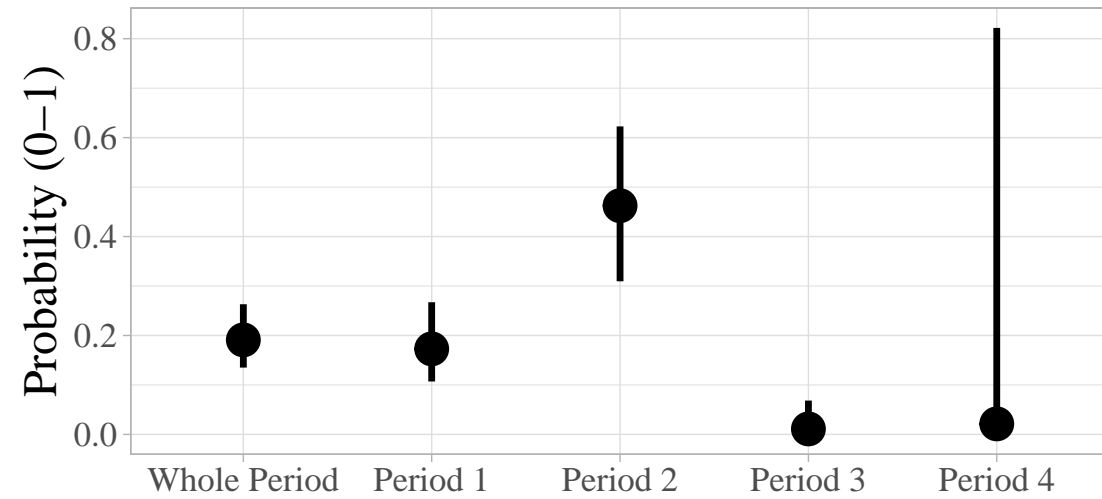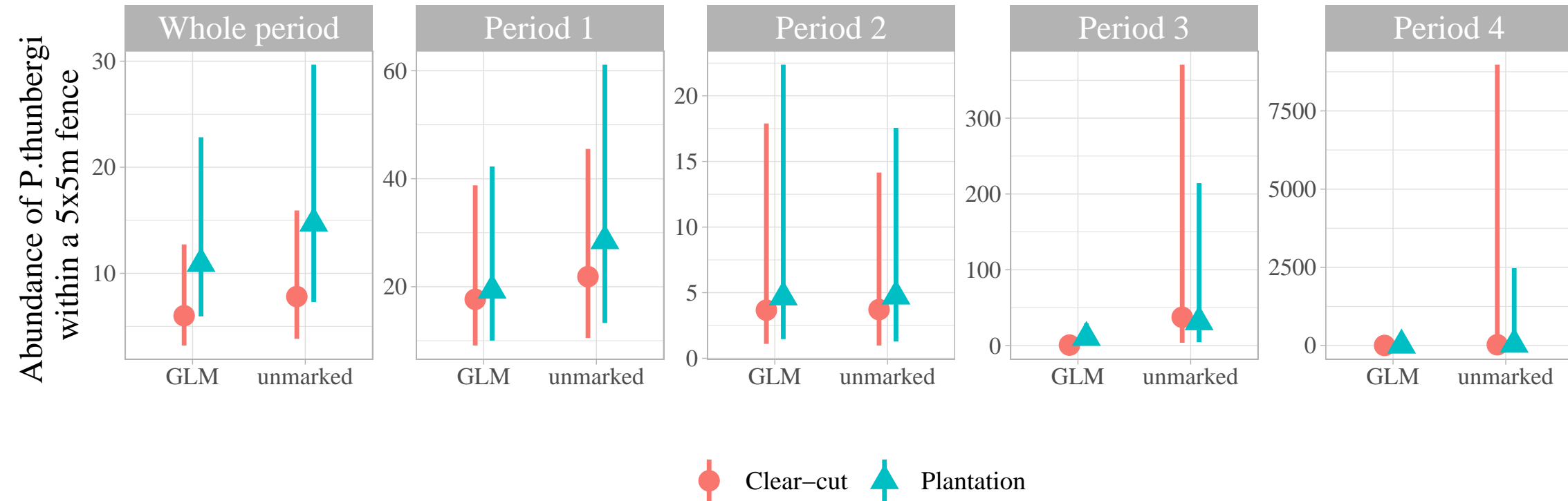Sampling grid without fence

1.5 m

1 m

> 5 m

Pitfall trap

5 × 5 m fence
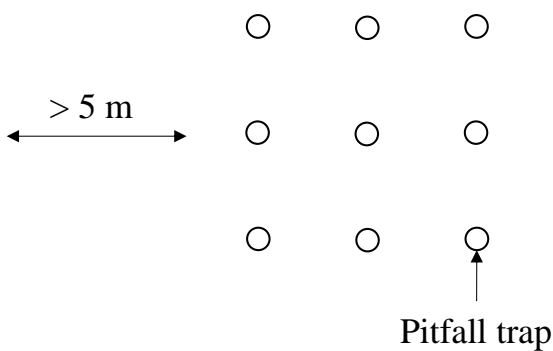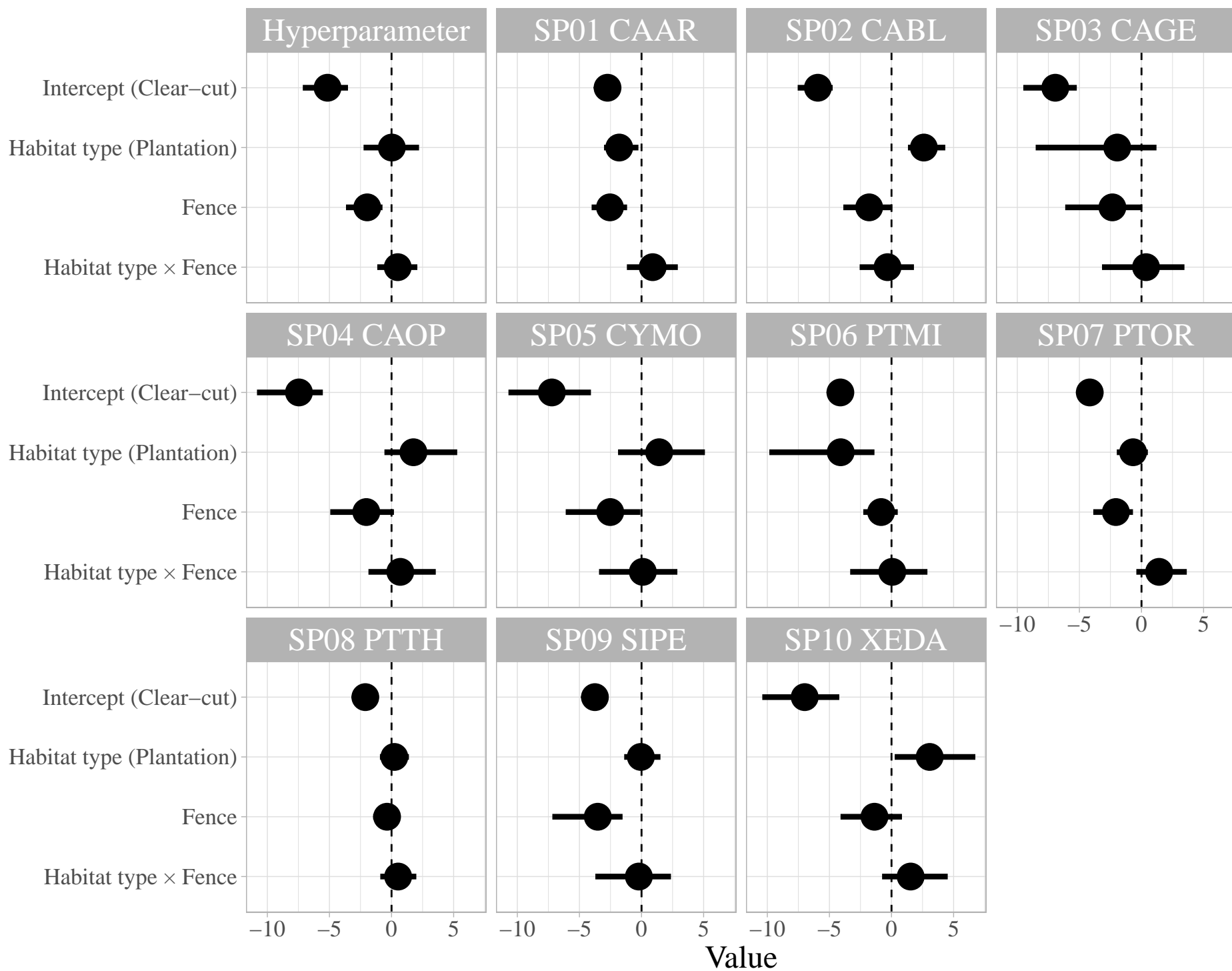
(a) Effect of soil temperature on removal probability
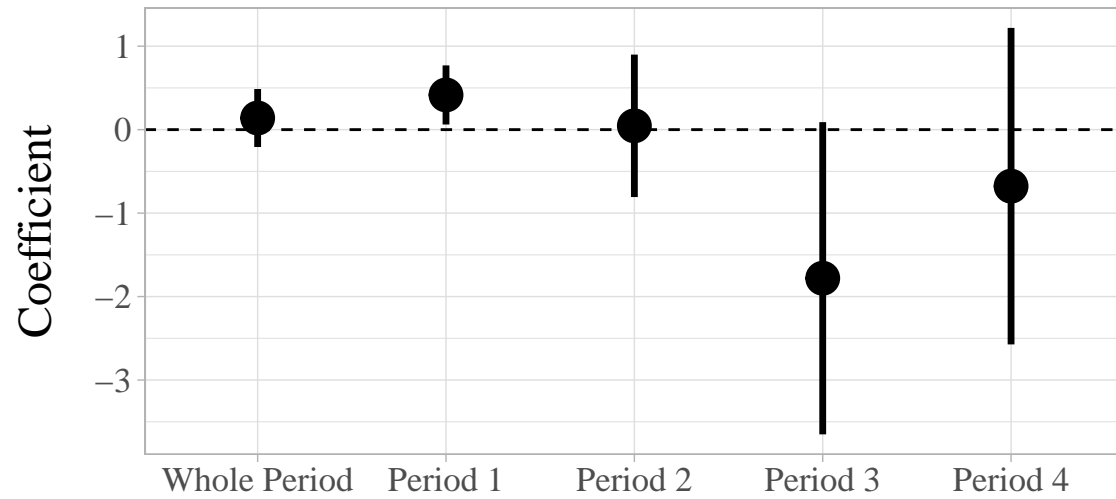
(b) Estimated removal probability

(c) Abundance estimates

Clear−cut   Plantation

1 **Table**

2 Table 1 Glossary of terms used in this study.

Terms	Explanation
Initial abundance	• The number of individuals present in a certain area during an arbitrary time. • In this study, we regarded initial abundance as the number of individuals present within the fences when the fences were shut down, and we estimated it using removal sampling.
Sampled abundance	• The number of individuals actually collected by pitfall traps. • It is determined through the sampling process of pitfall traps, which is influenced by various factors (sampling design and targeted site- and species-specific characteristics).
Removal probability	• The probability that individuals within effective trap area are caught and removed by pitfall traps during a certain period. • It depends on a sampling design and the movement activity of each species. • In this study, we regard the removal probability as the probability that an individual is collected by traps per day in an enclosure experiment in the absence of a temporary migration process.
Movement activity	• It represents the degree of activity of each species, which is dependent on intrinsic factors (e.g., their body size, species-specific movement distance or frequency) and extrinsic factors (e.g., soil temperature, vegetation structures). • It affects both the temporary migration and removal processes.
Sampled abundance within fence	• The total number of individuals collected within fences. • It is determined by the initial abundance and removal probability within fences, and thus it is expected to be lower than the initial abundance but close to the initial abundance with a longer survey period.

	• The movement of individuals over fences is prevented, and thus sampled abundance within fence is not affected by temporary migration process.
Sampled abundance without fence	• The total number of individuals collected without fences. • It is the common measure of comparison in pitfall trap survey.

3

Table 2 Mean value of the sampled abundance of each species per day at clear-cut and unharvested plantation sites

ID	Species name	Abbreviation	Habitat	Taxa	Clear-cut		Plantation	
					Within fence	Without fence	Within fence	Without fence
1	*Carabus arcensis hokkaidoensis*	CAAR	Forest	Carabid	0.004 (0.0072)	0.0757 (0.0625)	0.0026 (0.0092)	0.0093 (0.0143)
2	*Carabus blaptoides rugipennis*	CABL	Forest	Carabid	0.0013 (0.0046)	0.0013 (0.0046)	0.004 (0.0072)	0.0384 (0.0386)
3	*Carabus gehinii gehinii*	CAGE	Forest	Carabid	0 (0)	0.0013 (0.0047)	0 (0)	0 (0)
4	*Carabus opaculus opaculus*	CAOP	Forest	Carabid	0 (0)	0 (0)	0.0013 (0.0046)	0.004 (0.0072)
5	*Cychrus morawitzi morawitzi*	CYMO	Forest	Carabid	0 (0)	0 (0)	0 (0)	0.004 (0.0137)
6	*Pterostichus microcephalus*	PTMI	NonForest	Carabid	0.0093 (0.0197)	0.0146 (0.023)	0 (0)	0 (0)
7	*Pterostichus orientalis antiquus*	PTOR	Forest	Carabid	0.0013 (0.0046)	0.0186 (0.0309)	0.0053 (0.0078)	0.0066 (0.0106)
8	*Pterostichus thunbergi*	PTTH	Forest	Carabid	0.0952 (0.1463)	0.1067 (0.1492)	0.1733 (0.1401)	0.1455 (0.0593)
9	*Silpha perforata*	SIPE	Forest	Silphid	0 (0)	0.0274 (0.0448)	0 (0)	0.0238 (0.0441)

10	*Xestagonum daisetsuzanus*	XEDA	Forest	Carabid	0 (0)	0 (0)	0.0278 (0.0479)	0.0132 (0.0223)

Values indicate the mean value of sampled abundance per day and per 1 pitfall trap. Values with parentheses indicate the standard deviations. These values show the sampled abundance of 7 continuous days in four survey periods (not including extended sampling in periods 3 and 4). Mean values were calculated with the data of whole periods (each 7-sampling day in June and July 2018 and 2019). The scientific name of each species was in accordance with Suzuki (2022). Carabid species are categorized into forest and nonforest species according to the literature (Hori 2001; Hori 2003; Hori 2012; Yamanaka et al. 2021). Silphid species (*Silpha perforata*) are categorized as forest species according to Katakura et al. (1986). *Pterostichus microcephalus* is a wing polymorphic species (Shibuya et al. 2018), but most of the individuals we captured were brachypterous (only 2 of 18 individuals were macropterous). Thus, P. microcephalus was included in the analysis.

Appendix

Examining the bias of pitfall traps with enclosure experiments and removal

sampling

Satoshi YAMANAKA, Yuichi YAMAURA, Kenichi OZAKI

Contents

26   7 days ("Data2.txt")

27 3. Data of body size of each species ("Splist.txt")

28

29 Script for analysis

30 1. Script for HCMs ("Rcode1.R")

31 2. Script for removal sampling models ("Rcode2.R")

32 3. Script for classic removal sampling models ("Rcode3.R")

33 4. Stan code for HCMs ("Stancode1.stan")

34 5. Stan code for removal sampling models with the whole period data

35   ("Stancode2.stan")

36 6. Stan code for removal sampling models with each period data

37   ("Stancode3.stan")

38 7. Stan code for classic removal sampling models ("Stancode4.stan")

39

Appendix 1 Study site

     Our survey was conducted a clear-cut site and a plantation site (Figure S1). At the clear-cut site, a mature plantation of Sakhalin fir was harvested in 2015, and 3 or 4 years had passed at the time of the survey. In clear-cut site, logging residue produced by the harvesting remained (Figure S1a). The unharvested plantation site mainly consists of mature Sakhalin fir.

Figure S1 Study sites

(a) clear-cut site. (b) plantation site.

Appendix 2 Abundance-based hierarchical community models

In order to examine the effects of temporary emigration process (i.e., fence installation) on sampled abundance of each species, we constructed the abundance-based hierarchical community models (HCMs) according to Yamaura *et al.* (2016). HCMs can estimate a community-level response based on species-level responses.

Here, we pooled the sampled abundance of each species at 4 survey periods. We assumed that the total sampled abundance of species i at grid j (Y_{ij}) follows a negative binomial distribution:

$$Y_{ij} \sim NegativeBinomial(\lambda_{ij}, \sigma_i), \qquad (1)$$

where λ_{ij} is an expected sampled abundance of species i in grid j, and σ_i is a dispersion parameter of species i. We modeled λ_{ij} as a function of an intercept (α_i), habitat type (binary variable H_j; 0: clear-cut, 1: plantation), installed fence (binary variable F_j; 0: absent, 1: present), and the interaction of habitat type and installed fence variables. We also included the log-transformed number of the valid traps as an offset term because several traps without fences were disturbed by mammals:

$$\log(\lambda_{ij}) = \alpha_i + \beta_{h_i} \times H_j + \beta_{f_i} \times F_j + \beta_{hf_i} \times H_j \times F_j + \log(T_j), \qquad (2)$$

where β_{h_i}, β_{f_i}, and β_{hf_i} are coefficients of habitat type, installed fence, and the interaction of habitat type and installed fence variables, respectively. These coefficients indicate the changes in sampled abundance in unharvested plantation site compared to clear-cut site, abundance changes due to fence installation, and abundance changes due to fence installation in plantation site, respectively. T_j is the number of valid traps in grid j, and $\log(T_j)$ is the offset term.

In order to estimate species- and community-level responses, we assumed that the species level parameters (α_i, β_{h_i}, β_{f_i}, and β_{hf_i}) follow normal distributions shared by all species,

$$\alpha_i \sim Normal[\mu_\alpha, \sigma_\alpha^2],$$

$$\beta_{h_i} \sim Normal[\mu_{\beta_h}, \sigma_{\beta_h}^2], \quad .... \qquad (3)$$

where, μ_α is the mean value of α_i, showing the community-level response (i.e.,

hyperparameter), and σ_α is its standard deviation.

We used normal distributions $(0, 100^2)$ for μ_α, μ_{β_h}, μ_{β_f} and $\mu_{\beta_{hf}}$, and half-

Cauchy distributions $(0, 5)$ for the standard deviation of each coefficient $(\sigma_\alpha, \sigma_{\beta_h}, \sigma_{\beta_f},$

and $\sigma_{\beta_{hf}})$ and dispersion parameter (σ_i) as weakly informative prior distributions

(Gelman 2006). We used four chains that had 20,000 iterations following 5,000 burn-in

with 20 thinning rate.

References

Gelman, A. (2006) Prior distributions for variance parameters in hierarchical models

      (Comment on an Article by Browne and Draper). *Bayesian Analysis,* **1,** 515-533.

Yamaura, Y., Kery, M. & Royle, J.A. (2016) Study of biological communities subject to

      imperfect detection: bias and precision of community N-mixture abundance

      models in small-sample situations. Ecological Research, 31, 289-305.

Appendix 3 Explanation of removal sampling models

1.　Removal sampling models considering the changes in removal probability

　　We constructed and fitted removal sampling models using three methods: (1) the R package "`unmarked`" version 1.0.1 (Fiske & Chandler 2011) with a Poisson distribution (hereafter, `unmarked` Poisson model), (2) the R package "`ubms`" version 1.0.2 (Kellner et al. 2022), and (3) the custom model code in the R package "`RStan`" (Stan Development Team 2020). As well as `unmarked` models in the main text, we used two types of data: (1) the whole period data, which covered the four survey periods, and (2) each period's data.

1-1. `unmarked` Poisson models

　　We used the daily number of individuals collected as the response variable, following Poisson distributions, and categorical habitat type (clear-cut vs. unharvested plantation) and standardized daily mean soil temperature as explanatory variables for initial abundance and removal probability, respectively. We used the "`gmultmix`" function of the R package "`unmarked`" using maximum likelihood estimation (Fiske & Chandler 2011).

1-2. `ubms` models

　　We used the "`stan_multinomPois`" function of the R package "`ubms`" using Bayesian estimation and included random effects in the models (Kellner et al. 2022). The response variables and explanatory variables are the same as `unmarked` models; however, as random effects, we added grid ID and period ID to explanatory variables for the initial abundance in the model with the whole period data and grid ID

117 to an explanatory variable in the models with each period data. We assumed that the

118 response variables followed a Poisson distribution because "`ubms`" does not support a

119 negative binomial distribution for removal sampling models. For each model, we used

120 four chains that had 4,000 iterations with no burn-in and one thinning rate.

121

122 1-3. `RStan` model

123   We developed custom codes according to Kéry and Royle (2015). In the

124 models, the response variables followed a Poisson distribution, and we included grid

125 and/or period IDs as in the `ubms` models. It is noted that the `RStan` models had the

126 same structure as the `ubms` models. For the model using the data set of the whole

127 survey period, we modeled expected value of the initial abundance of *Pterostichus*

128 *thunbergi* at grid *i* and period *j* (λ_{ij}) as a function of habitat types and random effects

129 of sampling grids and survey periods:

$$\log(\lambda_{ij}) = \alpha_i + \varepsilon_{Grid_i} + \varepsilon_{Period_j}, \quad (1)$$

131 where, α_i is a categorical variable showing the initial abundance in clear-cut or

132 plantation sites. $\varepsilon_{Transect_i}$ and ε_{Period_j} are random effects to account for the variation

133 among sampling grids and survey periods and were assumed to follow a normal

134 distribution:

$$\varepsilon_{Grid_i} \sim \text{Normal}(0, \sigma^2_{Grid}),$$

$$\varepsilon_{Period_j} \sim \text{Normal}(0, \sigma^2_{Period}), \quad (2)$$

137 where, σ indicates the standard deviation.

138   We assumed that the removal probability on day *t* in grid *i* at period *j* is

139 determined by the standardized daily mean value of soil temperature on day *t* in grid *i* at

140 period *j* (S_{ijt}):

$$\text{logit}(p_{ijt}) = \alpha_p + \beta_p \times S_{ijt}, \quad (3)$$

142 where, p_{ijt} is the removal probability on day t in grid i at period j, and its value is

143 ranged from 0 to 1. α_p and β_p indicate an intercept and a coefficient of soil

144 temperature, respectively. We calculated the conditional cell probabilities of

145 multinomial models on each sampling day (π_t). The conditional cell probability on a

146 certain day depends on the probability that the individual was not removed before that

147 day and the removal probability on that day. For example, the conditional cell

148 probability on day 2 (π_{ij2}) depends on the probability that the individuals were not

149 removed on day 1 $(1 - p_{ij1})$ and the removal probability on day 2 (p_{ij2}):

150 $$\pi_{ij1} = p_{ij1},$$

151 $$\pi_{ij2} = (1 - p_{ij1}) \times p_{ij2}, \ \dots,$$

152 $$\pi_{ij7} = (1 - p_{ij1}) \times (1 - p_{ij2}) \times (1 - p_{ij3}) \times (1 - p_{ij4}) \times (1 - p_{ij5}) \times$$

153 $$(1 - p_{ij6}) \times p_{ij7}. \quad\quad\quad (4)$$

154 We summed the conditional cell probability of each sampling day to calculate the

155 total removal probability $(\sum_{t=1}^{7} \pi_{ijt})$, which indicates the net probability that the

156 individual in grid i at period j was removed in any of 7 sampling days. In addition, π_{ij0}

157 is the probability that the individual in grid i at period j was not removed during

158 sampling days and is shown as $1 - \sum_{t=1}^{7} \pi_{ijt}$.

159 We assumed that sampled abundance on day t in grid i at period j (Y_{ijt}) is

160 determined by the total sampled abundance (n_{ij}) and rate of collected individuals on

161 day t out of the total sampled abundance $(\pi_{ijt}^c = \pi_{ijt}/(1 - \pi_{ij0}))$. We also assume that

162 total sampled abundance (n_{ij}) depends on the initial abundance (N_{ij}) and total removal

163 probability $(1 - \pi_{ij0})$, and that the initial abundance follows a Poisson distribution:

164 $$Y_{ijt}|n_{ij} \sim Multinom(n_{ij}, \pi_{ijt}^c),$$

165 $$n_{ij} \sim Binomial(N_{ij}, 1 - \pi_{ij0}),$$

166 $$N_{ij} \sim Poisson(\lambda_{ij}). \quad\quad\quad (5)$$

167   As prior distributions, we used normal distributions $(0, 100^2)$ for α_i, α_p, and

168 β_p. We also used half-Cauchy distributions $(0, 5)$ for any variance of coefficients as

169 weakly informative prior distributions (Gelman 2006). For each model, we used four

170 chains that had 50,000 iterations following 25,000 burn-in with 20 thinning rate. We

171 used the "R-hat" and "N_eff/N" statistics (R-hat < 1.1 and N_eff/N > 0.1) to assess

172 model convergence.

173   We also constructed models using the data set of each survey period. In the

174 models, we assumed that the expected initial abundance of *P. thunbergi* at grid i (λ_i)

175 was a function of habitat types and random grid effects:

176     $$\log(\lambda_i) = \alpha_i + \varepsilon_{Transect_i}. \qquad (1)'$$

177

178 2. Classic removal sampling models

179   We also constructed classic removal sampling models with four model-fitting

180 methods (`unmarked` with a Poisson and negative-binomial distribution, `ubms`, and

181 `RStan` models). These models were simpler than the above-mentioned models because

182 the classic models do not consider effects of daily soil temperature on removal

183 probability ("Rcode3.R" and "Stancode4.stan" in Script for analysis), meaning that in

184 these models the daily removal probability is assumed to be constant through all survey

185 periods and among sites. We pooled the sampled abundance across survey periods, and

186 the total of sampled abundance on each sampling day and at each grid was used as the

187 response variables.

188

189 References

190 Gelman, A. (2006) Prior distributions for variance parameters in hierarchical models

191   (Comment on an Article by Browne and Draper). *Bayesian Analysis,* **1,** 515-533.

192   Fiske, I.J. & Chandler, R.B. (2011) Unmarked: An R Package for Fitting Hierarchical

193   Models of Wildlife Occurrence and Abundance. Journal of Statistical

194   Software, 43, 1-23.

195   Kellner, K.F., Fowler, N.L., Petroelje, T.R., Kautz, T.M., Beyer, D.E. & Belant, J.L.

196   (2022) ubms: An R package for fitting hierarchical occupancy and N-mixture

197   abundance models in a Bayesian framework. Methods in Ecology and

198   Evolution, 13, 577-584.

199   Kéry, M. & Royle, J.A. (2015) Applied Hierarchical Modeling in Ecology: Analysis of

200   distribution, abundance and species richness in R and BUGS: Volume 1:

201   Prelude and Static Models. Academic Press, Boston.

202   Stan Development Team (2020) "Rstan: the R interface to Stan." R package version

203   2.21.2.

204

205

Appendix 4 Sampled abundance of *Pterostichus thunbergi* within fences

We collected totally 203 individuals of *P. thunbergi* within fences during each 7-sampling day within 4 periods (Figure S4-1). The sampled abundance was highest at period 1, June 2018 (111 individuals), and the abundance at the other periods was relatively small. In fact, 34, 33 and 25 individuals were caught at period 4, period 3, and period 2, respectively (Figure S4-1). At period 1 and 2, the daily sampled abundance was highest on the first day tended to decrease after the following days. On the other hand, at period 3 and 4, the sampled abundance was highest on the third day and maintained after the following days (Table S4 and Figure S4-1).

In period 3 and period 4, we conducted extended sampling after day 7 and additionally collected a total of 5 and 42 individuals of *P. thunbergi*, respectively (Figure S4-2), suggesting that in these periods (especially period 4), the 7-day sampling did not remove all the individuals within fences. These results were consistent with the results of the removal sampling models showing that the estimated removal probability was overly low in periods 3 and 4 (see Figure 3b and S7-1b in Appendix 7).

Table S4 Mean value of daily sampled abundance of *Pterostichus thunbergi* at each period

Day	Period			
	Period 1	Period 2	Period 3	Period 4
Day 1	5.5 (1-16)	2.5 (0-7)	0.8 (0-2)	0.7 (0-2)
Day 2	1.7 (0-4)	0.5 (0-3)	0.7 (0-3)	1.0 (0-2)
Day 3	4.0 (0-9)	0.2 (0-1)	1.3 (0-5)	1.5 (0-4)
Day 4	2.5 (0-5)	0.5 (0-2)	0.8 (0-3)	0.5 (0-2)

Day 5	2.5 (0-6)	0.3 (0-1)	0.8 (0-4)	0.3 (0-2)
Day 6	1.2 (0-3)	0.2 (0-1)	0.7 (0-2)	0.7 (0-3)
Day 7	1.2 (0-3)	0.0 (0-0)	0.5 (0-1)	0.8 (0-2)

224 Values indicate the mean value of daily sampled abundance and using 9 pitfall traps.

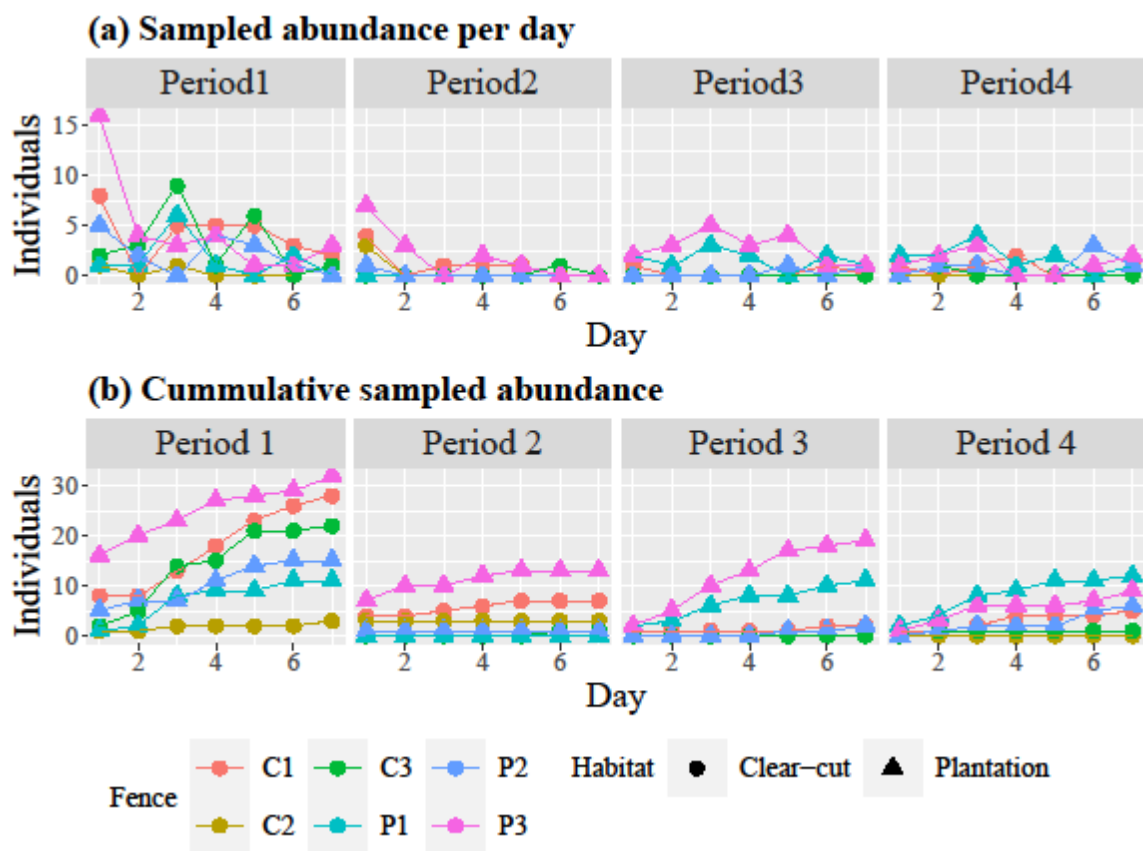225 Values with parenthesis indicate the max and minimum values of the sampled abundance.

226

227

228 Figure S4-1 Sampled abundance (a) and cumulative sampled abundance (b) of *P.*

229 *thunbergi*

230 Circles and triangles indicate clear-cut and unharvested plantation sites, respectively.

231 Different colors indicate different fences.

Cummulative sampled abundance

Figure S4-2 Cumulative sampled abundance of *P. thunbergi* on days 1-19 and 1-21 in

periods 3 and 4

Circles and triangles indicate clear-cut and unharvested plantation sites, respectively.

Different colors indicate different fences. In periods 3 and 4, the survey was continued

after the 7th day, and samples were collected on days 10, 12, and 19 in period 3 and on

days 14 and 21 in period 4. We collected 5 and 42 individuals of *P. thunbergi*

additionally, respectively.

Appendix 5 Weather factors (soil and air temperature and precipitation)

Daily mean values of soil temperature were higher in the clear-cut site than at the unharvested plantation site, and standard deviations were also relatively higher in the clear-cut site (Table S5). The ranges of daily mean and maximum values of soil temperature were overlapped among survey periods, although the minimum values in period 3 were relatively lower than those in other periods (Figure S5-1). The daily mean values of soil temperature were correlated with its maximum and minimum values, respectively (Figure S5-2).

Comparing the mean values of soil temperature among the all-day, day, and night time, the difference in soil temperature in the all-day time reflected the soil temperature in day time (from 6:00 to 18:00), and the difference among fences was small in night time (from 18:00 to 6:00) (Figure S5-3). We also examined air temperature at several fences. The daily mean values of air temperature had similar patterns with those of soil temperature (Figure S5-4).

Table S5 Daily mean values and its standard deviation of soil temperature

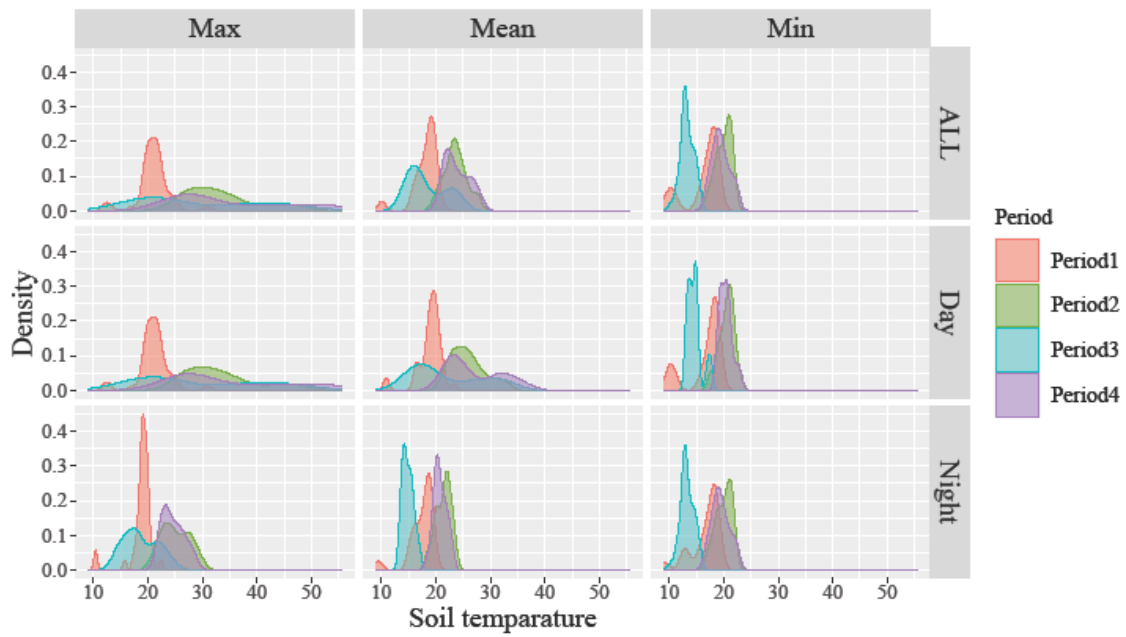| Period		Clear-cut		Plantation	
		Mean	SD	Mean	SD
Period1	2018 June	18.90	1.33	17.38	2.73
Period2	2018 July	25.04	1.54	22.15	1.34
Period3	2019 June	20.95	2.98	15.74	1.14
Period4	2019 July	25.79	1.48	22.00	0.67

258

259   Figure S5-1 Distribution of mean values of soil temperature

260   All: all-day time (24h), Day: day time (6:00-18:00, 12h), Night: night time (18:00-6:00,
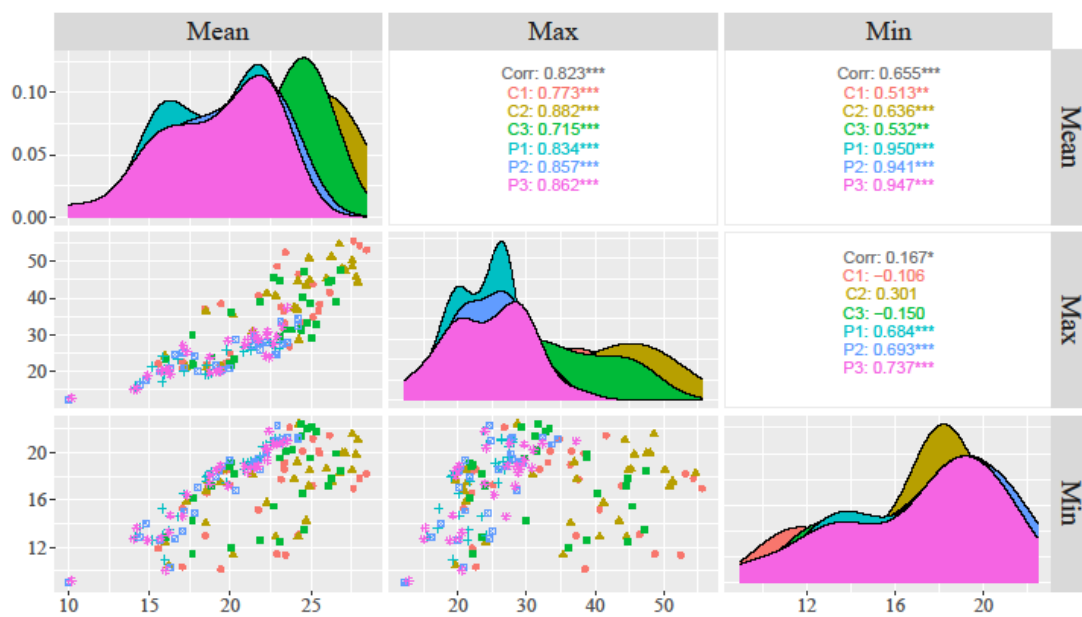
261   12h)

262

263

264   Figure S5-2 Correlation of mean values of soil temperature in the all-day time with

265   maximum and minimum values

266   Different symbols indicate each fence. The values at the right panels indicate the
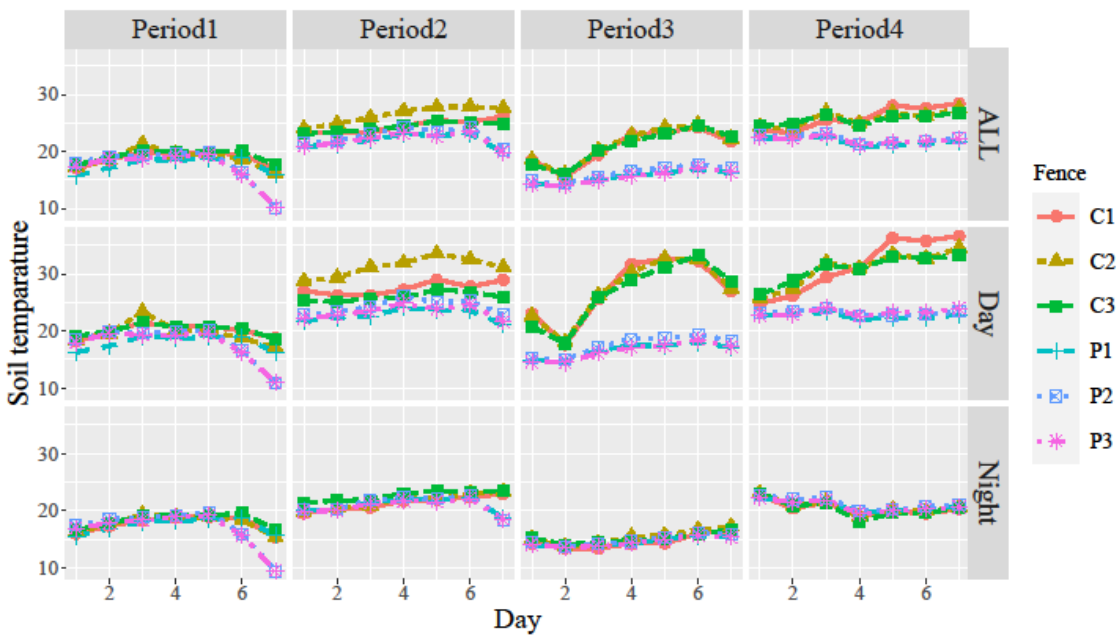
267   correlation coefficients.

268

269

270   Figure S5-3 Mean values of soil temperature at the all-day, day, and night time.

271   All: all-day time (24h), Day: day time (6:00-18:00, 12h), Night: night time (18:00-6:00,

272   12h). Different symbols indicate each fence.

273
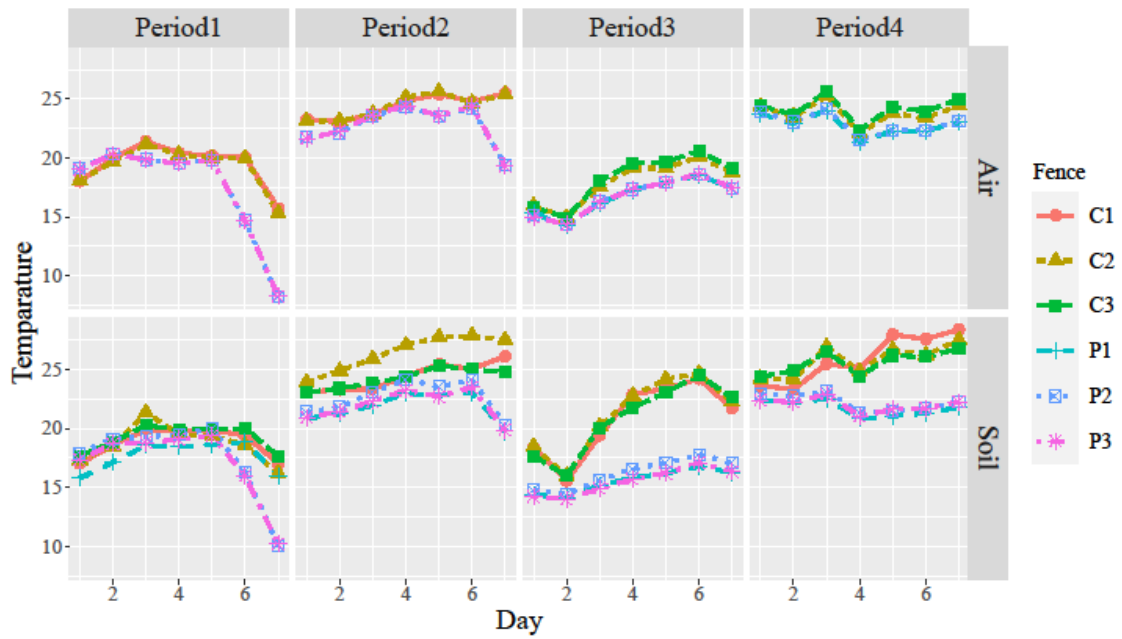
Figure S5-4 Daily mean values of air and soil temperature

Values indicate daily mean values. Different symbols indicate each fence.

2018

2019
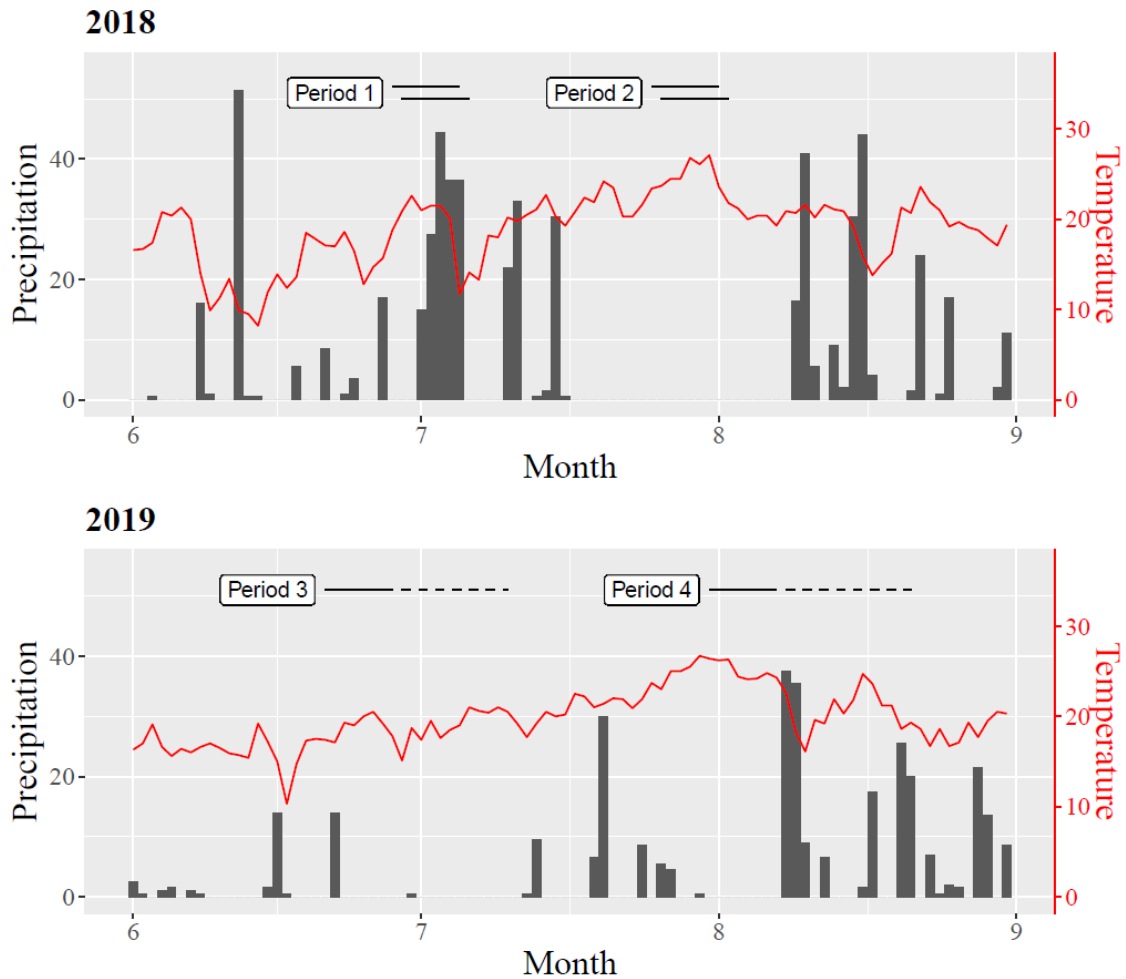
Figure S5-5 Daily total precipitation and mean temperature of the study area during the

surveyed period

Black bars and red lines indicate daily total precipitation and mean temperature,

respectively. These data were obtained from the Ashibetsu observatory (Japan

Meteorological Agency 2021), which is the closest study area. Horizontal solid and

dashed lines indicate 7-day continuous sampling (at periods 1-4) and extended sampling

(at only periods 3-4), respectively. In period 1, sampling at grids C1, C2, C3, and P1

started on 28 June 2018 and ended on 5 July 2018, and sampling at grids P2 and P3

started on 29 June 2018 and ended on 6 July 2018. In period 2, sampling at Clear-cut

site (C1, C2, and C3) and Plantation site (P1, P2, and P3) started on 25 and 26 July

289   2018 and ended on 1 and 2 August 2018, respectively. In period 3, sampling started on

290   21 June 2019 and ended on 10 July 2019. In period 4, sampling started on 31 July 2019

291   and ended on 21 August 2019.

292

293   Reference

294   Japan Meteorological Agency (2021) Historical weather data,

295   http://www.data.jma.go.jp/obd/stats/etrn/index.php.

296

Appendix 6 Relationship between body size and coefficients of the effects of fences

on sampled abundance
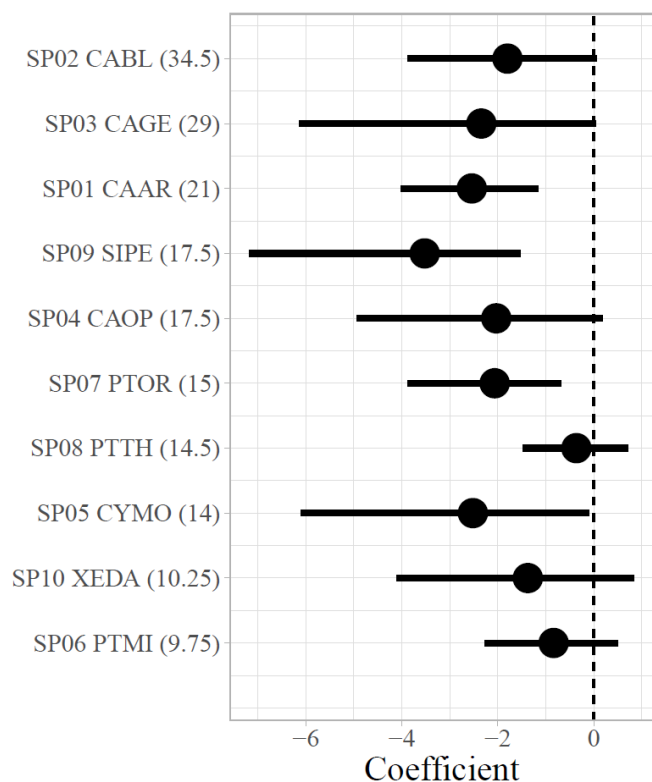
301 Figure S6 body size and coefficients of the effects of fences on sampled abundance of

302 each species

303 Y-axis indicates each species, sorted from top to bottom by body size (numbers in

304 parentheses next to species names represent the mean body length). X-axis indicates

305 coefficient of the effects of fences on sampled abundance. Black circles indicate mean

306 values, and horizontal lines represent 95% credible intervals of the coefficients. Mean

307 body length of each species was calculated by averaging the maximum and minimum

308 sizes that reported by Ueno, Kurosawa and Sato (1985).

309

310 Reference

311 Ueno, S., Kurosawa, Y. & Sato, M. (1985) *The Coleoptera of Japan in Color, Vol. II (in*

312   *Japanese)*. Hoikusha, Osaka.

313

Appendix 7 Results of removal sampling models

1. the coefficients of removal sampling models with different model-fitting methods

    The `ubms` and `RStan` models converged; however, a poor model fit for all `ubms` models was suggested based on Pareto smoothed importance-sampling leave-one-out cross-validation (PSIS-LOO). Most of the estimated coefficients were similar among the different model-fitting methods (Figure S7-1 and S7-3). As well as `unmarked` models in the main text, in other models in periods 3 and 4, the estimated removal probability and the initial abundance estimates were overly low and high, respectively (Figure S7-1c and S7-2). This suggests that these models in these periods also could not estimate the removal probability and initial abundance precisely. Unlike other models, in the `unmarked` Poisson model, the effect of soil temperature was negative for the whole period data (Figure S7-1a) likely due to the coefficient of period 3.

2. Comparing classic removal sampling models

    In the result of classic removal sampling models, estimated coefficients did not differ among model-fitting methods (`unmarked`, `ubms`, and `Rstan`) (Figure S7-4). Moreover, the coefficients did not largely differ from that of the abovementioned removal sampling models with the whole period data (Figure S7-3 and S7-4). This suggests that effects of daily soil temperature on removal probability were not large when considering over the whole survey periods, and this was consistent with our main conclusion.

338
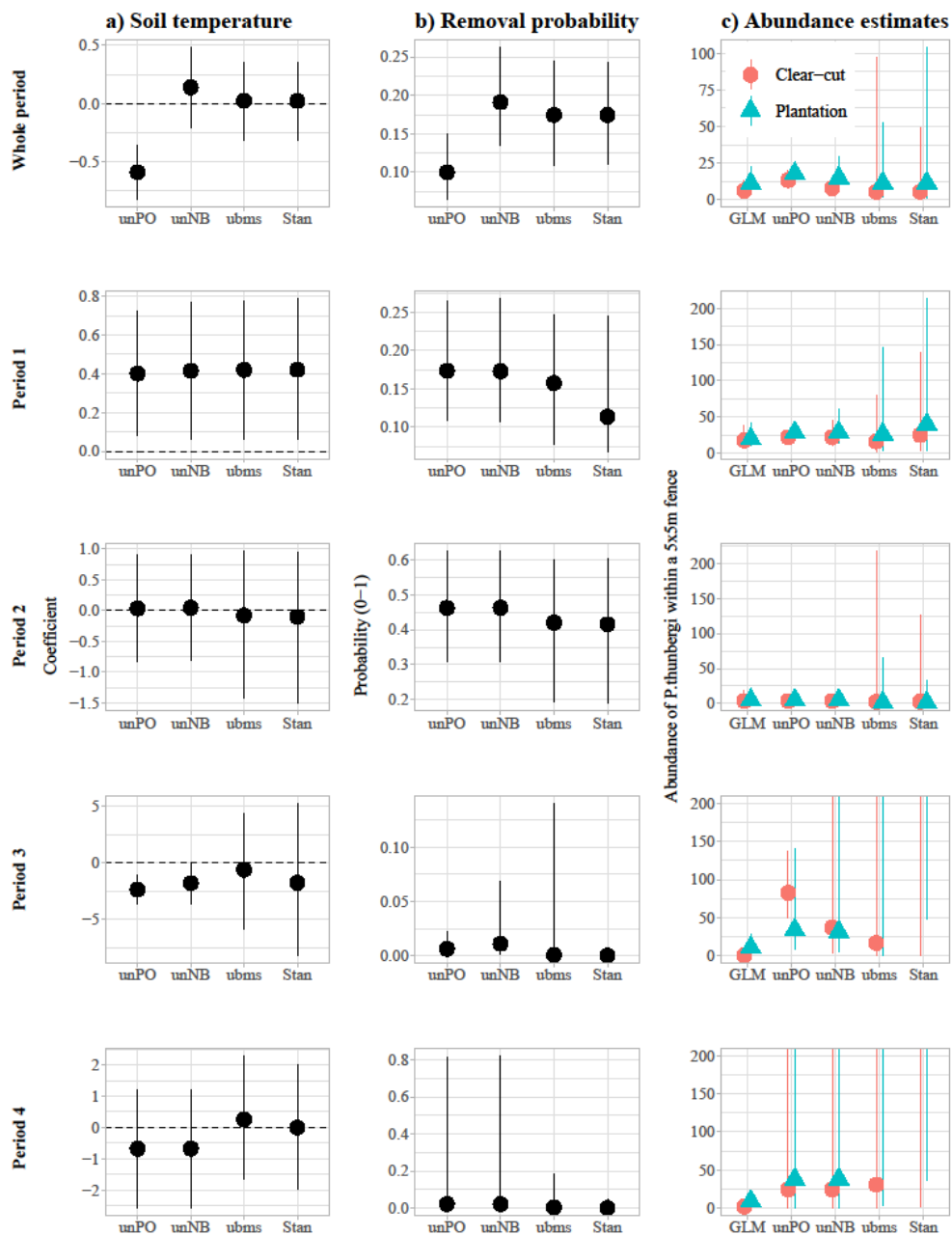
Figure S7-1 Comparison of estimates of four removal sampling models and GLMs with

the whole period data (Whole period) and each period data (Periods 1, 2, 3, and 4) in the

analysis of *P. thunbergi*

342   The mean values of estimates are denoted by circles or triangles, and their 95% CIs are

343   denoted by vertical bars. (a) Effects of daily soil temperature on removal probability, (b)

344   estimated per-day removal probability (given the mean soil temperature), and (c)

345   abundance estimates are shown separately for different methods and distributions.

346   Abbreviation: `unmarked` Poisson (unPO) and negative binomial (unNB), `ubms`

347   (ubms), and `RStan` model (Stan). It is noted that unNB is the `unmarked` models in

348   the main text. In periods 3 and 4, some mean values and their CIs were overly large, and

349   thus, the figures show estimates with a limited range on the y-axis (0-200) to clarify the

350   difference in estimates among models. Figures with the complete range of the y-axis are
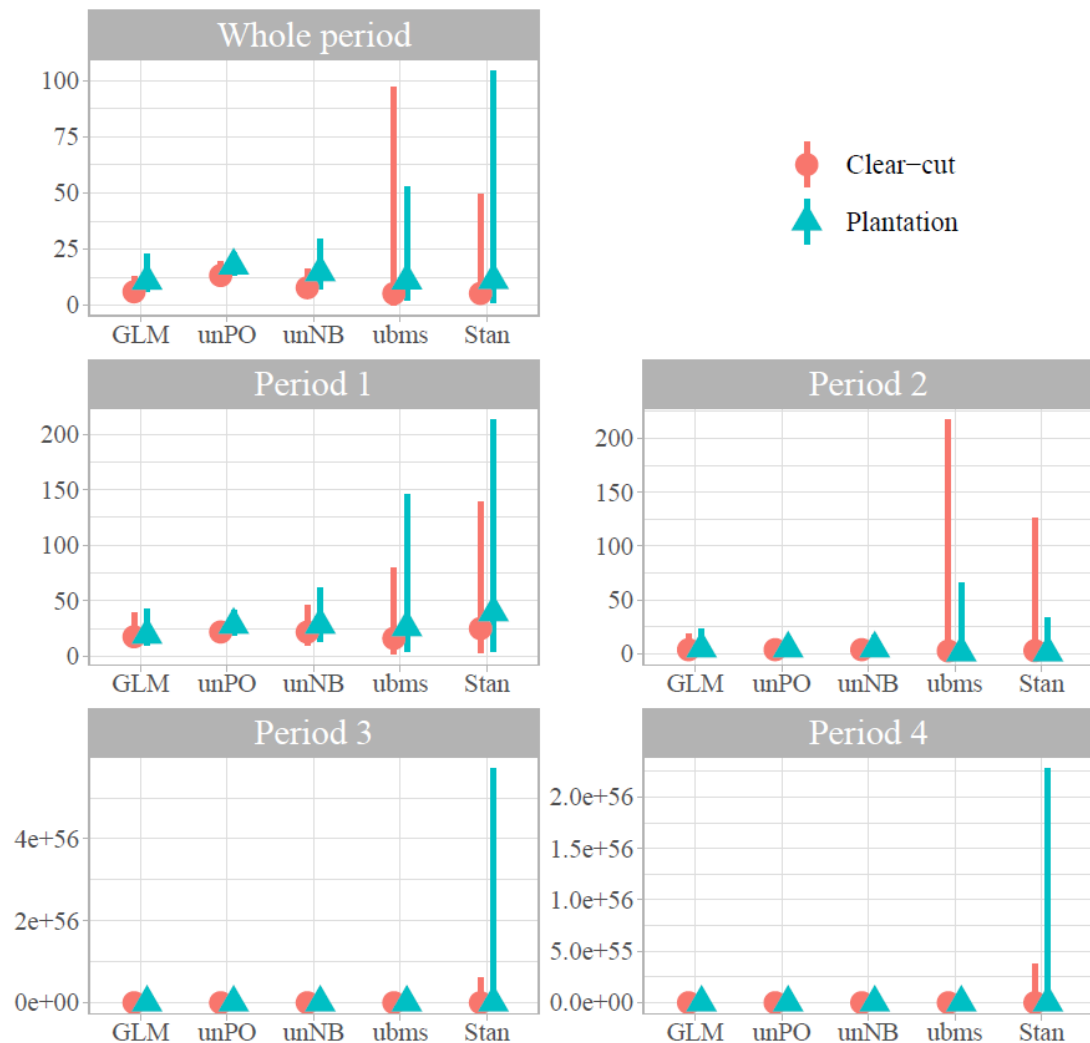
351   shown in Figure S7-2.

Figure S7-2 Initial abundances estimated by removal sampling models and expected

sampled abundance by GLMs (with full-range y-axis)

The estimates of GLM indicate the expected sampled abundance estimated by GLMs.

Other estimates (unPO, unNB, ubms, and Stan) indicate the initial abundance estimated

by each removal sampling model. unPO and unNB indicate `unmarked` model with a

Poisson and negative binomial distribution, respectively. Red circles and blue triangles

indicate the mean values of clear-cut and unharvested plantation sites, respectively.

360 Vertical bars show 95% CIs of estimates for GLMs and `unmarked` models or `ubms`

361 and `RStan` models, respectively.

362
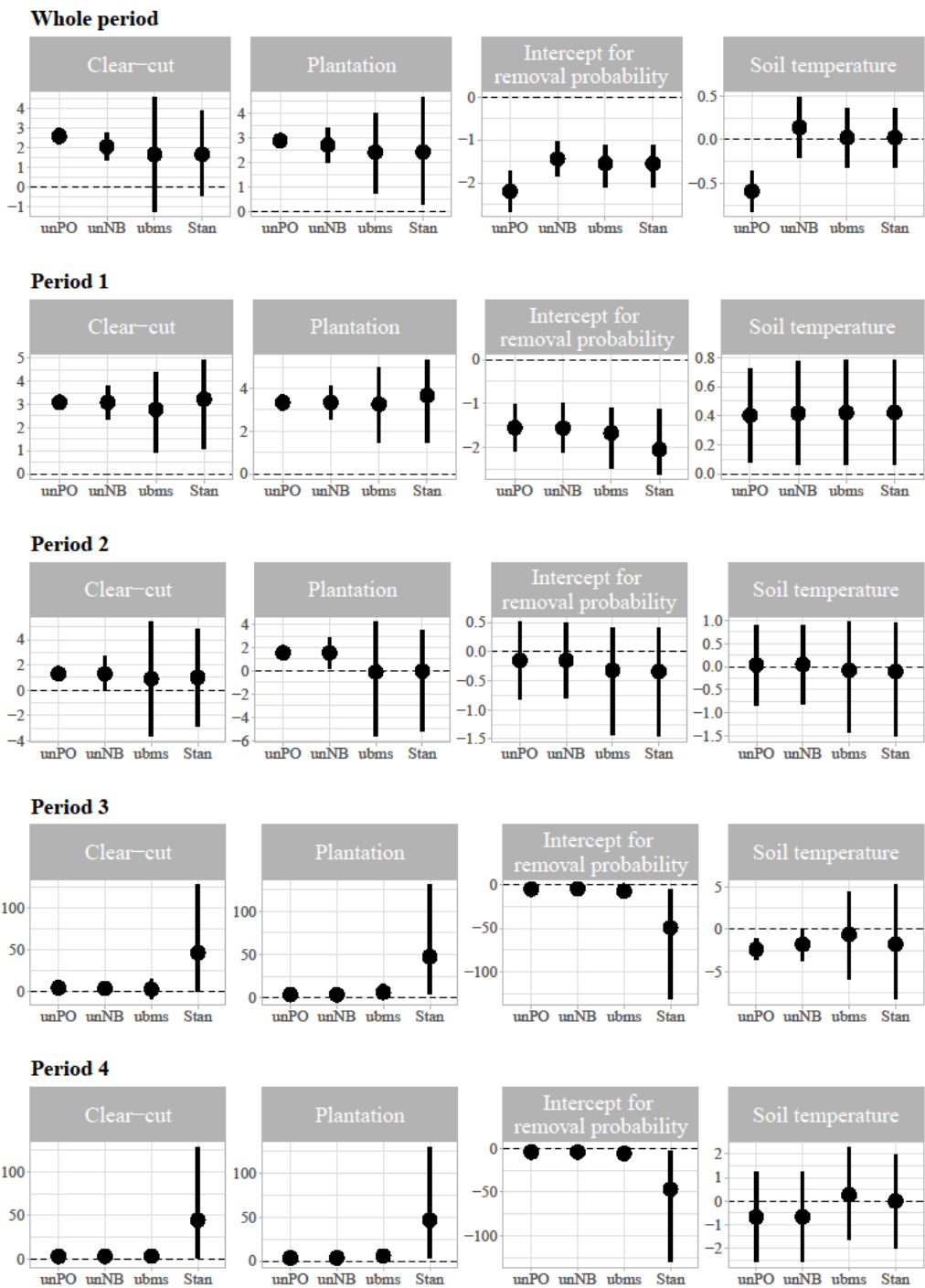
363

364 Figure S7-3 Estimated coefficients of parameters of removal sampling models

365 Black circles indicate mean values of the coefficients. Vertical bars show 95%

366 confidence intervals or credible intervals of the coefficients for `unmarked` models or

367 `ubms` and `RStan` models, respectively. Clear-cut and plantation indicate the initial

368 abundance of clear-cut and unharvested plantation sites, respectively. Soil temperature

369 indicates the coefficients of the effects of daily soil temperature on removal probability.

370 unPO and unNB indicate `unmarked` models with a Poisson and negative binomial

371 distribution, respectively.
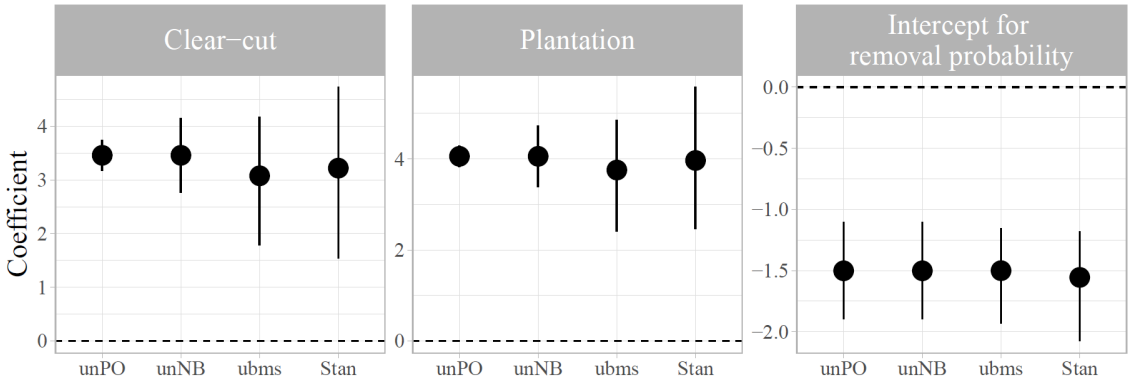
372

373

374 Figure S7-4 Estimated coefficients of parameters of classic removal sampling models

375 (without considering the daily changes in removal probability)

376 Black circles indicate mean values of the coefficients. Vertical bars show 95% CIs of the

377 coefficients for `unmarked` models or `ubms` and `RStan` models, respectively. Clear-

378 cut and plantation indicate the initial abundance of clear-cut and unharvested plantation

379 sites, respectively. unPO and unNB indicate `unmarked` models with a Poisson and

380 negative binomial distribution, respectively.

381

382