1 **Title**

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3 Mass attack by the ambrosia beetle *Platypus quercivorus* occurs in single trees and in

4 groups of trees

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33   **Abstract**

34

35   Bark and ambrosia beetles sometimes kill trees by attacking them *en masse*;

36   however, their attack is not necessarily successful.   Less than half of the fagaceous

37   trees attacked by the ambrosia beetle, *Platypus quercivorus*, die, and the factors

38   affecting this mortality are still unknown.   To examine this issue, the survival of all

39   stems of fagaceous trees attacked by the ambrosia beetle was investigated in a

40   secondary forest from 2008 to 2010.   In an area of 93 ha, 2130 stems (1278 genets) of

41   fagaceous trees were attacked by *P. quercivorus* during the study period, and 813 of

42   these stems died.   A generalized additive mixed model was constructed to predict the

43   probability of mortality of the attacked stems.   A best-fit model showed that the

44   probability of mortality was higher in *Quercus crispula* than in *Castanea crenata*.   A

45   positive correlation was determined between the density of the attacked trees and the

46   probability of mortality, suggesting that mass attack of *P. quercivorus* occurs not only

47   on individual trees, but also on groups of trees.   Assuming that trees attacked earlier in

48   the season have a higher probability of mortality, the observed negative effects of

49   altitude suggest that *P. quercivorus* initially seeks hosts at lower elevations.

50

Introduction

In general, the search pattern of animals consists of 2 parts. Firstly, when animals search a wide area without any resource cues, they move in a relatively straight path without turning (ranging). Secondly, after they detect resources, they scour a local area (local search), and then repeat their ranging and local search until they reach or gather the necessary resources (Jander 1975). This search pattern is also followed by ambrosia and bark beetles, with tree selection usually consisting of multiple phases—detection of host trees, evaluation of tree suitability, and acceptance of the host (Schoonhoven et al. 2005). Visual, olfactory, mechanosensory, and gustatory cues are considered to be involved in each phase.

Cues that ambrosia and bark beetles use to locate host trees can be predicted from differences in characteristics between attacked and intact trees. These differences have been determined in *Pinus* trees attacked by *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae) (Coops et al. 2006; Negrón et al. 2008; Negrón and Popp 2004; Olsen et al. 1996; White et al. 2007), and the information can be used to assess risk (Coops et al. 2009; Robertson et al. 2008; Wulder et al. 2006; Wulder et al. 2009). However, analysis of damaged and intact trees without considering the multiple phases of host selection by the beetle may lead to incorrect interpretation of the results, because the cues in each phase are different. For example, the chemical factors involved in each phase of host selection by the conifer bark beetle were presumed to be different (Zhang and Schlyter 2004). Even within the same phase, different mechanisms may occur. Two conflicting mechanisms for the first phase of host selection by *Dendroctonus* beetles have been proposed: (1) attraction to host volatiles

75   (Pureswaran and Borden 2005; Pureswaran et al. 2004); and (2) random landing on

76   trees (Moeck et al. 1981; Wood 1982).   This contradiction was explained by the

77   difference in timing of these two behaviors within the first phase (Saint-Germain et al.

78   2007).

79   In Japan, the ambrosia beetle, *Platypus quercivorus* (Murayama) (Coleoptera:

80   Platypodidae), causes Japanese oak wilt by transporting the pathogenic fungus

81   *Raffaelea quercivora* Kubono et Shin-Ito (Ito et al. 1998; Kinuura and Kobayashi 2006;

82   Kubono and Ito 2002; Saito et al. 2001).   The disease has spread throughout Japan

83   since the 1980s (Kobayashi and Ueda 2005).   From June to October, adult males of *P.*

84   *quercivorus* fly to their host trees and bore shallow holes in them.   Adult females join

85   the males and, after mating, the males and females make galleries in the sapwood and

86   deposit eggs at the terminal parts of these galleries.   Hatched larvae feed on fungi that

87   have been transported from old host trees by adult females.   The larvae grow into the

88   5th larval stage by winter, and then enter hibernation.   Pupation starts in spring, and

89   new adults emerge starting in June (Soné et al. 1998).

90   Infection by *P. quercivorus* occurs in 3 successive phases—initial attack (Fig.

91   1a–b), mass attack (Fig. 1b–c), and cessation of attack.   During the initial attack phase,

92   some male beetles find a host tree, excavate a hole in the bark, and use an aggregation

93   pheromone to attract their conspecifics (Tokoro et al. 2007).   During the mass attack

94   phase, aggregated beetles attack the host tree *en masse*, and cause death.   It has been

95   suggested that the attractiveness of trees bored by male beetles decreases after mating of

96   the beetles, and this leads to the cessation of attack (Ueda and Kobayashi 2001).

97   Some trees survive the initial attack without receiving a mass attack, while

98   other trees die because of the mass attack induced by the aggregation pheromone.   In

99   the case of *Quercus crispula* Blume, the mortality of attacked trees was about 40%

100   (Kamata et al. 2002).   It is interesting to speculate under which situations the attack

101   status of trees shifts from initial attack to mass attack.   Factors that could affect the

102   attack sequence include tree species, tree size, local environment, and timing of the

103   attack.

104   It has been suggested that *P. quercivorus* can discriminate between tree

105   species (Yamasaki and Futai 2012) with different susceptibilities (Kobayashi et al.

106   2004); therefore, a difference in the probability of initiation of a mass attack may be

107   observed among tree species.   The preference of *P. quercivorus* for targeting trees with

108   wider trunks (Akaishi et al. 2006; Yamasaki and Sakimoto 2009) may be explained by

109   the requirement of the species for large volumes of sapwood to construct galleries (Hijii

110   et al. 1991).   A similar preference might also be observed in the initiation of a mass

111   attack.

112   *Platypus quercivorus* shows positive phototaxis (Igeta et al. 2003), and

113   therefore the host selection behavior of the beetle may depend on forest light

114   environments, which change temporally and spatially.   Moreover, trees at different

115   topographies are subjected to varying levels of drought stress (Eckhardt and Menard

116   2008; Guarín and Taylor 2005), and this might affect the probability of their death after

117   attack.   The initiation of a mass attack might also be affected by the density of the

118   attacked trees (DEA).   A high DEA could expose surrounding trees to high levels of

119   aggregation pheromone, and result in a high probability of a mass attack.   In addition,

120   at sites where the attack by *P. quercivorus* begins early in the season, trees will be

121   exposed to the attack for a longer period, which might increase their mortality risk.

122   In the present study, we investigated the factors affecting the initiation of a

123   mass attack by *P. quercivorus*.   We analyzed the survival data of attacked fagaceous

124   trees collected from a 93-ha area, surveyed over 3 years.   Among the proposed factors,

125   the timing of the attack was impossible to measure throughout the wide area.

126   Therefore, based on our results, we discuss the indirect effect of topography related to

127   the timing of the attack.

128

129   **Material and methods**

130

131   *Study site and search for infected trees*

132

133   The present study was conducted in a secondary forest near the Hacchodaira

134   bog, located in eastern Kyoto Prefecture, Japan (35°14' N, 135°50' E, Fig. 2a).   The

135   altitude of the study area ranged from 800 m to 970 m above sea level.   The forest is in

136   a cool-temperate forest zone, and is dominated by *Q. crispula* and *Castanea crenata*

137   Sieb. et Zucc., which are highly susceptible and weakly susceptible, respectively, to

138   Japanese oak wilt.

139   Damage caused by *P. quercivorus* in the study area was first observed in 2008.

140   The 93-ha area was thoroughly searched from April to June in 2009, 2010, and 2011, to

141   identify fagaceous trees that had been attacked by *P. quercivorus* in the previous year.

142   The search effort was approximately 0.5 ha/h per person.   Attacks by *P. quercivorus*

143   were identified by the presence of holes bored by the beetle, and frass accumulation at

144   the base of the tree.   We identified the tree species and measured the diameter of each

145   attacked tree at 130 cm above the ground (diameter at breast height [DBH]).   The

146 survival of each attacked tree was determined and recorded, by checking the leaf flush

147 of the investigated year.   For multi-stemmed trees, DBH and survival were recorded

148 for each individual stem.   Differences in the mortality rate among trees species were

149 tested using a 2-sample test for equality of proportions.

150   The location of each attacked tree was mapped using a global positioning

151 system (GPS; GPS map 60 CSx, Garmin International, Inc., Olathe, Kansas).   The

152 longitude and latitude of each tree were projected onto a Transverse Mercator

153 coordinate system in meter units.   The altitude, topographic wetness index, and slope

154 aspect of each location were calculated from a digital elevation model provided by the

155 Geospatial Information Authority of Japan.   The topography projection and calculation

156 were performed using GRASS geographic information system (GIS) software (GRASS

157 Development Team 2010).

158

159 *Preparation of explanatory variables*

160

161   Although it was presumed that the DEA affected the probability of mortality

162 of an individual tree, the scale of this was unclear.   Therefore, we prepared the basal

163 area of attacked fagaceous trees (BA) by generating buffers around each stem, using 10

164 different scales ranging from a 2.5-m to a 25-m radius at 2.5-m intervals, and summing

165 the BA of stems included in each buffer.   When the generated buffer crossed the

166 boundary of the study area, the BA was corrected by dividing the cumulative basal area,

167 by the proportion of the buffer area inside the study area to the total buffer area.

168   We mapped the locations of attacked fagaceous trees (gray and black trees in

169 Fig. 1c) in the study area, and calculated the surrounding BA of each attacked tree as a

170   candidate explanatory variable for predicting its mortality. The locations of intact

171   fagaceous trees (trees drawn with dotted lines in Fig. 1c) were not mapped; therefore,

172   the density of fagaceous trees, including intact and attacked trees (density of probable

173   host trees [DEP]), could not be calculated. As a substitute for DEP, we prepared the

174   categorical variable of vegetation type at the location of each attacked tree. Vegetation

175   type was determined using the vegetation map created by the national survey on the

176   natural environment, conducted by the Biodiversity Center of Japan, Ministry of the

177   Environment. Five types of vegetation were observed in the study area—(1)

178   secondary forest dominated by *C. crenata* and *Q. crispula*, (2) secondary forest

179   dominated by Japanese cedar (*Cryptomeria japonica*) and *Q. crispula*, (3) secondary

180   forest dominated by *F. crenata* and *Q. crispula*, (4) bog, and (5) grassland. Fagaceous

181   trees were not observed in the grasslands.

182   The candidate explanatory variables for predicting the probability of mortality

183   of trees attacked in the present year did not include the distance from trees attacked in

184   the previous year, because of the lack of information regarding attacked trees outside

185   the study area, and the prevention control of beetle emergence conducted in the study

186   area. In the study area, diameter measurements of the trees have been recorded at

187   3-year intervals since 1980, in 13 fixed plots (boxes in Fig. 2b). No damage caused by

188   *P. quercivorus* was observed in these plots or their surroundings, until the 10th

189   measurements were conducted in 2007. In 2008, trees killed by *P. quercivorus* were

190   first observed in the surrounding plot; therefore, nearly all the damage in 2008 was

191   thought to be caused by beetles from outside the study area. It was difficult to check

192   the locations of trees outside the study area that had been attacked in the previous year,

193   i.e., 2007. In addition, irrespective of the present study, damage control trials were

194   conducted in the study area by Kyoto City, a conservator of this area.   From May to

195   July in 2009 and 2010, the basal parts of trunks of all dead trees attacked in the previous

196   year were covered by vinyl sheets, up to 3 m or 4 m above the ground, to prevent beetle

197   emergence and minimize damage to other trees.   Therefore, it was difficult to evaluate

198   the potential of trees attacked in the previous year to be sources of infection.

199

200   *Model construction and selection*

201

202   We modeled the probability of mortality of trees attacked by *P. quercivorus*

203   by using a generalized additive mixed model (GAMM) with the package *gamm4* in R

204   2.15.3 (R Core Team 2013).   The response variable used in the model was the survival

205   of stems (0 for surviving stems and 1 for dead stems).   The response variable follows a

206   binomial distribution, and therefore we set the link function of the model as a logit link.

207   The candidate explanatory variables were tree species, DBH, BA within a 2.5–25-m

208   radius, altitude, topographic wetness index, slope aspect, and vegetation type.   We

209   assumed a nonlinear effect of slope aspect, and used a cyclic cubic regression spline as

210   a smoother, to ensure that the values of the smoother at each end of slope aspect—0°

211   and 360°—were the same.

212   The data for analysis were prepared at the individual stem level.   We

213   observed a high frequency of multi-stemmed fagaceous trees in the study area; further,

214   stems of the same genet (individual tree) were basally connected with each other,

215   implying a dependent structure.   Therefore, the genet of trees, nested within tree

216   species, was included in the model as a random intercept (Zuur et al. 2009).   Model

217   selection was performed in 2 steps, to obtain the best-fit model for predicting the

218 probability of mortality of trees attacked by *P. quercivorus*.   In the first step, the best

219 scale to calculate the density of attacked trees as an explanatory variable in the model

220 for predicting the probability of mortality was evaluated.   In the second step, the

221 best-fit model with the lowest Akaike's information criterion (AIC) was selected from

222 various combinations of candidate explanatory variables.

223   In the first step, 10 models were constructed—including the BA values at 10

224 different scales and all other candidate explanatory variables— and the model with the

225 lowest AIC was selected as the full model.   In the second step, the best-fit model was

226 selected from the full model, by comparing the AIC of all candidate models with

227 various combinations of explanatory variables.   We used 7 candidate explanatory

228 variables (tree species, DBH, BA, altitude, topographic wetness index, slope aspect, and

229 vegetation type), and therefore the inclusion or exclusion of each variable resulted in

230 128 combinations.   Among these 128 models, the model with the lowest AIC was

231 selected as the best-fit model.   The relative variable importance (RVI) of each

232 candidate explanatory variable was calculated using the Akaike weights of the 128

233 models.   Comparisons of AIC and calculation of RVI were performed using the

234 *MuMIn* package in R.

235

236 **Results**

237

238   In the study area, *P. quercivorus* attacks were observed on 3 fagaceous

239 species, namely, *Q. crispula*, *Q. serrata* Murray, and *C. crenata*.   In 2008, 2009, and

240 2010, we recorded 366 (227), 531 (320), and 1,233 (731) stems (numbers within

241 parentheses are the number of genets), respectively (Table 1).   In general, the mortality

242   rate of the attacked stems was higher in *Q. crispula* than in *C. crenata* (Table 1), and

243   these differences were significant for all 3 years (2-sample test for equality of

244   proportions: Chi-squared = 4.368, *P* = 0.037 for 2008; Chi-squared = 24.328, *P* < 0.001

245   for 2009; Chi-squared = 25.4, *P* < 0.001 for 2010).   The study forest was dominated by

246   *Q. crispula* and *C. crenata*; the density of *Q. serrata* was low.   In comparison with *Q.*

247   *crispula* and *C. crenata*, *Q. serrata* showed a much lower number of attacked stems

248   (Table 1); therefore, data on *Q. serrata* were excluded from the statistical analyses.   In

249   2010, 40 stems of *Q. crispula* with a previous infection history (20 stems attacked in

250   2008 and 20 stems attacked in 2009) were reattacked by *P. quercivorus*.   Data on these

251   40 stems were also excluded from the statistical analyses, because trees with a previous

252   infection history are known to be resistant to *P. quercivorus* (Soné et al. 1998; Urano

253   2000).   Thus, data on the remaining 2063 stems were used for the statistical analyses.

254   The annual distribution of attacked *Q. crispula* in the study area differed from

255   that of *C. crenata* (Fig. 3).   Clumps of attacked *Q. crispula* were observed at the lower

256   edges of the ridge face on the bog (Fig. 3).   Generally, the density of attacked *Q.*

257   *crispula* was low on the west side of the study area (Fig. 3), where the vegetation was

258   dominated by Japanese cedar and *Q. crispula* (Fig. 2b).   Similar to this area, the center

259   area (bog) was distinguished by a low density of attacked *Q. crispula* (Fig. 3).   In 2008,

260   attacked *C. crenata* trees were distributed only on the north side; however, after 2009,

261   their distribution range extended to the south (Fig. 3).

262   We compared the ability of 10 models to predict the probability of mortality

263   of the attacked trees, by using tree species, DBH, altitude, topographic wetness index,

264   slope aspect, vegetation type, and BAs calculated at 10 different scales as explanatory

265   variables (Fig. 4).   The AIC of the model decreased with an increase in the radius of

266   the area used to calculate the BA, reaching its lowest value at a 15-m radius; thereafter,

267   the AIC increased (Fig. 4).   Therefore, the BA within a 15-m radius was used as a

268   candidate explanatory variable for modeling the probability of mortality of the attacked

269   trees.

270   DBH, topographic wetness index, slope aspect, and vegetation type were not

271   selected as explanatory variables in the best-fit model to predict the probability of

272   mortality of the attacked trees.   When *C. crenata* was set as a baseline, the estimated

273   coefficient for *Q. crispula* was positive (tree species in Table 2).   The estimated

274   coefficient for the BA was also positive, indicating that this variable had significant

275   positive effects on the probability of mortality of the attacked trees (Table 2).   A

276   significant negative effect on the probability of mortality was detected for altitude

277   (Table 2).   Tree species, BA, and altitude were equally important predictors in the

278   model (RVI = 0.99 or 1.00, Table 2).   Among the variables not selected for the best-fit

279   model, DBH showed the highest RVI (0.51), while vegetation type showed the lowest

280   RVI (0.16).

281

282   **Discussion**

283

284   In the present study, we showed that the mortality of trees attacked by *P.*

285   *quercivorus* was significantly higher in *Q. crispula* than in *C. crenata* (Table 1); further,

286   tree species was included in a best-fit model to predict the probability of mortality

287   (Table 2), implying that the probability of mortality was higher in *Q. crispula* than in *C.*

288   *crenata*.   *Quercus crispula* is a more suitable host for *P. quercivorus* than is *C. crenata*

289   (Tarno et al. 2011); therefore, the beetle is more inclined to use *Q. crispula* as an attack

290   target (Yamasaki and Futai 2012), resulting in a higher probability of death for this

291   species.

292   We demonstrated a positive effect of DEA on the probability of mortality

293   (Table 2), suggesting that mortality is low when the tree is individually attacked (i.e.,

294   with a low density of surrounding attacked trees), and high when the tree is attacked

295   together with surrounding individuals (i.e., with a high density of surrounding attacked

296   trees).   In other words, changes in infection phases, from initial attack to mass attack

297   (and subsequent death of the attacked tree), tend to occur when groups of trees are

298   attacked.   Therefore, it is likely that mass attacks of *P. quercivorus* occur not only in

299   individual trees, but also in groups of trees.   The ambrosia and bark beetles are thought

300   to attack trees *en masse* to break down the host tree's resistance; further, the male

301   beetles use an aggregation pheromone to attract conspecifics to an individual tree

302   (Wood 1982).   When attacked trees are clumped together (Fig. 3), the effects of the

303   aggregation pheromone might also work on a larger scale, and the beetle might be

304   attracted primarily to a group of trees.   The BAs calculated at a 15-m-radius scale, i.e.,

305   706.5 m^2 in area, were good predictors of the probability of mortality of the attacked

306   trees (Fig. 4), and may show the effective scale of clumped attacked trees as attractants

307   to the beetle.   In the case of initial attack by *P. quercivorus*, the effective DEP scale

308   was 900 m^2 (Yamasaki and Sakimoto 2009), which is slightly higher than the scale

309   suggested in the present study.   Beetles might begin to search for a suitable host tree

310   within a wide range, and after detecting clumped host trees, might narrow the target,

311   and precipitate a mass attack.

312   Previous studies showed negative effects of altitude on the probability of

313   mortality of ponderosa pine caused by *Ips* beetles (Negrón et al. 2009).   These

314 negative effects were explained by the shorter growing season for the beetles, caused by

315 the cooler temperatures at higher altitude (Williams et al. 2008).   A similar negative

316 effect of altitude was determined in the present study (Table 2); however, considering

317 the small range of altitude (800–970 m) in the study area, it is improbable that the

318 length of the beetle's growing season differs among trees at different altitude.   The

319 decrease in the probability of mortality of the attacked trees with an increase in altitude

320 may have arisen because of the host-seeking process of *P. quercivorus* in forests.   A

321 previous study showed that *P. quercivorus* moves upward along slopes (Esaki et al.

322 2004).   *Platypus quercivorus* might initially seek hosts at lower elevations in a forest,

323 and trees at the lower elevations might have a higher probability of mortality because of

324 their longer exposure to the beetle.

325   As reviewed in Fettig et al. (2007), insect resistance mechanisms are damaged

326 in trees that are stressed by factors such as drought, and this causes high susceptibility

327 to attack by the bark beetle.   Moreover, under severe drought conditions, susceptibility

328 to beetle attack is further increased by other stress factors (Eatough Jones et al. 2004).

329 In the present study, we determined no effect of wetness on the mortality of the attacked

330 trees (the topographic wetness index was not selected in the best-fit model, Table 2).

331 Vegetation type was also not selected in the best-fit model (Table 2).   The model

332 confirmed the lack of a relationship between water availability and the mortality of the

333 attacked trees.   The dataset for the present study included 4 vegetation types, namely,

334 bog and 3 types of secondary forest.   Water availability was evidently higher for trees

335 growing in a bog than for trees growing with other vegetation types; however, the

336 mortality of the attacked trees did not differ among vegetation types.   The mortality of

337 trees attacked by *P. quercivorus* is considered to be mainly affected by the occurrence

338   of mass attacks, and the local environment of trees may have little effect once a mass

339   attack is initiated.

340   *Platypus quercivorus* shows positive phototaxis, and might concentrate in

341   stands with more light (Igeta et al. 2003).   A study conducted at Hacchodaira—the

342   same site as that used in the present study—showed a negative effect of DEP at a large

343   scale on the probability of beetle attack (Yamasaki et al. in press), suggesting a beetle

344   preference for bright stands with low DEP.   Assuming that phototaxy functions during

345   the host-seeking process, the heterogeneity of light environments in a forest interior

346   caused by differences in slope aspect might have some effects on beetle aggregation.

347   However, in the present study, the mortality of attacked trees was not affected by slope

348   aspect (Table 2).   Therefore, positive phototaxis may function at an earlier time, such

349   as immediately after beetle emergence from holes, in order to orient them toward the

350   sky.   Nevertheless, many uncertainties regarding the flight behavior and flight height

351   of *P. quercivorus* exist.

352   Assuming that the DEP was uniform within the area of the same vegetation

353   type, exclusion of vegetation type (which showed the lowest RVI; Table 2) from the

354   model indicated no difference in mortality among attacked trees with different DEP

355   values.   However, even for the same vegetation types, DEP differed at a local scale.

356   Therefore, the possibility that DEP affects the mortality of attacked trees cannot be

357   excluded.   The inclusion of DEP at various scales as a candidate explanatory variable

358   for the model may clarify this issue.   Moreover, to elucidate a more precise host

359   selection process of *P. quercivorus*, the inclusion of variables not measured in the

360   present study (for example, the distance from trees attacked in the previous year) as

361   candidate explanatory variables is required.

362

Conclusion

364

365   Previous studies on trees attacked by *P. quercivorus* have considered all

366   probable host trees in a certain area as subjects of analysis, and have shown the

367   preferences of the beetles during their attack process with regard to species (Yamasaki

368   and Futai 2012), size (Akaishi et al. 2006; Yamasaki and Sakimoto 2009), and infection

369   history (Yamasaki and Futai 2008).   However, the attack process of the beetles is

370   thought to be divided into 2 phases—the initial attack and the mass attack (Fig. 1).   In

371   the present study, by analyzing only attacked trees, we clarified the factors affecting the

372   initiation of mass attack.   The exclusion of DBH and vegetation type from the best-fit

373   model for predicting the probability of mortality of the attacked trees suggests that *P.*

374   *quercivorus* selects clumped, wide trees not as a mass attack target, but as an initial

375   attack target.   The inclusion of BA in the best-fit model showed that *P. quercivorus*

376   selects dense stands of attacked trees as mass attack targets.   The results of a 3-year

377   survey of beetle infection over wide areas revealed the detailed host selection process of

378   the ambrosia beetle, *P. quercivorus*.

379

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Table 1 Mortality rate of stems attacked by *Platypus quercivorus*, and number of

attacked stems (within parentheses), in a secondary forest near the Hacchodaira bog,

located in eastern Kyoto Prefecture, Japan.   Data are separately shown for 3

fagaceous species, in 2008, 2009, and 2010.   In all 3 years, the mortality rate was

significantly higher in *Q. crispula* than in *C. crenata* (2-sample test for equality of

proportions: Chi-squared $= 4.368$, $P = 0.037$ for 2008; Chi-squared $= 24.328$, $P <$

0.001 for 2009; Chi-squared $= 25.4$, $P < 0.001$ for 2010).

	2008	2009	2010
Quercus crispula	40.3% (325)	45.5% (453)	39.5% (1124)
Quercus serrata	50.0% (2)	0% (8)	0% (17)
Castanea crenata	23.1% (39)	14.3% (70)	13.0% (92)

Table 2 Estimated coefficients, their standard errors, and z-statistics of variables selected for a best-fit model (n = 2063, AIC = 2196.764) to predict the probability of mortality of fagaceous trees caused by the ambrosia beetle, *Platypus quercivorus*, in a secondary forest near the Hacchodaira bog, located in eastern Kyoto Prefecture, Japan.

Variable	Estimate[a]	SE	z	P[b]		RVI[c]
Tree species[d]	3.85180	1.05806	3.640	0.00027	***	1.00
BA[e]	4.03259	0.73263	5.504	<0.00001	***	1.00
Altitude	−0.02997	0.00904	−3.316	0.00091	***	0.99
DBH[f]	-	-	-	-		0.51
Topographic wetness index	-	-	-	-		0.39
Slope aspect	-	-	-	-		0.39
Vegetation type	-	-	-	-		0.16

[a]Variables without estimates were not selected as explanatory variables for a best-fit model

[b]Significant differences from zero were tested using z-statistics (**$P < 0.01$, ***$P < 0.001$)

[c]RVI = relative variable importance, calculated using Akaike weights of all candidate models

[d]Tree species = species of attacked tree (estimated intercept for *Quercus crispula*, when *Castanea crenata* is set as a baseline, is shown)

[e]BA = basal area of attacked fagaceous trees within a 15-m radius

[f]DBH = diameter at breast height, i.e., diameter of the attacked tree at 130 cm above ground

Fig. 1 Course of infection by *Platypus quercivorus*.   (a) Intact fagaceous trees distributed in a forest.   (b) Some trees receive an initial attack by the beetle.   (c) Mass attack occurs on some of the trees that received the initial attack.   White, gray, and black trees show intact trees, trees that received an initial attack, and trees that received a mass attack subsequent to the initial attack, respectively.   Trees drawn with a dotted line are not a target of the mass attack.
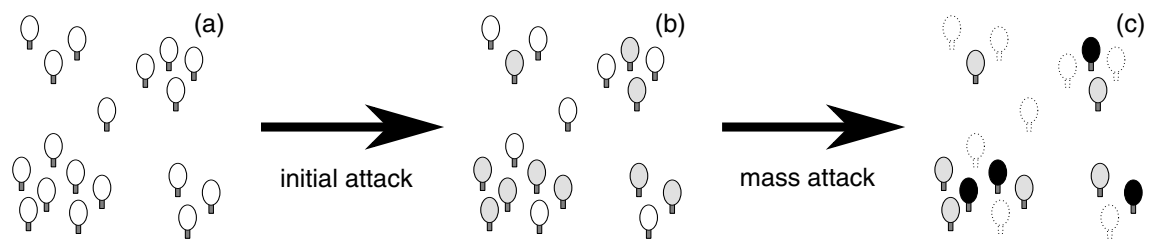
Fig. 2 (a) Location of the study site in Japan.　(b) Vegetation type in and around the study area.　The thick line shows the study area.　The white, gray, dark gray, black, and light gray areas show the secondary forest dominated by *Castanea crenata* and *Quercus crispula*, other types of secondary forest, artificial forest, bogs, and other types of vegetation such as grasslands, respectively.　Gray lines show contour lines at 10-m intervals.　Boxes show the location of 13 fixed plots set up in 1980.

☐ Secondary forest dominated by fagaceous trees
▨ Other types of secondary forest
▧ Artificial forest
■ Bogs
☐ Grasslands, etc.
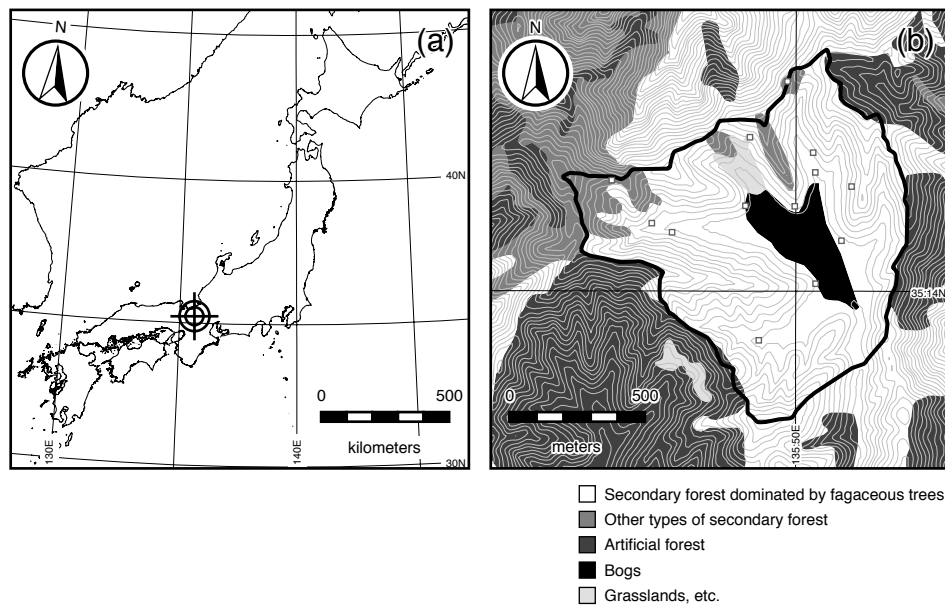
Fig. 3 Distribution of *Quercus crispula* (top) and *Castanea crenata* (bottom) attacked by *Platypus quercivorus* in 2008 (left), 2009 (center), and 2010 (right) in a secondary forest near the Hacchodaira bog, located in eastern Kyoto Prefecture, Japan.   Circle, surviving tree; cross, dead tree.
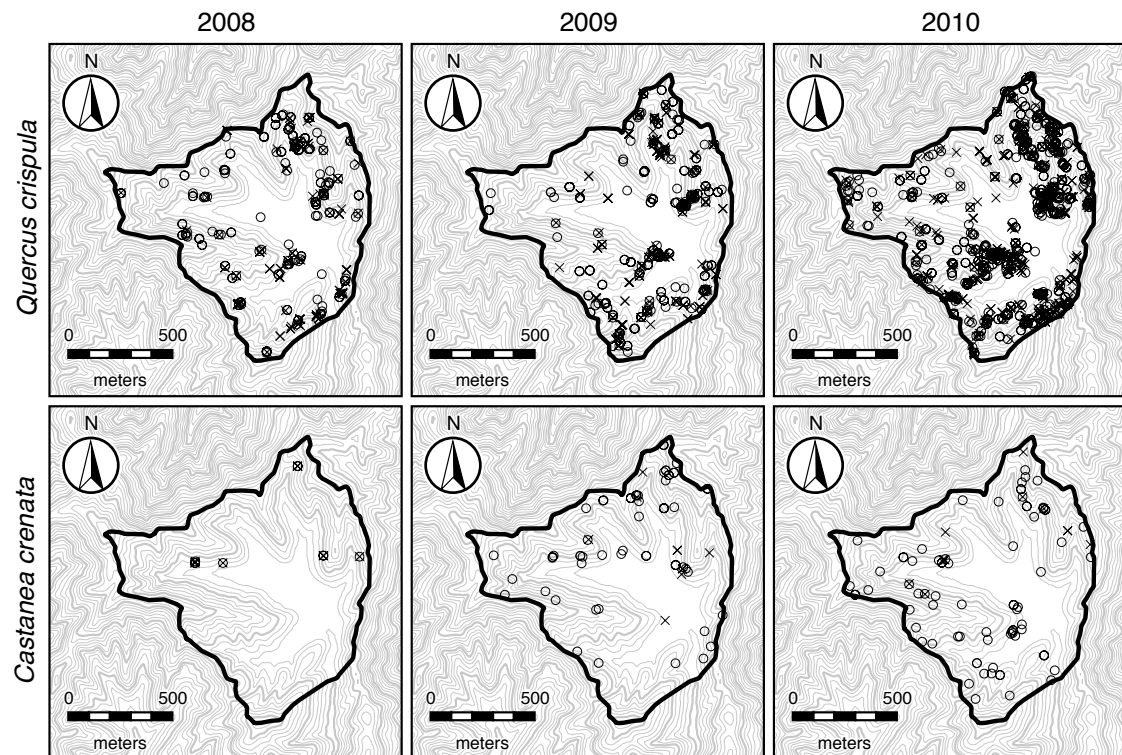
Fig. 4 Akaike's information criterion (AIC) of 10 different models to predict the mortality probability of fagaceous trees attacked by *Platypus quercivorus* in a secondary forest near the Hacchodaira bog, located in eastern Kyoto Prefecture, Japan.　The basal areas of attacked trees calculated within a radius of 2.5–25 m of the target tree were included in each model, together with the other candidate explanatory variables.