

A peer-reviewed version of this preprint was published in PeerJ on 22 December 2016.

[View the peer-reviewed version](https://peerj.com/articles/2816) (peerj.com/articles/2816), which is the preferred citable publication unless you specifically need to cite this preprint.

Itô H. (2016) Changes in understory species occurrence of a secondary broadleaved forest after mass mortality of oak trees under deer foraging pressure. PeerJ 4:e2816 <https://doi.org/10.7717/peerj.2816>

Changes in understory species occurrence of a secondary broadleaved forest after mass mortality of oak trees under deer foraging pressure

Hiroki Itô ^{Corresp.} 1

¹ Hokkaido Research Center, Forestry and Forest Products Research Institute, Sapporo, Hokkaido, Japan

Corresponding Author: Hiroki Itô
Email address: abies.firma@gmail.com

The epidemic of mass mortality of oak trees has affected secondary deciduous broadleaved forests that have been used as coppices in Japan. The dieback of oak trees formed gaps in the crown that would be expected to enhance the regeneration of shade-intolerant pioneer species. However, foraging by sika deer *Cervus nippon* has also affected forest vegetation, and the compound effects of both on forest regeneration should be considered when they simultaneously occur. A field study was conducted in Kyôto City, Japan, to investigate how these compound effects affected the vegetation of the understory layer of such a forest. The presence/absence of seedlings and saplings was observed for 200 quadrats sized 5 m × 5 m for each species in 1992, before the mass mortality and deer encroachment, and in 2014 after these effects. A hierarchical Bayesian model was constructed to explain the occurrence, survival, and colonization of each species with their responses to the gaps created or affected by the mass mortality of oak trees. The species that occurred most frequently in 1992, *Eurya japonica*, *Quercus glauca*, and *Cleyera japonica*, also had the highest survival probability. Deer-unpalatable species such as *Symplocos prunifolia* and *Triadica sebifera* had higher colonization rates in the gaps, while the deer-palatable species *Aucuba japonica* had the smallest survival probability. The gaps thus resulted in promoting the colonization of deer-unpalatable plant species such as *Symplocos prunifolia* and *Triadica sebifera*. It might be forecasted that such deer-unpalatable species will dominate the gaps created or affected by the mass mortality of oak trees.

1 Changes in understory species occurrence 2 of a secondary broadleaved forest after 3 mass mortality of oak trees under deer 4 foraging pressure

5 Hiroki Itô¹

6 ¹Hokkaido Research Center, Forestry and Forest Products Research Institute, Toyohira,
7 Sapporo 305-8687, Japan. Email address: abies.firma@gmail.com

8 ABSTRACT

9 The epidemic of mass mortality of oak trees has affected secondary deciduous
10 broadleaved forests that have been used as coppices in Japan. The dieback of
11 oak trees formed gaps in the crown that would be expected to enhance the regen-
12 eration of shade-intolerant pioneer species. However, foraging by sika deer *Cervus*
13 *nippon* has also affected forest vegetation, and the compound effects of both on forest
14 regeneration should be considered when they simultaneously occur. A field study was
15 conducted in Kyôto City, Japan, to investigate how these compound effects affected the
16 vegetation of the understory layer of such a forest. The presence/absence of seedlings
17 and saplings was observed for 200 quadrats sized 5 m × 5 m for each species in
18 1992, before the mass mortality and deer encroachment, and in 2014 after these
19 effects. A hierarchical Bayesian model was constructed to explain the occurrence,
20 survival, and colonization of each species with their responses to the gaps created or
21 affected by the mass mortality of oak trees. The species that occurred most frequently
22 in 1992, *Eurya japonica*, *Quercus glauca*, and *Cleyera japonica*, also had the high-
23 est survival probability. Deer-unpalatable species such as *Symplocos prunifolia* and
24 *Triadica sebifera* had higher colonization rates in the gaps, while the deer-palatable
25 species *Aucuba japonica* had the smallest survival probability. The gaps thus resulted
26 in promoting the colonization of deer-unpalatable plant species such as *Symplocos*
27 *prunifolia* and *Triadica sebifera*. It might be forecasted that such deer-unpalatable
28 species will dominate the gaps created or affected by the mass mortality of oak trees.

29 Keywords: deer-unpalatable plant species, gap, Japanese oak wilt, sika deer, under-
30 story vegetation

31 INTRODUCTION

32 Many coppices have been abandoned for socio-economic reasons, such as the replace-
33 ment of woody fuels with fossil fuels in Europe (Rackham, 2008; Müllerová et al., 2015;
34 Svátek and Matula, 2015). This abandonment parallels that of Japan (Suzuki, 2013),
35 and a considerable number of deciduous oak forests grown from such coppices have
36 suffered from the mass mortality of oak trees (Kuroda et al., 2012; Nakajima and Ishida,
37 2014). This mass mortality has been caused by Japanese oak wilt (Kuroda et al., 2012),

38 a pathogenic species of fungus *Raffaelea quercivora* Kubono et Shin. Ito, which is
39 carried by the ambrosia beetle *Platypus quercivorus* Murayama (Kubono and Ito, 2002;
40 Kinuura and Kobayashi, 2006).

41 The mass mortality altered the structures of damaged oak forests. The two major
42 deciduous oak species in Japan, *Quercus crispula* Blume and *Quercus serrata* Murray,
43 are vulnerable to the pathogenic fungus. Nakajima and Ishida (2014) showed that 80
44 $\pm 19\%$ (mean \pm standard deviation) stems of *Quercus crispula* died while $34 \pm 19 \%$
45 stems of *Quercus serrata* died. How such damaged oak forests are regenerated depends
46 on circumstance; sub-canopy trees might grow to canopy trees in some cases (Itô et al.,
47 2009), and dense floor vegetation such as dwarf bamboo might inhibit regeneration in
48 other cases (Itô et al., 2011; Saito and Shibata, 2012). In the latter case, the damaged
49 forests may lack a canopy layer for a long time.

50 For the last several decades, one of the most serious problems for forest vegetation is
51 impact by deer in Europe and North America (Rooney, 2001; Côté et al., 2004; Rackham,
52 2008). This is also paralleled in Japan: sika deer (*Cervus nippon* Temminck) is the major
53 inhibitor of forest regeneration (Takatsuki, 2009; Iijima and Nagaike, 2015). However,
54 little is known about how regeneration proceeds after mass mortality under deer foraging
55 pressure (Obora et al., 2013). Gap formations should improve light conditions on the
56 forest floor and promote the regeneration of many tree species (Suzuki, 2013). However,
57 deer browsing should inhibit regeneration except for unpalatable species (Shimoda et al.,
58 1994). Therefore, a combination of both factors might promote the regeneration of
59 species that are unpalatable to deer. This in turn may change the species composition of
60 damaged forests in the future.

61 It is important for the management of secondary forests to predict what tree or
62 shrub species will be recruited in forest stands damaged by the mass mortality of oak
63 trees and deer impact. In a previous study, Itô (2015) described the changes in the
64 canopy/sub-canopy and understory layers of a damaged forest by comparing before and
65 after the occurrence of mass mortality of oak trees and deer foraging. It was found for the
66 understory layer that regenerating species were limited to the originally abundant species,
67 such as *Quercus glauca* Thunb., *Cleyera japonica* Thunb., and *Eurya japonica* Thunb.
68 var. *japonica*, as well as to species unpalatable to deer, such as *Symplocos prunifolia*
69 Siebold et Zucc. and *Triadica sebifera* (L.) Small. However, the study only described the
70 changes in species occurrence and failed to estimate the specific probabilities of survival
71 and colonization. In this study, the previous data were reanalyzed using a statistical
72 model to more precisely estimate those parameters for each species in the understory
73 layer. This should enable us to forecast which species will dominate such stands in the
74 future.

75 MATERIALS AND METHODS

76 Study site

77 The field data were collected in the Ginkakuzi-san National Forest located in Kyôto
78 City, Japan (35.029°N, 135.801°E). The yearly average temperature from 1981 to 2010
79 was 15.9°C and the average precipitation in the same term was 1491.3 mm at the Kyôto
80 Local Meteorological Office. Altitude of the forest was about 100-290 m above sea
81 level, and the forest was in the warm temperate zone. The national forest was protected

82 for its landscape and the prevention of earth outflow, and most of it was situated in
83 the buffer zone of the UNESCO world heritage, historic monuments of ancient Kyôto.
84 The Kyôto-Ôsaka District Forest Office and Forestry and the Forest Products Research
85 Institute agreed to conduct the study cooperatively in the national forest.

86 In the 1930s, most of the forest was covered with a mix of pines (*Pinus densiflora*
87 Siebold et Zucc.) and broadleaved trees including oak (*Quercus serrata*). After the
88 1960s, many pine trees had died due to the pine wilt disease. Recently, most of the
89 national forest has been covered with a secondary broadleaved forest consisting of
90 many species such as evergreen oak *Quercus glauca*, evergreen subcanopy species
91 *Symplocos prunifolia*, and deciduous tree species *Ilex macropoda* Miq., although conifers
92 (*Cryptomeria japonica* (L.f.) D.Don and *Chamaecyparis obtusa* (Siebold et Zucc.)
93 Endl.) were planted in a small part of the area (Itô, 2007). In the last decade, the mass
94 mortality of oaks has damaged the forest. In addition, damages by sika deer such as
95 browsing and bark-stripping have been noticeable over the same period (Itô, 2015).

96 In 1992, a study plot sized 0.5 ha (100 m × 50 m) was settled on a south-facing slope
97 in the national forest at an altitude of about 142-194 m. The average slope inclination
98 was about 30° and the surface geology was granite. All the stems in the plot were marked
99 and their diameters at breast height (dbh) were measured in 1993, 1996, 1999, 2002,
100 2005, and 2014. Mainly due to the mass mortality of oak trees *Q. serrata*, the basal
101 area in the plot was decreased from 43.3 m²/ha in 2005 to 39.5 m²/ha in 2014, while
102 the number of stems in the plot increased from 1554 to 1645. There were 36 *Quercus*
103 *serrata* stems in the plot in 2005, and 21 of them died by 2014. Almost all seemed
104 to be killed by Japanese oak wilt. This affected the forest structure in the plot via the
105 formation of new canopy gaps or additive disturbance to existing gaps Itô (2015). On
106 the other hand, none of the evergreen oaks *Quercus glauca* died from the disease though
107 some were attacked by the ambrosia beetles, being less vulnerable than *Quercus serrata*
108 (Murata et al., 2005, 2009). In the understory layer, *Quercus glauca* and some evergreen
109 shrub species such as *Eurya japonica* and *Cleyera japonica* were frequently observed.
110 Overall changes in the stand composition of the site from 1990s to 2010s were reported
111 in Itô (2015).

112 Data collection

113 The plot was divided into 200 quadrats sized 5 m × 5 m. In 1992, all woody plant
114 seedling or saplings (age ≥ 1 year and dbh < 3 cm) were searched for throughout each
115 quadrat, and the species names of found seedlings and saplings were recorded. The
116 same observation was conducted again in 2014. In 2004, each quadrat was classified
117 into inside or outside of the gaps, which were formed by death of oak trees, or had been
118 gaps at least since 2005 and were affected in addition by fallen dead oak trees. Twenty
119 of 200 quadrats were classified as gaps created or affected by oak death. The size of the
120 largest gap was approximately 250 m² consisting of 10 adjacent quadrats.

121 In 1992, 55 species were observed and 58 species in 2014 (Itô, 2015). The following
122 analysis was conducted for 42 of the species that were observed in more than 5 of 400
123 occasions (200 quadrats × 2 observations).

124 **Statistical Modeling**

125 A hierarchical Bayesian model was constructed to explain which species benefited or
126 were damaged in the understory layer by the recent environmental changes in the forest.

127 The presence/absence (presence = 1, absence = 0) of species i in quadrat j in the
128 year 1992 (y_{1ij}) and 2014 (y_{2ij}) was assumed to follow the Bernoulli distribution given
129 the occurrence probability ψ_{1ij} and ψ_{2ij} , as follows,

$$y_{1ij} \sim \text{Bernoulli}(\psi_{1ij})$$

$$y_{2ij} \sim \text{Bernoulli}(\psi_{2ij}).$$

130 To be exact, the “presence/absence” was “detection/nondetection” (Dorazio et al.,
131 2006; Kéry and Schaub, 2012). It has been pointed out that detection probability should
132 be considered to correctly estimate population properties such as the occurrence rate
133 or survival rate, even if the observed objects are plants (Kéry, 2004; Chen et al., 2009,
134 2013). The present study had, regrettably, only one observation for each survey year.
135 However, the quadrat size was rather small (5 m × 5 m) and the whole of each quadrat
136 was explored, so I expected that the detection probability should be near to one and
137 therefore “detection/nondetection” was regarded as “presence/absence” in this study.
138 Chen et al. (2009) showed that the detection probability asymptotically approaches one
139 with larger survey efforts.

The parameter of occurrence in 1992, ψ_{1ij} , was formulated as follows,

$$\text{logit}(\psi_{1ij}) = \beta_0 + \varepsilon_{oi} + r_j,$$

140 where β_0 denotes an intercept or overall mean of ψ_1 on the logit scale, and ε_{oi} denotes
141 the species random effect on the intercept of species i . The parameter r_j denotes a
142 spatially autocorrelated random effect of quadrat j .

The parameter of occurrence in 2014, ψ_{2ij} , was formulated as follows,

$$\psi_{2ij} = y_{1ij}\phi_{ij} + (1 - y_{1ij})\gamma_j,$$

143 where parameter ϕ_{ij} denotes the ‘survival’ probability that species i was present in
144 quadrat j in 1992 and still present in 2014. The parameter γ_j denotes the ‘colonization’
145 probability that species i was absent in quadrat j in 1992 but present in 2014.

The parameters of survival ϕ_{ij} and colonization γ_j were formulated as follows,

$$\text{logit}(\phi_{ij}) = \beta_s + \varepsilon_{si} + (\beta_{sg} + \varepsilon_{sgi})g_j$$

$$\text{logit}(\gamma_j) = \beta_c + \varepsilon_{ci} + (\beta_{cg} + \varepsilon_{cgi})g_j,$$

146 where the parameters β_s and β_c are intercepts or overall means of ϕ and γ on the
147 logit scale, respectively. The parameters ε_{si} and ε_{ci} are species random effects on the
148 intercepts, β_{sg} and β_{cg} are coefficients of the gap covariate g_j (0: non-gap quadrats, 1:
149 gap quadrats affected by oak mortality), and ε_{sgi} and ε_{cgi} are species random effects on
150 the coefficients.

151 Priors of the species random effects were defined hierarchically; hyperparameters,
152 σ_0 , σ_s , σ_{sg} , σ_c and σ_{cg} , scaled the distribution of ε_{oi} , ε_{si} , ε_{sgi} , ε_{ci} and ε_{cgi} , respectively,
153 as follows,

$$\varepsilon_{oi} \sim \text{Normal}(0, \sigma_o^2)T(-10, 10),$$

154 where $\text{Normal}(0, \sigma^2)T(-10, 10)$ denote a normal distribution truncated between -10
 155 and 10; the truncation was incorporated to stabilize the logit scale parameters (Kéry and
 156 Schaub, 2012). Priors of the parameters β_o , β_{op} , β_{os} , β_s , β_{sg} , β_c , and β_{cg} were defined as
 157 $\text{Normal}(0, 10^4)T(-10, 10)$. The prior of the spatial effect r_j was defined as an intrinsic
 158 conditional autoregressive model as follows,

$$r_j | r_{-j} \sim \text{Normal} \left(\sum_{k \neq j} \frac{w_{jk} r_j}{w_{j+}}, \frac{\sigma_r^2}{w_{j+}} \right),$$

159 where r_{-j} denote the values of r except the quadrat j , a variable w_{jk} was defined to be 1
 160 if quadrat j and quadrat k are adjacent, and 0 if not, and w_{j+} was defined to be $\sum_k w_{jk}$.
 161 The parameter σ_r^2 denotes a variance of the random effect.

162 Presence/absence data of 42 species, which were observed in more than 5 quadrats
 163 in total combining 2 survey occasions, 1992 and 2014, were used for the parameter
 164 estimation. The parameters were estimated using the Markov chain Monte Carlo
 165 (MCMC) method. Four parallel chains were generated, and each of them had 13,000
 166 iterations while the first 3,000 iterations were dropped as burn-in. The MCMC sample
 167 was taken from the three chains with 10 thinning intervals, so that the sample size was
 168 4,000. OpenBUGS 3.2.3 (Lunn et al., 2009) was used for the computation. The BUGS
 169 code is available in List S2.

170 RESULTS

171 The MCMC calculation seemed to be successfully converged; Gelman-Rubin statistics
 172 (\hat{R}) were no larger than 1.1 for each parameter (Gelman and Rubin, 1992; Brooks and
 173 Gelman, 1998). However, some random species effects on coefficients of gaps had
 174 rather wide posteriors such as in *Quercus glauca* (Fig. 3B). Those parameters might lack
 175 enough information to estimate precise posteriors due to the small number of colonizers
 176 in the gap quadrats for those species.

177 Posterior mean, median, and 95% CI (Credible Interval) of the overall occurrence
 178 probability in 1992, β_o , was estimated to be -3.25 for the posterior mean, -3.25 for the
 179 median, and -3.99 – -2.54 for the 95% CI, equivalent to 0.037, 0.037, and 0.018 – 0.073
 180 on the probability scale, respectively (Table 1). The overall survival probability, β_s , was
 181 estimated to be -2.60 for the posterior mean, -2.57 for the median, and -4.11 – -1.44
 182 for the 95% CI, equivalent to 0.069, 0.071, and 0.016 – 0.019 on the probability scale,
 183 respectively. The overall colonization probability, β_c , was estimated to be -3.81 for the
 184 posterior mean, -3.81 for the median, and -4.45 – -3.18 for the 95% CI, equivalent to
 185 0.022, 0.022, and 0.012 – 0.040 on the probability scale, respectively.

186 Posterior mean of coefficients of the gap on the survival β_{sg} and colonization β_{cg}
 187 were -0.17 and 1.51, respectively, and β_{cg} did not include zero in the 95% CI (0.86 –
 188 2.08), while β_{sg} included zero in the 90% CI (-1.27 – 0.81).

189 Random species effects on occurrence probability in 1992 (ε_o) are shown in Fig. 1.
 190 *Eurya japonica*, and *Quercus glauca* had the largest value, followed by *Aucuba japonica*,

Table 1. Parameter estimates other than random effects

	Mean	SD	2.5%	5%	50%	95%	97.5%
β_o	-3.25	0.37	-3.99	-3.88	-3.25	-2.65	-2.54
β_s	-2.60	0.67	-4.11	-3.81	-2.57	-1.61	-1.44
β_{sg}	-0.17	0.65	-1.54	-1.27	-0.14	0.81	1.04
β_c	-3.81	0.32	-4.45	-4.33	-3.81	-3.28	-3.18
β_{cg}	1.51	0.31	0.86	0.98	1.53	1.99	2.08
σ_o	2.27	0.30	1.76	1.82	2.24	2.81	2.95
σ_s	2.89	0.57	1.97	2.07	2.84	3.91	4.13
σ_{sg}	1.51	0.84	0.19	0.31	1.40	3.07	3.48
σ_c	1.89	0.28	1.43	1.48	1.86	2.40	2.51
σ_{cg}	1.35	0.32	0.81	0.88	1.32	1.93	2.07
σ_r	0.44	0.10	0.27	0.29	0.44	0.60	0.65

SD: Standard Deviation.

191 *Cleyera japonica*, *Ilex crenata*, *Photinia glabra*, and so on. On the other hand, *Carpinus*
 192 *tschonoskii*, *Celtis sinensis*, *Zanthoxylum ailanthoides*, and *Triadica sebifera* had the
 193 smallest values because these species were not detected in 1992 (Fig. 1). Random
 194 species effects on intercept of survival (ϵ_s) are shown in Fig. 2A. *Quercus glauca* had
 195 the largest value, and *Cleyera japonica*, *Eurya japonica*, *Camellia japonica* L., and
 196 *Symplocos prunifolia* followed. The posterior of *Aucuba japonica* Thunb. var. *japonica*
 197 was less than zero within 95% CI (Fig. 2A). Random species effects on the survival
 198 coefficients of gap covariates were rather small and included zero in their 90% CI for
 199 all species (Fig. 2B). Random species effects on intercepts of colonization were the
 200 largest in *Quercus glauca*, followed by *Eurya japonica*, *Cleyera japonica*, *Symplocos*
 201 *prunifolia*, *Photinia glabra* (Thunb.) Maxim., and so on (Fig. 3A). Random species
 202 effects on the colonization coefficient of the gap were the largest in *Callicarpa mollis*
 203 Siebold et Zucc., followed by *Zanthoxylum ailanthoides* Siebold et Zucc., *Carpinus*
 204 *tschonoskii* Maxim., *Triadica sebifera* and so on. They were the smallest in *Cleyera*
 205 *japonica* (Fig. 3B).

206 Complete estimates of random effects are available in Table S3.

207 DISCUSSION

208 The posterior mean of overall occurrence probability in 1992 was estimated to be -3.25,
 209 equivalent to 0.037 on the probability scale; this meant that a species was expected
 210 to occur in only 3.7% of quadrats. However, the random species effect on occurrence
 211 widely varied; the posterior mean of ϵ_o ranged from -3.21 (*Carpinus tschonoskii*) to
 212 5.71 (*Eurya japonica*) (Fig. 1). The expected occurrence probability would be 0.00
 213 ($= \text{logit}^{-1}(-3.25 - 3.21)$) for *Carpinus tschonoskii* and 0.92 ($= \text{logit}^{-1}(-3.25 + 5.71)$)
 214 for *Eurya japonica*. The most frequent species in 1992 were all evergreen tree or shrub
 215 species such as *Eurya japonica*, *Quercus glauca*, *Aucuba japonica*, *Cleyera japonica*,
 216 *Ilex crenata* Thunb., and *Photinia glabra*. On the other hand, the least occurring
 217 species were deciduous trees or shrubs such as *Castanopsis tschonoskii*, *Zanthoxylum*
 218 *ailanthoides*, *Celtis sinensis* Pers., and *Triadica sebifera*; these species were not detected

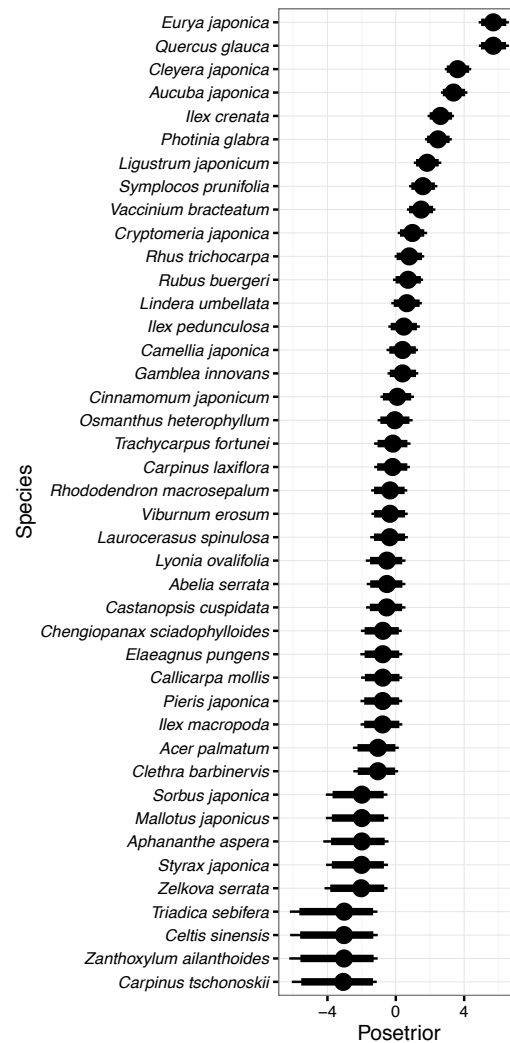


Figure 1. Random species effects on occurrence in 1992 ϵ_0 .

Thin lines denote 95% credible intervals (CI), thick lines denote 90% CI, and circles denote medians.

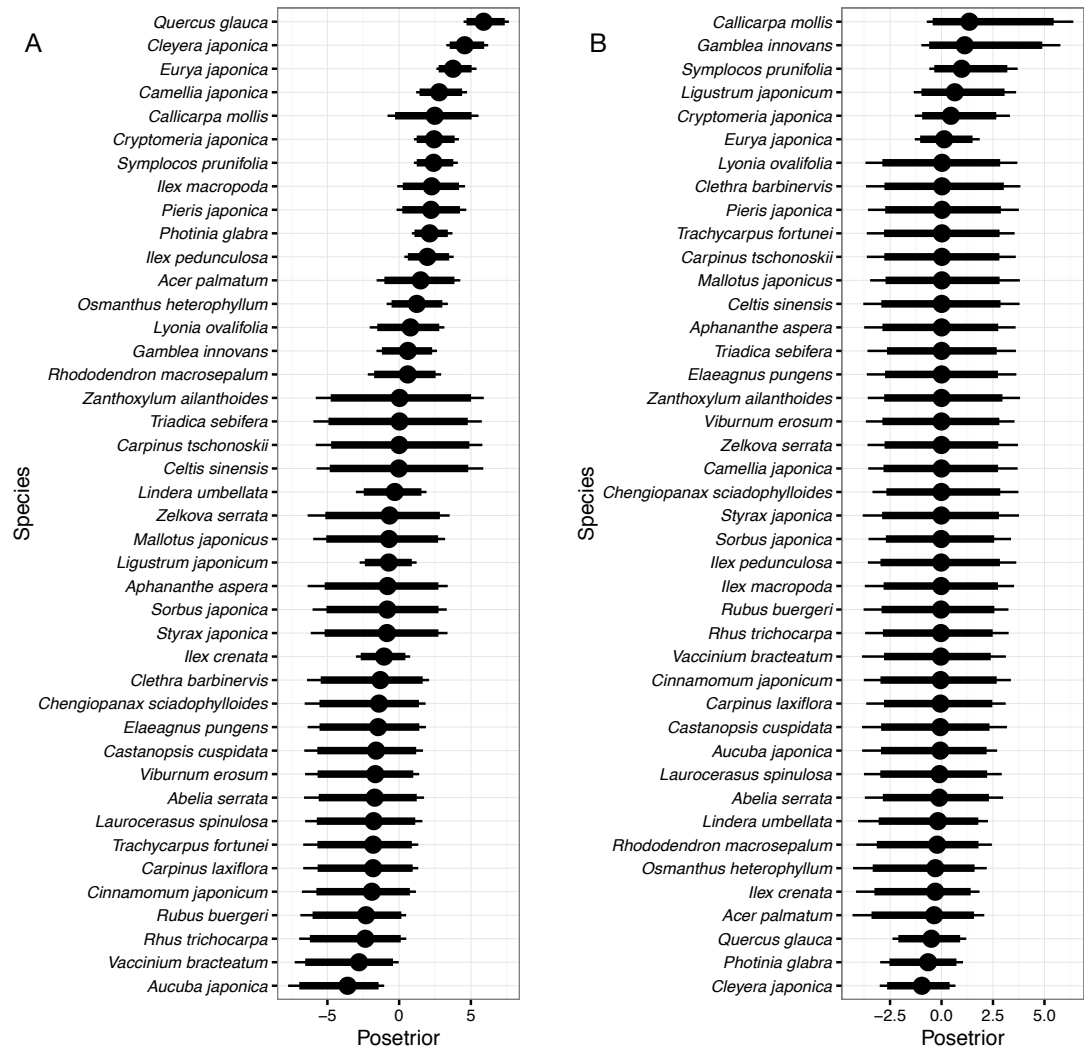


Figure 2. Random species effects on survival.

(A) ϵ_s , on the intercept, (B) ϵ_{sp} and (B) ϵ_{sg} , on the coefficient of the gap. Thin lines denote 95% credible intervals (CI), thick lines denote 90% CI, and circles denote medians.

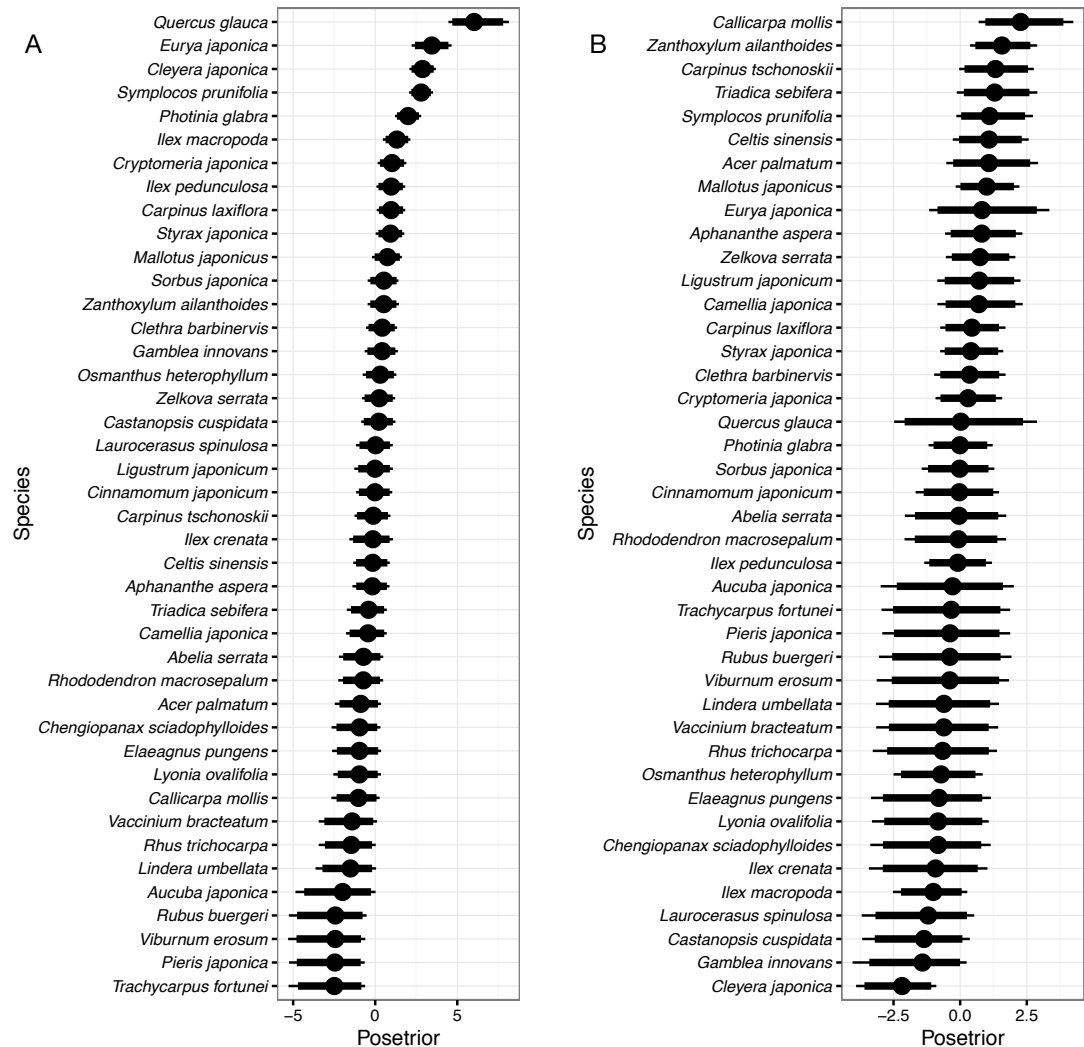


Figure 3. Random species effects on colonization.

(A) ϵ_c , on the intercept and (B) ϵ_{cg} , on the coefficient of the gap. Thin lines denote 95% credible intervals (CI), thick lines denote 90% CI, and circles denote medians.

219 in the quadrats in 1992. The canopy of the forest was almost closed in 1992, so that
220 shade-tolerant evergreen tree or shrub species dominated the understory layer and
221 deciduous early-successional species infrequently occurred.

222 The posterior mean of survival intercept was largest in *Quercus glauca* (Fig. 2A);
223 the posterior mean was 5.484 and the expected survival probability without the gap
224 effects was estimated to be 0.97 ($= \text{logit}^{-1}(-2.60 + 5.93)$). *Cleyera japonica*, *Eurya*
225 *japonica*, and *Camellia japonica* followed. These are all evergreen broadleaved species
226 that can survive under a closed canopy, as shown by their occurrence. On the other hand,
227 *Aucuba japonica*, a species of evergreen shrub, had the smallest survival probability;
228 the posterior mean of the random effect was -3.80 and the expected value of survival
229 probability was 0.00 (the calculation was the same as above). *Aucuba japonica* is known
230 to be a food plant for sika deer and is vulnerable to deer browsing (Hashimoto and Fujiki,
231 2014). The encroachment of deer likely explains its small survival probability. The
232 posterior mean of the random effect was the second smallest in *Vaccinium bracteatum*
233 Thunb. There are relatively small amounts of data on the palatability of *Vaccinium*
234 *bracteatum* for sika deer, and some reports refer to it as a food plant while others refer
235 to it as unpalatable (Nakajima, 1929; Kabaya, 1988; Takatsuki, 1989; Hashimoto and
236 Fujiki, 2014). The present results suggest that the species is vulnerable to deer impacts.

237 The random species effects on the coefficients of gap covariates seemed relatively
238 small (Fig 2B). They contained 0 within their 90% CI for all species. This indicates that
239 species heterogeneity in survival may be small within gaps, but that may be due to few
240 light-demanding species occurring in 1992.

241 The posterior mean of colonization intercept was largest also in *Q. glauca* (Fig. 3A);
242 the posterior mean was 6.09 and the expected survival probability without the gap effects
243 was estimated to be 0.91 ($= \text{logit}^{-1}(-3.81 + 6.09)$).

244 Random species effects on the colonization coefficient of the gap covariate was
245 the largest in *Callicarpa mollis*, followed by *Zanthoxylum ailanthoides*, *Carpinus*
246 *tschonoskii*, and *Triadica sebifera* (Fig. 3B). The four species whose colonization
247 probabilities were largest in the gaps are all shade-intolerant (Shimoda et al., 1994;
248 Shibata and Nakashizuka, 1995). In addition, the following *Symplocos prunifolia* is also
249 considered a shade-intolerant species though it is an evergreen species (Fujii, 1994).
250 However, *Symplocos prunifolia* and *Triadica sebifera* are unpalatable plants for sika deer
251 (Shimoda et al., 1994; Hashimoto and Fujiki, 2014). *Triadica sebifera* is an alien species
252 in Japan. The species is unpalatable for sika deer (Shimoda et al., 1994; Hashimoto and
253 Fujiki, 2014), and it is increasing on Mt. Kasugayama (Maesako et al., 2007). Shimoda
254 et al. (1994) studied the deer effects on pioneer species on Mt. Kasugayama in Nara,
255 which is located about 40 km south of the study site and is inhabited by many deer; the
256 authors found that pioneer species including *Zanthoxylum ailanthoides* and *Callicarpa*
257 *mollis* emerged in gaps but rarely survived or matured due to deer foraging pressure.
258 *Quercus glauca* originally occurred in most parts of the site, and the survival probability
259 of the species was large, but it also food plant for sika deer (Hashimoto and Fujiki,
260 2014).

261 In the study site, small amounts of large plants (height ≥ 50 cm) of *Zanthoxylum*
262 *ailanthoides*, *Callicarpa mollis*, and *Carpinus tschonoskii* were found, though large
263 amounts of those of *Quercus glauca*, *Cleyera japonica*, and *Eurya japonica* were found
264 in the quadrats that were not affected by the mass oak mortality (Itô, 2015). The latter

265 species are evergreen trees or shrubs, and they had been dominant at least since 1992.
266 In addition to these species, large plants of *Symplocos prunifolia* and *Triadica sebifera*
267 were found in the gap quadrats created or affected by the mass mortality (Itô, 2015), and
268 the large amounts of their saplings and seedlings might contribute to their survival.

269 CONCLUSION

270 Gaps created or affected by the mass mortality of oak trees might be beneficial for pioneer
271 species. Shade-intolerant species such as *Callicarpa mollis*, *Zanthoxylum ailanthoides*,
272 *Carpinus tschonoskii*, *Triadica sebifera*, and *Symplocos prunifolia* were estimated to
273 more frequently colonize the gaps. In addition, deer-unpalatable species *Symplocos*
274 *prunifolia* and *Triadica sebifera* may be more likely to survive or mature under foraging
275 pressure of deer, and this may change the species composition in regenerated stands.

276 In the future, deer-unpalatable species such as *Symplocos prunifolia* and *Triadica*
277 *sebifera* may dominate the understory rather than the current dominant species such
278 as *Eurya japonica* and *Quercus glauca* within the gaps created or affected by mass
279 mortality of oak trees.

280 ACKNOWLEDGEMENTS

281 I thank Dr. K. Hirayama (Kyôto Prefectural University) for cooperating with the
282 fieldwork and the Kyôto-Ôsaka District Forest Office for supporting this work. I also
283 thank Dr. H. Iijima (Yamanashi Forest Research Institute) for reading a previous version
284 of the manuscript and for comments. Computational calculations were conducted on the
285 high performance cluster computing system of AFFIT, Ministry of Agriculture, Forestry
286 and Fisheries, Japan.

287 REFERENCES

- 288 Brooks, S. P. and Gelman, A. (1998). General methods for monitoring convergence of
289 iterative simulations. *Journal of Computational and Graphical Statistics*, 7(4):434–
290 455.
- 291 Chen, G., Kéry, M., Plattner, M., Ma, K., and Gardner, B. (2013). Imperfect detection is
292 the rule rather than the exception in plant distribution studies. *Journal of Ecology*,
293 101(1):183–191.
- 294 Chen, G., Kéry, M., Zhang, J., and Ma, K. (2009). Factors affecting detection probability
295 in plant distribution studies. *Journal of Ecology*, 97(6):1383–1389.
- 296 Côté, S. D., Rooney, T. P., Tremblay, J.-P., Dussault, C., and Waller, D. M. (2004).
297 Ecological impacts of deer overabundance. *Annual Review of Ecology and Systematics*,
298 35:113–147.
- 299 Dorazio, R. M., Royle, J. A., Söderström, B., and Glimskär, A. (2006). Estimating
300 species richness and accumulation by modeling species occurrence and detectability.
301 *Ecology*, 87(4):842–854.
- 302 Fujii, T. (1994). Stand development process and flowering patterns of a *Symplocos*
303 *prunifolia* population. *Humans and Nature*, 3:79–83. (in Japanese with English
304 summary).

- 305 Gelman, A. and Rubin, D. B. (1992). Inference from iterative simulation using multiple
306 sequences. *Statistical Science*, 7(4):457–472.
- 307 Hashimoto, Y. and Fujiki, D. (2014). List of food plants and unpalatable plants of sika
308 deer (*Cervus nippon*) in Japan. *Humans and Nature*, 25:133–160. (in Japanese).
- 309 Iijima, H. and Nagaïke, T. (2015). Appropriate vegetation indices for measuring the
310 impacts of deer on forest ecosystems. *Ecological Indicators*, 48:457–463.
- 311 Itô, H. (2007). Twelve-years change of a broad-leaved secondary forest in Ginkakuji-san
312 National Forest. *Bulletin of FFPRI*, 6:93–100. (in Japanese with English summary).
- 313 Itô, H. (2015). Effects of sika deer (*Cervus nippon*) on the dynamics of a broadleaved
314 secondary forest after mass mortality of oak trees. *Journal of Japanese Forest Society*,
315 97:304–308. (in Japanese with English summary).
- 316 Itô, H., Igarashi, T., and Kinuura, H. (2009). Changes in stand structure after the mass
317 mortality of oak trees in Keihoku area, Kyoto City, Japan. *Journal of Japanese
318 Forestry Society*, 91:15–20. (in Japanese with English summary).
- 319 Itô, H., Kinuura, H., and Oku, H. (2011). Stand structure of a broadleaved forest with
320 *Sasa*-type floor after mass mortality by oak wilt disease. *Journal of Japanese Forestry
321 Society*, 93:84–87. (in Japanese with English summary).
- 322 Kabaya, H. (1988). Changes of undergrowth of a broadleaved evergreen forest in relation
323 to grazing effects by sika deer. *Bulletin of the Tokyo University Forests*, 78:67–82. (in
324 Japanese with English summary).
- 325 Kéry, M. (2004). Extinction rate estimates for plant populations in revisitation studies:
326 importance of detectability. *Conservation Biology*, 18(2):570–574.
- 327 Kéry, M. and Schaub, M. (2012). *Bayesian population analysis using WinBUGS: a
328 hierarchical perspective*. Academic Press, Waltham.
- 329 Kinuura, H. and Kobayashi, M. (2006). Death of *Quercus crispula* by inoculation with
330 adult *Platypus quercivorus* (Coleoptera: Platypodidae). *Applied Entomology and
331 Zoology*, 41(1):123–128.
- 332 Kubono, T. and Ito, S.-i. (2002). *Raffaelea quercivora* sp. nov. associated with mass mor-
333 tality of Japanese oak, and the ambrosia beetle (*Platypus quercivorus*). *Mycoscience*,
334 43(3):255–260.
- 335 Kuroda, K., Osumi, K., and Oku, H. (2012). Reestablishing the health of secondary
336 forests “Satoyama” endangered by Japanese oak wilt: A preliminary report. *Journal
337 of Agricultural Extension and Rural Development*, 4:192–198.
- 338 Lunn, D., Spiegelhalter, D., Thomas, A., and Best, N. (2009). The bugs project:
339 Evolution, critique, and future directions. *Statistics in Medicine*, 28:3049–3067.
- 340 Maesako, Y., Nanami, S., and Kanzaki, M. (2007). Spatial distribution of two invasive
341 alien species, *Podocarpus nagi* and *Sapium sebiferum*, spreading in a warm-temperate
342 evergreen forest of the Kasugayama Forest Reserve, Japan. *Vegetation science*,
343 24(2):103–112.
- 344 Müllerová, J., Hédli, R., and Szabó, P. (2015). Coppice abandonment and its implications
345 for species diversity in forest vegetation. *Forest Ecology and Management*, 343:88–
346 100.
- 347 Murata, M., Matsuda, Y., Yamada, T., and Ito, S. (2009). Differential spread of dis-
348 coloured and non-conductive sapwood among four Fagaceae species inoculated with
349 *Raffaelea quercivora*. *Forest Pathology*, 39(3):192–199.
- 350 Murata, M., Yamada, T., and Ito, S.-i. (2005). Changes in water status in seedlings of

- 351 six species in the Fagaceae after inoculation with *Raffaelea quercivora* Kubono et
352 Shin-Ito. *Journal of Forest Research*, 10(3):251–255.
- 353 Nakajima, H. and Ishida, M. (2014). Decline of *Quercus crispula* in abandoned coppice
354 forests caused by secondary succession and Japanese oak wilt disease: Stand dynamics
355 over twenty years. *Forest Ecology and Management*, 334:18–27.
- 356 Nakajima, M. (1929). The feeding experiments of Japanese deer in the university forest
357 in Chiba prefecture. *Bulletin of the Tokyo University Forests*, 8:95–114. (in Japanese).
- 358 Obora, T., Watanabe, H., and Yokoi, S. (2013). The effect of Sika deer browsing damage
359 on regeneration in mass mortality area of Japanese oak trees. *Journal of Japanese
360 Society of Revegetation Technology*, 39(2):260–263. (In Japanese).
- 361 Rackham, O. (2008). Ancient woodlands: Modern threats. *New Phytologist*, 180(3):571–
362 586.
- 363 Rooney, T. P. (2001). Deer impacts on forest ecosystems: a North American perspective.
364 *Forestry*, 74(3):202–208.
- 365 Saito, S. and Shibata, M. (2012). The forest structure and tree death rate of forest stands
366 damaged by Japanese oak wilt in Yamagata prefecture. *Journal of Japanese Forest
367 Society*, 94(5):223–228. (in Japanese with English summary).
- 368 Shibata, M. and Nakashizuka, T. (1995). Seed and seedling demography of four
369 co-occurring *Carpinus* species in a temperate deciduous forest. *Ecology*, 76(4):1099–
370 1108.
- 371 Shimoda, K., Kimura, K., Kanzaki, M., and Yoda, K. (1994). The regeneration of
372 pioneer tree species under browsing pressure of Sika deer in an evergreen oak forest.
373 *Ecological Research*, 9(1):85–92.
- 374 Suzuki, M. (2013). Succession of abandoned coppice woodlands weakens tolerance of
375 ground-layer vegetation to ungulate herbivory: A test involving a field experiment.
376 *Forest Ecology and Management*, 289(0):318–324.
- 377 Svátek, M. and Matula, R. (2015). Fine-scale spatial patterns in oak sprouting and
378 mortality in a newly restored coppice. *Forest Ecology and Management*, 348:117–123.
- 379 Takatsuki, S. (1989). Effects of deer on plants and plant communities. *Japanese Journal
380 of Ecology*, 39:67–80. (in Japanese with English summary).
- 381 Takatsuki, S. (2009). Effects of sika deer on vegetation in Japan: A review. *Biological
382 Conservation*, 142(9):1922–1929.