Outstanding performance of an invasive alien tree *Bischofia javanica* relative to native tree species and implications for management of insular primary forests

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Invasive alien tree species can exert severe impacts, especially in insular biodiversity hotspots, but have been inadequately studied. Knowledge of the life history and population trends of an invasive alien tree species is essential for appropriate ecosystem management. The invasive tree *Bischofia javanica* has overwhelmed native trees on Haha-jima Island in the Ogasawara Islands, Japan. We explored forest community dynamics 2 years after a typhoon damaged the Sekimon primary forests on Haha-jima Island, and predicted the rate of population increase of *B. javanica* using a logistic model from forest dynamics data for 19 years. During the 2 years after the typhoon, only *B. javanica* increased in population size, whereas populations of native tree species decreased. Stem diameter growth of *B. javanica* was more rapid than that of other tree species, including native pioneer trees. Among the understory stems below canopy trees of other species, *B. javanica* grew most rapidly and *B. javanica* canopy trees inhibited growth of the dominant native *Ardisia sieboldii*. These competitive advantages are indicated to be the main mechanism by which *B. javanica* replaces native trees. The logistic model predicted that *B. javanica* would reach 30% of the total basal area between 2017 (in the eastern plot adjacent to a former *B. javanica* plantation) and 2057 (in the western plot distant from the plantation site), which is a maximum percentage allowing to eradicate under the present guideline of the National Forest. The results suggest immediate removal of *B. javanica* is required to preserve native biodiversity in these forests.

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2   implications for management of insular primary forests

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16

18 **Abstract**

19   Invasive alien tree species can exert severe impacts, especially in insular biodiversity hotspots, but

20 have been inadequately studied. Knowledge of the life history and population trends of an invasive alien tree

21 species is essential for appropriate ecosystem management. The invasive tree *Bischofia javanica* has

22 overwhelmed native trees on Haha-jima Island in the Ogasawara Islands, Japan. We explored forest community

23 dynamics 2 years after a typhoon damaged the Sekimon primary forests on Haha-jima Island, and predicted the

24 rate of population increase of *B. javanica* using a logistic model from forest dynamics data for 19 years. During

25 the 2 years after the typhoon, only *B. javanica* increased in population size, whereas populations of native tree

26 species decreased. Stem diameter growth of *B. javanica* was more rapid than that of other tree species, including

27 native pioneer trees. Among the understory stems below canopy trees of other species, *B. javanica* grew most

28 rapidly and *B. javanica* canopy trees inhibited growth of the dominant native *Ardisia sieboldii*. These

29 competitive advantages are indicated to be the main mechanism by which *B. javanica* replaces native trees. The

30 logistic model predicted that *B. javanica* would reach 30% of the total basal area between 2017 (in the eastern

31 plot adjacent to a former *B. javanica* plantation) and 2057 (in the western plot distant from the plantation site),

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33 results suggest immediate removal of *B. javanica* is required to preserve native biodiversity in these forests.

36   **Introduction**

37   Invasive alien species have diverse impacts on biodiversity and ecosystems worldwide (Chapin et al.

38   2000; Mack et al. 2000; Lockwood et al. 2007; Bellard et al. 2016). Invasive trees act as ecosystem engineers

39   by altering biological interactions, water runoff, litter quality, and nutrient cycling (Vitousek and Walker 1989;

40   Binggeli 1996; Fleischmann 1997; Crooks 2002; Lepš et al. 2002; Wiser et al. 2002; Meyer and Lavergne 2004;

41   Gaertner et al. 2014; Motard et al. 2015). Such impacts on native ecosystems are amplified on oceanic islands

42   owing to an inherent vulnerability to alien species (D'Antonio and Dudley 1995; Lonsdale 1999; Sax et al. 2002;

43   Pyšek and Richardson 2006; Kier et al. 2009; Walsh et al. 2012). As examples of the serious consequences of

44   an invasive tree species, *Miconia calvescens* attracts seed dispersers, shows high shade tolerance, and threatens

45   native plant biodiversity in Pacific insular mesic forests (Meyer and Florence 1996; Medeiros et al. 1997). The

46   alien nitrogen fixer *Myrica faya* changes nutrient cycling and alters development of the forest vegetation on

47   Hawaiian volcanic lava flows (Vitousek and Walker 1989). On Réunion Island, *Casuarina equisetifolia* disturbs

48   primary succession on lava flows (Potgieter et al. 2014) and *Ligustrum robustum* subsp. *walkeri* can become the

49   dominant woody species in natural forests on this island (Lavergne et al. 1999). Despite many examples of their

50   ecological impacts, research on invasive trees has not progressed sufficiently (Richardson et al. 2014), probably

51   because of the long lifespan of trees, which leads to a long time-lag between the initial invasion and expansion

52   in distribution (Webster et al. 2005; Wangen and Webster 2006).

53   The expansion mechanism of invasive tree species is a critical research focus. Although encroachment

54   of primary forests by invasive tree species is not common, it can cause a vegetation shift initially in canopy gaps

55   that result from wind storms (Knapp and Canham 2000; Bellingham et al. 2005; Brown et al. 2006). Even without

56   gap formation, shade-tolerant alien trees sometimes spread under the closed canopy of a mature native forest

57   (Wangen and Webster 2006; Martin et al. 2010). Invasion of insular native forests by such alien tree species will

58   exacerbate ecological deterioration of native forests in addition to the fragmentation caused by human activity

59   since the initial colonization of the island (Mueller-Dombois 2008). Given that ecosystem degradation generally

60   progresses as alien species invade, a conservation plan should take into account the invasion rate. However, few

61   case studies have estimated the rate of invasion from stand dynamics data (Webster et al. 2005). Additional

62   studies of invasive tree species are needed to understand details of the invasion dynamics and rate of invasion

63   (Martin et al. 2009; Richardson and Rejmánek 2011; Richardson et al. 2014).

64   The Ogasawara Islands host insular ecosystems with high endemic biodiversity, but several invasive

65   tree species are causing drastic changes to the vegetation (Hata et al. 2006; Fukasawa et al. 2009; Abe et al.

66   2011). *Bischofia javanica* (Phyllanthaceae) is one such invasive tree species in this island group (Yamashita et

67   al. 2000; Shimizu 2003). The species is invasive in the mountainous area of the islands, which are covered by

68   rich forest soils, with relatively high atmospheric humidity and frequent fogging (Shimizu 2003; Fukasawa et

69   al. 2009; Tanaka et al. 2010). *Bischofia javanica* exhibits moderate shade tolerance, and can quickly shift

70   photosynthetic mode between shade and direct sunlight (Yamashita et al. 2000). Such flexibility helps

71   individuals to outcompete native trees after a disturbance event. The distribution of *B. javanica* on Haha-jima

72   Island overlaps with that of mesic forests in which several endemic species are aggregated and thus poses a

73   serious threat to the native ecosystem. In contrast, the forests in the Sekimon area of Haha-jima have experienced

74   minimal anthropogenic disturbance and thus still resemble the original primary mesic forests (Shimizu 2003;

75   Abe et al. 2018).

76   To develop effective eradication strategies for an invasive species for biodiversity conservation, its

77   life history and population trend should be clarified (Sakai et al. 2001). We employed a permanent plot census,

78   which is a standard method to describe forest dynamics (Losos and Leight 2004), and explored the dynamics of

79   trees focusing on the relationships between alien and native species. Generally, the ecological risks posed by

80   invasive tree species tend to be underestimated because of the usual lag period following their introduction

81   (Frappier et al. 2003). Management of invasive alien species must be strategic to reduce the high social costs

82   (Higgs et al. 2000; Pimentel et al. 2000). These observations suggest that appropriate prediction of the expansion

83   of invasive tree species will contribute to effective forest management. In this study, we first investigated the

84   short-term (2 years) dynamics to clarify the mechanism of aggressive invasion by *B. javanica* in insular primary

85   forests on the Ogasawara Islands. As a result of an unexpected typhoon impact, the observed forest dynamics

86   included responses to the disturbance and later crown shading. Second, we predicted the rate of expansion of *B.*

87   *javanica* based on longer-term (19 years) population trends in the census plot. On the basis of our findings, we

88   propose an effective strategy for forest management framed as a time limit for eradication.

89

90   **Methods**

91   **Study site**

92   The oceanic Ogasawara Islands are located in a subtropical region of the Pacific Ocean (between

93   24º14'N and 27º44'N, and 140º52'E and 142º16'E). The resident biota contains a high percentage of endemic

94   species (Shimizu 2003). Haha-jima Island is one of the two inhabited islands in the archipelago. It covers 20 km²

95   and has a maximum elevation of 463 m above sea level. The island's central mountains are covered by mesic

96   forests that consist of relatively tall trees (about 15 m in height) compared with that of other forests in the

97   Ogasawara Islands. The Sekimon mesic forests cover uplifted limestone in the northeastern corner of Haha-jima.

98   The uplifted limestone has a doline-like central depression. Relatively thick sedimentary soil (Okamoto et al.,

99   1995) and protection from wind by the walls of the doline have favored the growth of dense, tall forest on the

100 base of the doline. This environment provides habitat for many plant species that are endemic to the Sekimon

101 (Abe et al. 2018). Although there is no record of planting *B. javanica* in the Sekimon in the forest management

102 ledger, a participator attested that *B. javanica* had been planted before 1935 (Toyoda 2003). In 1997, the seaward

103 edge of the doline collapsed (Fig. 1a) and, subsequently, many trees have been exposed to salt-bearing onshore

104 wind, causing desiccation and salt damage to the trees.

105   This area was struck by a strong typhoon in late 2006. Typhoon 0614 YAGI was spawned on 19

106 September in the northwestern Pacific (20.3ºN, 159.2ºE), about 1800 km southeast of the Ogasawara Islands.

107 The typhoon was closest to Haha-jima Island on 22 and 23 September when it passed about 100 km west of

108   Haha-jima. At that time, the atmospheric pressure decreased to 930 hPa, the maximum wind velocity attained

109   45 m s^{-1}, and the 170 km radius of storm area experienced a wind velocity $\geq$ 25 m s^{-1} estimated by the Dvorak

110   method (Japan Meteological Agency, 2019).

111

112   **Field survey**

113   We selected a survey area in the central portion of the primary forests in the Sekimon area and

114   established two 2-ha census plots (100 m $\times$ 200 m) because there is a steep limestone ridge difficult to traverse

115   between the two plots. We surveyed all trees with diameter at breast height (DBH) $\geq$ 10 cm in 2006 and described

116   the status of each individual's crown in terms of whether it formed part of the forest canopy or understory. We

117   defined canopy trees as individuals in which more than half of the crown surface was exposed to direct sunlight

118   (i.e., not shaded by neighboring trees); for individuals classified as an understory tree, we recorded the tree

119   species that covered the largest proportion of its crown. This judgement was conducted by eyesight, aided by

120   observation using binoculars when necessary. In 2008, we conducted a second census following the same method

121   of the first census.

122   Shimizu (1994) surveyed a portion of our study site in 1987 using a 100 m $\times$ 50 m plot (Fig. A.1). The

123   southern portion of this plot disappeared in a landslide in 1997 (Fig. 1a). The present study plot included the

124   remaining portion (60 m $\times$ 50 m) of the Shimizu plot in the southeastern part of the western plot. Our

125   reconstruction of the Shimizu plot was based on a map of individual trees that was created in 1987 (Shimizu

126   1994). We checked the position of characteristic large trees (e.g., *Melia azedarach*) and old stumps of *Morus*

127   *boninensis* that had been cut about 130 years previously but had not decomposed because of the strong, decay-

128   resistant wood (Yoshida and Oka 2000). The 1987 data enabled us to analyze changes in species composition in

129   terms of the number of stems and basal area. However, we could not analyze individual mortality and growth

130   since 1987 because Shimizu (1994) did not label individual trees.

131   To detect the impacts of typhoon 0614 YAGI, we surveyed the damage soon after the first tree census

132   (November and December 2006). We recorded the types of damage for individual trees with DBH ≥ 10 cm in

133   the northern half of the western plot (1 ha, $N = 2675$). The damage to each tree was classified as defoliated,

134   snapped, uprooted, or trapped (under one or more uprooted trees).

135   Field survey was approved for the Ogasawara National Park by the Ministry of Environment (No.

136   0606328007, No.080507006) and for the Ogasawara National Forest by the Forest Agency (No.18-2-50 and

137   No.20-1-32).

138

139   **Statistical analyses**

140   We evaluated the annual growth rate in 2-year period as ((DBH in 2008)-(DBH in 2006))/2 for each

141   tree species. We examined the effects of crown position on diameter growth of understory tree stems using two

142   types of analysis: the effect of the canopy tree species on a given understory species and the growth differences

143   among the understory tree species under a given canopy species. Both analyses used a general linear model

144   (GLM) with a Gaussian link function and a multiple-comparison test using R ver. 3.3.2 (R Core Team 2016).

145   To evaluate the suppression intensity of a crown, we estimated the effect of crown width (CW) of each

146   canopy species using the average number of stems below the canopy:

147   CW = NS/NC

148   where NS is the number of stems covered by the crown of the canopy species and NC is the number of canopy

149   stems of the species.

150

151   **Prediction of increase in *B. javanica* occupancy**

152   It is preferable to use highly accurate models, such as a population matrix, to predict the population

153   dynamics of an invasive tree species (e.g. Buckley et al. 2003). However, we could not use such a model in the

154   present analysis because we surveyed the seedlings only once. Instead, we used a simple logistic curve

155   (Radosevich et al. 2003; Webster and Wangen 2009) to predict future population growth of *B. javanica* in terms

156   of the number of stems and basal area. Given that it can be assumed that the spread of an invasive tree species

157   is random and continuous within the forest, a simple model prediction is considered to be sufficiently practicable

158   (Frappier et al. 2003). The model represented the proportion of *B. javanica* (D_{BJ}) with an upper limit of 1.0 for

159   the proportion, as follows:

160                          $D_{BJ} = 1/\{1 + a \times \exp(-b \times t)\}$

161   where t represents the number of years since 2006. The coefficients a and b were determined based on the data

162   from the 1987 measurements in the Shimizu (1994) plot and the 2006 measurements in Abe et al. (2018) (Table

163   A.1).

164   We predicted the time required for *B. javanica* to attain 30% and 50% of the number of stems and

165   basal area for the western plot and eastern plot, using logistic regression models. The lower percentage (30%)

166   was based on the guideline of the National Forest that restricts the proportion of tree removal less than 30% of

167   the total volume to prevent soil erosion. The higher percentage (50%) was based on data from the forests on Mt

168   Kuwanoki (Haha-jima Island), where the former forest type had been identical to that at Sekimon but now

169   resembles a *B. javanica* forest stand with more than 40% occupancy of the total basal area (Shimizu 1988). In

170   addition, as a property of the logistic model, the estimated year tends to include a smaller error in the central

171   portion of the logistic curve (e.g., between 30% and 70% occupancy) than that at each extreme (i.e., the first

172   year of invasion and the end of the simulation period). Therefore, forecast years reaching 30% and 50%

173   occupancy are expected to be most accurate and robust.

174

175   **Results**

176   **Survival, growth, and typhoon damage**

177   Typhoon 0614 YAGI was situated closest to Haha-jima Island on 22 and 23 September 2006. The

178   typhoon defoliated all standing stems (Fig. 1b), and snapped, uprooted, and trapped trees accounted for 7.1%,

179   2.7%, and 0.2% of the total, respectively (Table 1). Pioneer trees (sun-lit trees growing rapidly in the early stage

180   of succession or in the gaps) exhibited relatively high mortality (*Zanthoxylum ailanthoides* var. *inerme* at 16.7%,

181   *Trema orientalis* at 33.3%, and *Cyathea mertensiana* at 21.4%), as did some later-successional species (*Ochrosia*

182   *nakaiana* at 50.0% and *Psychotria homalosperma* at 21.4%). *Bischofia javanica* showed low mortality (1.9%)

183   in response to the typhoon disturbance.

184   The number of stems decreased between 2006 and 2008 among the most frequent tree species (more

185   than 30 stems in the plots) except for *B. javanica* (7.4% increase) (Fig. 2). The increment in *B. javanica* was the

186   result of recruitment of 44 individuals to the DBH ≥ 10 cm size class and the death of 10 individuals. Species

187   that showed the greatest decrease in number of stems were an endemic pioneer, *Z. ailanthoides* var. *inerme*

188   (−43.3%), and an endemic tree fern, *Cyathea mertensiana* (−34.8%). The proportion of the number of

189   recruitments into the stem size class DBH ≥ 10 cm was largest for the alien species *B. javanica* (8.8%) followed

190   by *Callicarpa subpubescens* (6.9%) and *Ficus boninsimae* (6.6%). Annual diameter growth rate (Fig. 3) was

191   largest in *B. javanica* (3.1 ± 0.1%, mean ± SE) followed by three pioneers, *C. mertensiana* (2.1 ± 0.4%), *Z.*

192   *ailanthoides* var. *inerme* (2.1 ± 0.3%), and *C. subpubescens* (2.0 ± 0.3%). The growth rates of dominant native

193   species were less than half that of *B. javanica* (e.g., *Ardisia sieboldii* at 0.8 ± 0.0%, *Elaeocarpus photiniifolius*

194   at 1.0 ± 0.1%, and *Pisonia umbellifera* at 1.3 ± 0.1%). Annual diameter growth rate was negatively correlated

195   with population growth rate when the data for *B. javanica* were omitted from those for the most frequent tree

196   species (Pearson's product-moment correlation, $r = -0.635$, $t = -3.182$, df = 15, $p = 0.006$), but no significant

197   relationship was observed when the data for *B. javanica* were included ($r = -0.225$, $t = -0.922$, df = 16, $p =$

198   0.370).

199

200   **Effects of crown shading**

201   The number of trees in which more than half of the crown was shaded by the crown of a neighboring

202   tree in 2008 was 2761 (39.9% of all stems, Fig. 4); the number was largest for *A. sieboldii* (1956), *P. umbellifera*

203   (301), and *B. javanica* (105). The most frequent canopy species were *E. photiniifolius* (793), *B. javanica* (685),

204   and *Celtis boninensis* (219).

205   The mean annual diameter growth of understory trees was significantly less than that of canopy trees

206   (GLM with a Gaussian link function; estimate = 0.059, t = 8.32, P < 0.001). The canopy of *B. javanica*

207   significantly inhibited the growth of several understory tree species: growth was also inhibited for *A. sieboldii*

208   under *E. photiniifolius* and under *Z. ailanthoides* var. *inerme*, and for *P. umbellifera* under *A. sieboldii* (Fig. 5).

209   On the other hand, understory individuals of *B. javanica* exhibited superior growth compared with that of native

210   understory tree species, regardless of the canopy tree species (Fig. 6). Although the CW index was much larger

211   in *M. azedarach* (CW = 5.3) and *C. boninensis* (4.9) compared with that of all other species (Fig. 7), the largest

212   values of CW among dominant species (i.e., those with ≥ 100 canopy individuals) were for *E. photiniifolius*

213   (2.2), followed by *B. javanica* (1.9) and *Planchonella obovata* var. *obovata* (1.1). The most frequent dominant

214   species, *A. sieboldii*, showed a small CW index (< 0.1).

215

216   **Prediction of invasion by *B. javanica***

217   In the Shimizu plot, *B. javanica* increased substantially in both the number of stems (176.4%) and basal area

218   (177.8%) for the 19-year period (Table A.1). We applied these changes for *B. javanica* to estimate the

219   coefficients of logistic curves (Fig. 8). The coefficients of the logistic model were $a = 36.214$ and $b = 0.038$

220   based on the number of stems, and $a = 36.155$ and $b = 0.051$ based on the basal area. The model predicted that

221   in the eastern plot, *B. javanica* will account for 30% of the number of stems in 2033 and 30% of the basal area

222   in 2017. In the eastern plot, *B. javanica* will account for 30% of the number of stems in 2087 and 30% of the

223   basal area in 2057. In the eastern plot, *B. javanica* will account for 50% of the number of stems in 2056 and 50%

224   of the basal area in 2034. In the western plot, *B. javanica* will account for 50% of the number of stems in 2109

225   and 50% of the basal area in 2074.

226

227   **Discussion**

228   The invasive tree species *B. javanica* showed increased performance relative to native trees after

229   typhoon 0614 YAGI. The diameter growth rate and survival rate of *B. javanica* were higher than those of other

230   tree species in the study plots, including native pioneer trees. Given that rapid growth is a strong indicator of

231   invasiveness (Lamarque et al. 2011), *B. javanica* showed high invasive ability in the Sekimon area of Haha-jima

232   Island. In addition, *B. javanica* showed the most rapid leaf flush after defoliation by the typhoon (Fig. 1d). As a

233   result, *B. javanica* increased in population size after the typhoon, whereas native tree species decreased in

234 population size. Surprisingly, dominant native tree species that were expected to be adapted to typhoon damage

235 mostly ceased growth for two years. The negative correlation between diameter growth rate and population

236 growth rate among the dominant native tree species is likely to reflect the well-known growth–survivorship

237 trade-off (Grubb 1977; Hubbell and Foster 1992; Wright et al. 2003). However, *B. javanica* showed exceptional

238 positive population growth despite the rapid diameter growth. This difference may be the result of an inherent

239 vulnerability to invasive species on oceanic islands that exhibit a high percentage endemicity (Berglund et al.

240 2009; Walsh et al. 2012). Windstorm disturbance usually creates the opportunity for invasive plant species to

241 spread in natural insular forests (Fine 2002; Denslow 2003; Lugo 2004; Bellingham et al. 2005; Shimizu 2005).

242 A high number of seedlings of *B. javanica* and two additional alien species, *Carica papaya* and *Morus australis*,

243 were observed on the Sekimon forest floor (Abe et al. 2018). This observation suggests that these alien species

244 show high propagule pressure. In particular, seedlings of *B. javanica* show high photosynthetic plasticity

245 (Kamaluddin and Grace 1992; Yamashita et al. 2000), which can promote their acclimation to a range of light

246 environments and permit a rapid growth response after forest disturbance (Pattison et al. 1998). Therefore, the

247 seedlings of *B. javanica* are likely to exhibit greater percentage survival than native species after typhoon

248 disturbance. Subsequently, young understory stems of *B. javanica* grew more rapidly than understory individuals

249 of native tree species regardless of the canopy tree species (Fig. 6).

250   The invasion rate of *B. javanica* was relatively slow in the Sekimon forests probably because the

251 species is still in an early stage of invasion. The number of stems and basal area of *B. javanica* increased by 1.4

252   times and 1.7 times, respectively, during the 19-year period in the Sekimon forests, whereas basal area of *B.*

253   *javanica* increased to 9 times the 1984 value during the subsequent 19 years and overwhelmed the native tree

254   species in secondary forests on Chichi-jima Island, located 50 km north of Haha-jima (Hata et al. 2006). Even

255   in the early stage of invasion, the rate of increase of *B. javanica* in the Sekimon forests has exceeded those of

256   native tree species, even though native species also have increased over the 19 years (Table A.1). During this

257   period, typhoons with a wind speed of more than 20 m s^{-1} struck 12 times and more than 30 m s^{-1} struck four

258   times in the Ogasawara Islands (Table A.2). A preliminary study of the Sekimon forests also reported significant

259   damage to the forest by a severe typhoon in 1983 (Shimizu 1994). Repeated wind-induced disturbance is likely

260   to have assisted the spread of *B. javanica* in the Sekimon forests.

261   Regarding crown position, the two dominant tree species, *A. sieboldii* and *P. umbellifera*, grew less

262   under a *B. javanica* crown than those under *E. photiniifolius* and *A. sieboldii* crowns, respectively. Given that

263   the defoliation damage caused by typhoon 0614 YAGI had recovered in 2008, the stem growth during the

264   preceding two years included the effects of both typhoon disturbance and later crown shading, which are difficult

265   to distinguish. A lower growth rate under a *B. javanica* crown is partly due to the more rapid recovery of *B.*

266   *javanica* crowns after the typhoon damage (Fig. 1d). In addition, *B. javanica* showed a relatively high CW index,

267   whereas few native tree species showed a high CW value in the Sekimon forests. The dominant species *A.*

268   *sieboldii* is a sub-canopy tree and develops a narrow crown. This may be the reason why *P. umbellifera*

269   individuals showed superior growth under *A. sieboldii* crowns than under *B. javanica* crowns. Other native tree

270   species (e.g., *Machilus boninensis*, *Melicope grisea* var. *grisea*, *O. nakaiana*, and *P. umbellifera*) also produce

271   narrow crowns and are likely to have similar effects on understory trees that we may have failed to detect (Fig.

272   5) because of the small sample sizes. Although spatiotemporal variation in forest structure caused by wind-

273   induced disturbance is an important mechanism of tree species coexistence (Kohyama, 1992), invasion by *B.*

274   *javanica* that outcompetes all other canopy tree species, such as *E. photiniipholius* and *P. umbellifera*, would

275   homogenize the various crown–understory relationships and disrupt the stable coexistence mechanism of native

276   tree species. *B. javanica* showed positive population growth after the typhoon and a high rate of diameter growth

277   in both canopy and understory individuals compared with those of native species, which would be an important

278   mechanism in the replacement of native forest by an invasive tree species.

279   The logistic regression curves suggested that *B. javanica* was currently in Phase II (expansion) of its

280   invasion, based on the results of Webster and Wangen (2009), and eradication will be difficult during this phase

281   (Webster et al., 2006). The present eradication plan of the Forest Agency prescribes that less than 30% of the

282   total volume can be removed to prevent soil erosion. Our logistic model predicted that *B. javanica* would account

283   for 30% of the basal area by 2017 in the eastern plot and by 2057 in the western plot. These estimations provide

284   important time limits at which it is possible to eradication all mature individuals at once, in compliance with the

285   guideline. In other forests on Haha-jima Island, *B. javanica* has become the dominant tree species (40% to 50%

286   of all individual stems or relative dominance) and has affected plant species diversity (Shimizu 1988; Toyoda

287   and Kawaoka 2005). In addition, this dominance range (30% to 50%) corresponds to the stage of most rapid

288   expansion in population size represented by the logistic curve. Therefore, these dominance values are considered

289   to be useful to set a time limit for action to eradicate both empirically and logically. It is of crucial scientific

290   importance that the population growth rate of invasive tree species can be estimated for a primary forest of high

291   conservation value.

292

293   **Conclusions**

294   This study presents a typical example of the expansion mechanism and quantitative prediction of the

295   time-limit to eradicate an invasive tree species in an insular primary forest. The differences in growth rates

296   among tree species and the relationships with crown position explained the mechanism by which *B. javanica*

297   outcompetes and excludes many of the native tree species. Understory individuals of *B. javanica* grew more

298   rapidly than native tree species and, once reaching the forest canopy, suppressed the growth of native species,

299   resulting in their gradual decline. This pattern of competition also explains how invasive tree species reduce

300   species diversity in natural forests. Prediction by a simple logistic regression model suggested the urgent need

301   for eradication and will contribute to decision-making to develop an effective conservation strategy (Higgins et

302   al. 2000; Bukley et al. 2003). The short settlement history (about 200 years) of the Ogasawara Islands has allowed

303   the primary forests to survive and retain many endemic endangered plants as in the case of the Sekimon forests

304   (Abe et al. 2018). Immediate eradication of *B. javanica* and long-term monitoring are required to prevent further

305   degradation of biodiversity in the Ogasawara Islands.

306

312

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458

460   **Fig. 1.** Photographs showing the situation of the Sekimon forests after the typhoon. (a) View of the mesic forests

461   on the Sekimon uplifted limestone on 4 October 2006. The southern part of the uplift collapsed in a landslide

462   in 1997. (b) Defoliation of canopy crowns by typhoon 0614 YAGI (22 November 2006). (c) Regeneration of

463   *Sambucus chinensis* var. *formosana* on the sunny forest floor after the typhoon (17 April 2007). (d) Rapid

464   flushing of *Bischofia javanica* after the typhoon damage (22 November 2006). (e) Defoliated crowns of *Pisonia*

465   *umbellifera* and *Ardisia sieboldii* (22 November 2006).

466

467   **Fig. 2.** Population growth rates (individuals of DBH $\geq$ 10 cm) of the most frequent tree species between 2006

468   and 2008. Values within parentheses after the species names represent the number of stems within the survey

469   area (4 ha) in 2006. Abbreviations for species names are defined in Table A.3.

470

471   **Fig. 3.** Annual growth rate of stem diameter from 2006 to 2008. The stem diameter was measured at breast

472   height. Error bars represent the SE. Abbreviations of species name are defined in Table A.3.

473

474   **Fig. 4.** Frequency of crown positions in the 4 ha survey area in 2008. "Above" is the total number of understory

475   stems (DBH $\geq$ 10 cm) that the species covered. "Below" is the number of understory stems of the species

476   that the crown is covered by other trees, including conspecifics. Abbreviations of species name are defined

477   in Table A.3.

478

479   **Fig. 5.** Annual growth rate of stem diameter in the six most frequent tree species under canopy trees. The stem

480   diameter was measured at breast height. Values within parentheses represent the number of canopy

481   individuals. Bars labeled with different letters differ significantly ($P < 0.05$, Tukey–Kramer test). Error bars

482   represent the SE. Abbreviations of species name are defined in Table A.3.

483

484   **Fig. 6.** Annual growth rate of stem diameter under the crown of the six most frequent tree species. The stem

485   diameter was measured at breast height. Values within parentheses represent the number of understory

486   stems. Bars labeled with different letters differ significantly ($P < 0.05$, Tukey–Kramer test). Error bars

487   represent the SE. Abbreviations of species name are defined in Table A.3.

488

489   **Fig. 7.** Crown width index values for the tree species in the survey area. Abbreviations of species name are

490   defined in Table A.3.

491

492   **Fig. 8.** Predictions of the increase in *Bischofia javanica* population size. Estimation of population size is based

493   on (a) the number of stems (N) and (b) the total basal area (BA). Data points were predicted by logistic

494   regressions based on data recorded in 1987 and 2006 in the Shimizu plot (filled circle). "West" and "East"

495   refer to the two plots in Fig. A.1.

496

497   **Table 1** Numbers of trees damaged by typhoon 0614 YAGI. "Uprooted" includes inclined individuals with at

498   least half of the root system exposed. Values of the number of damaged stems are "the number of damaged

499   stems including dead stems" / "the number of dead stems" in 1 ha area. E, Endemic to the Ogasawara

500   Islands; I, indigenous; A, alien. Typhoon YAGI was situated closest to Haha-jima Island on 22 September

501   2006 and the survey was conducted in November 2006. Species order is based on APG III (Yonekura and

502   Murata, 2012).

503

504   Fig. A.1. Location of study site. (a) Haha-jima Island and the Sekimon forests on uplifted limestone and (b) the

505   census plots in the Sekimon forests. Crosshatched rectangles are the two 2-ha plots surveyed in the present

506   study; the gray-shaded rectangle at the southern edge of the western plot represents the plot studied by

507   Shimizu (1994), of which the southernmost part was lost to a landslide. the irregular gray-shaded area at

508   the northeastern corner of the eastern plot represents a former *Bischofia javanica* plantation.

509

511   Table A.1. Changes in the number of stems (N) and basal area (BA) of trees (DBH $\geq$ 10 cm) between 1987 and

512   2006. The 1987 values are from the Shimizu (1994) and the 2006 values are collected by the present study

513   within the former Shimizu plot (60 m $\times$ 50 m). Species are listed in descending order of BA in 1987.

514   Numbers within parentheses after the BA values in 2006 represent the species order based on the BA in

515   2006. Only *Bischofia javanica* is an alien species. Species order is based on descending order of BA in 1987.

516

517   Table A.2: Typhoons for which a wind velocity of more than 20 m s^{-1} was recorded in the Ogasawara Islands

518   between 1987 and 2006. The data is from the Chichi-jima Weather Station (Japan Meteorological Agency,

519   2018).

520

521   Table A.3: Abbreviations for tree species names.

Figure 1

Photographs showing the situation of the Sekimon forests after the typhoon.

(a) View of the mesic forests on the Sekimon uplifted limestone on 4 October 2006. The southern part of the uplift collapsed in a landslide in 1997. (b) Defoliation of canopy crowns by typhoon 0614 YAGI (22 November 2006). (c) Regeneration of *Sambucus chinensis* var. *formosana* on the sunny forest floor after the typhoon (17 April 2007). (d) Rapid flushing of *Bischofia javanica* after the typhoon damage (22 November 2006). (e) Defoliated crowns of *Pisonia umbellifera* and *Ardisia sieboldii* (22 November 2006).

Fig. 1

Table 1(on next page)

Numbers of trees damaged by typhoon 0614 YAGI.

"Uprooted" includes inclined individuals with at least half of the root system exposed. Values of the number of damaged stems are "the number of damaged stems including dead stems" / "the number of dead stems" in 1 ha area. E, Endemic to the Ogasawara Islands; I, indigenous; A, alien. Typhoon YAGI was situated closest to Haha-jima Island on 22 September 2006 and the survey was conducted in November 2006. Species order is based on APG III (Yonekura and Murata, 2012).

Table 1

Species	Origin	N	The number of damaged stems			
			Defoliated	Snapped	Uprooted	Trapped
Cyathea mertensiana	E	28	28/1	4/3	2/2	0/0
C. spinulosa	E	8	8/1	0/0	0/0	0/0
Machilus boninensis	E	75	75/5	11/2	2/0	0/0
M. kobu	E	8	8/0	3/0	0/0	0/0
Rhaphiolepis indica var. *umbellata*	I	2	2/0	0/0	0/0	0/0
Celtis boninensis	E	23	23/0	0/0	0/0	0/0
Trema orientalis	I	3	3/1	0/0	0/0	0/0
Ficus boninsimae	E	51	51/3	1/0	4/3	0/0
Morus australis	A	2	2/0	0/0	0/0	0/0
Elaeocarpus photiniifolius	E	208	208/12	20/5	7/1	1/0
Bischofia javanica	A	54	54/1	3/0	4/0	0/0
Syzygium cleyerifolium	E	12	12/0	1/0	0/0	0/0
Melicope grisea var. *grisea*	E	96	96/8	3/2	0/0	0/0
Zanthoxylum ailanthoides var. *inerme*	E	6	6/1	0/0	0/0	0/0
Melia azedarach	I	1	1/0	0/0	0/0	0/0
Hibiscus glaber	E	27	27/0	3/1	4/1	0/0
Pisonia umbellifera	I	56	56/0	2/0	2/0	0/0
Planchonella obovata var. *obovata*	I	81	81/2	3/1	9/1	1/0
Ardisia sieboldii	I	1985	1985/149	132/35	34/19	3/0
Gardenia boninensis	E	1	1/0	0/0	0/0	0/0
Psychotria homalosperma	E	28	28/4	3/1	2/1	0/0
Ochrosia nakaiana	E	4	4/2	0/0	0/0	0/0
Ligustrum micranthum	E	1	1/0	0/0	0/0	0/0
Callicarpa subpubescens	E	5	5/0	1/0	2/1	0/0
Total		2675	2675/190	190/50	72/29	5/0

Figure 2

Population growth rates (individuals of DBH ≥ 10 cm) of the most frequent tree species between 2006 and 2008.

Values within parentheses after the species names represent the number of stems within the survey area (4 ha) in 2006. Abbreviations for species names are defined in Table A.3.
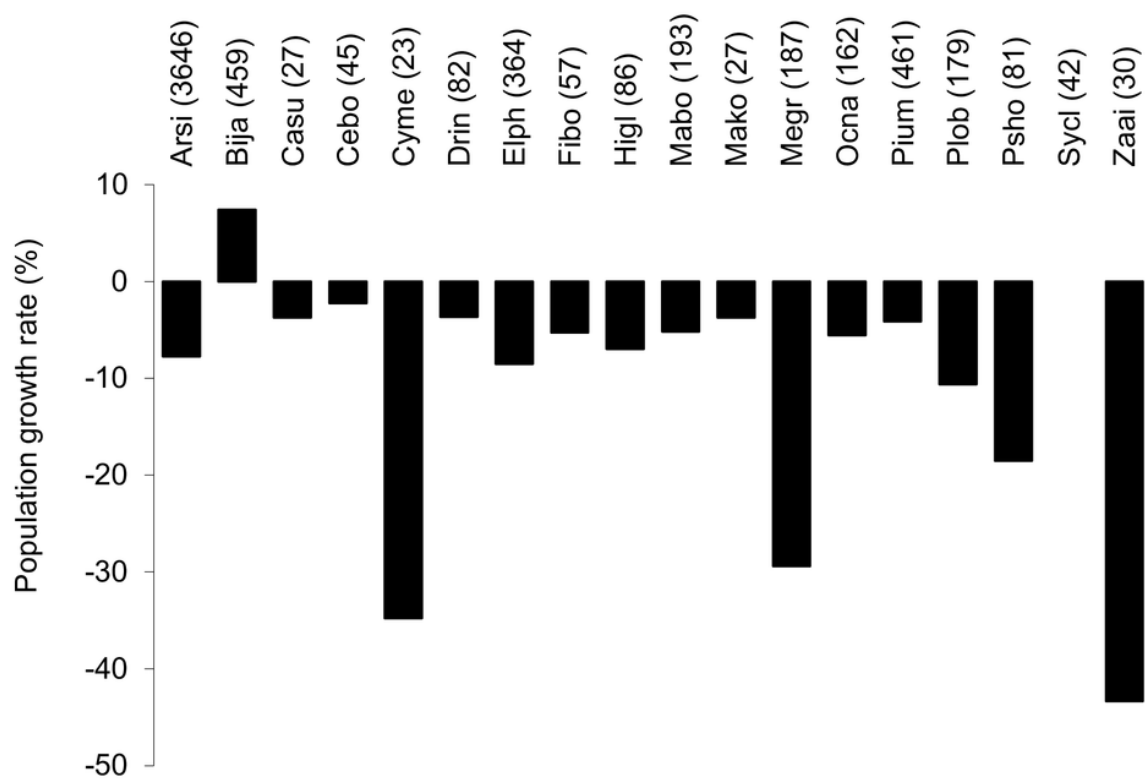
Fig. 2

Figure 3

Annual growth rate of stem diameter from 2006 to 2008.

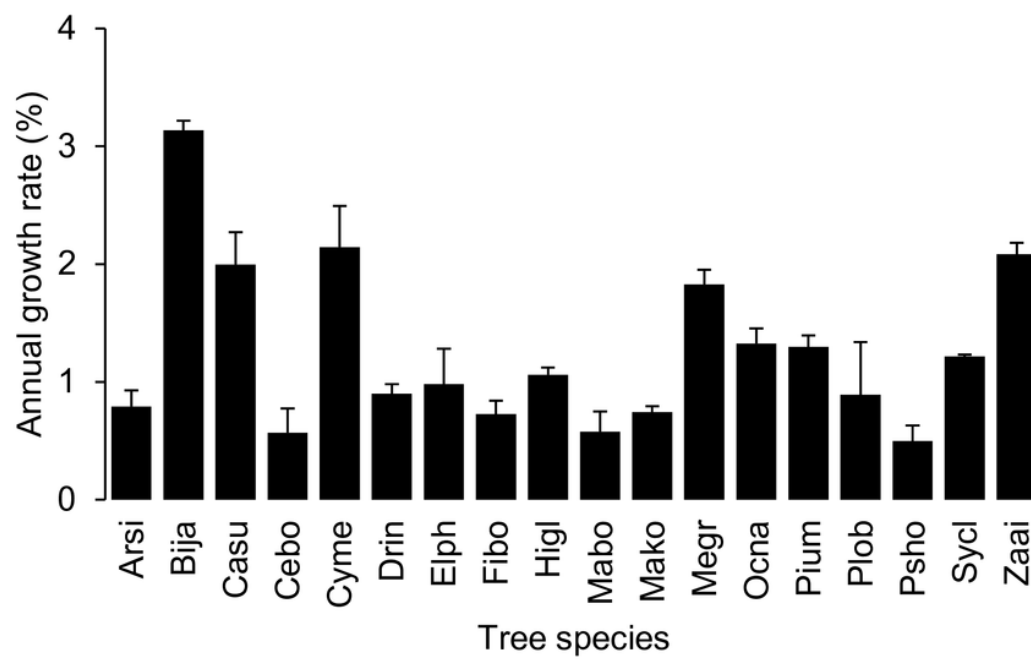The stem diameter was measured at breast height. Error bars represent the SE.

Abbreviations of species name are defined in Table A.3.

Fig. 3

Figure 4

Frequency of crown positions in the 4 ha survey area in 2008.

"Above" is the total number of understory stems (DBH ≥ 10 cm) that the species covered. "Below" is the number of understory stems of the species that the crown is covered by other trees, including conspecifics. Abbreviations of species name are defined in Table A.3.

Fig. 4

Figure 5

Annual growth rate of stem diameter in the six most frequent tree species under canopy trees.

The stem diameter was measured at breast height. Values within parentheses represent the number of canopy individuals. Bars labeled with different letters differ significantly ($P < 0.05$, Tukey–Kramer test). Error bars represent the SE. Abbreviations of species name are defined in Table A.3.
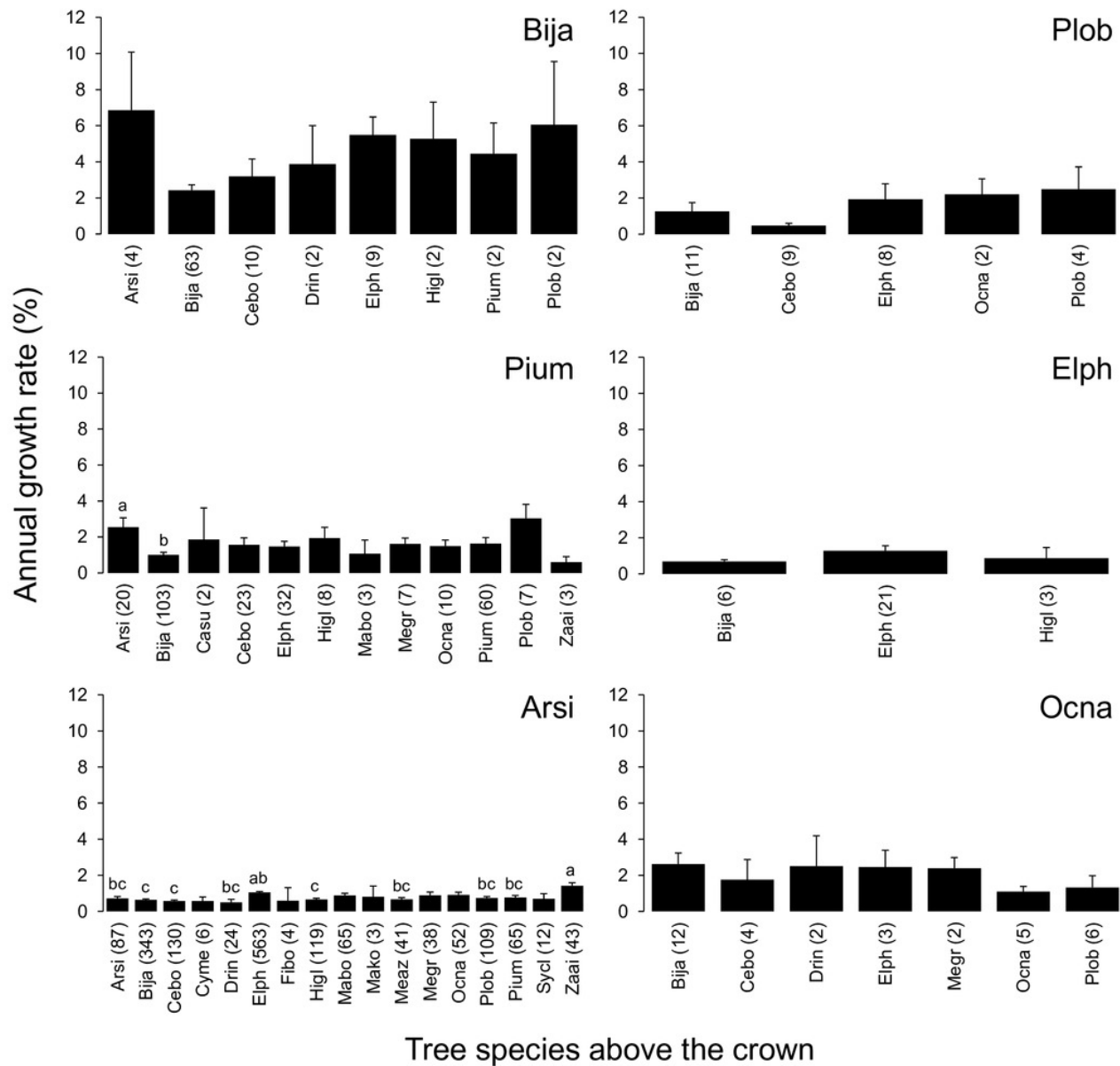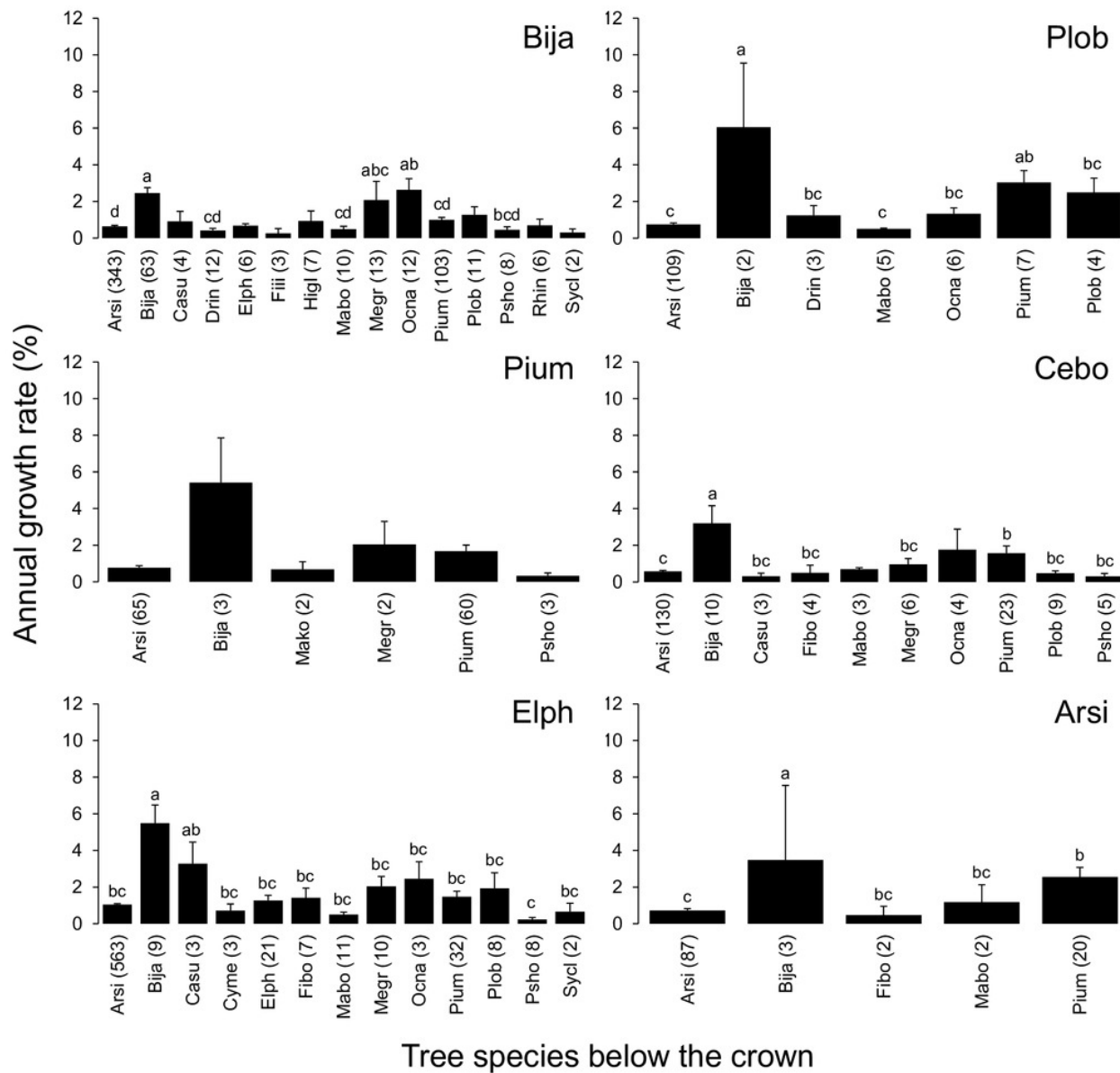
Fig. 5

Figure 6

Annual growth rate of stem diameter under the crown of the six most frequent tree species.

The stem diameter was measured at breast height. Values within parentheses represent the number of understory stems. Bars labeled with different letters differ significantly ($P < 0.05$, Tukey–Kramer test). Error bars represent the SE. Abbreviations of species name are defined in Table A.3.

Fig. 6

Figure 7

Crown width index values for the tree species in the survey area.

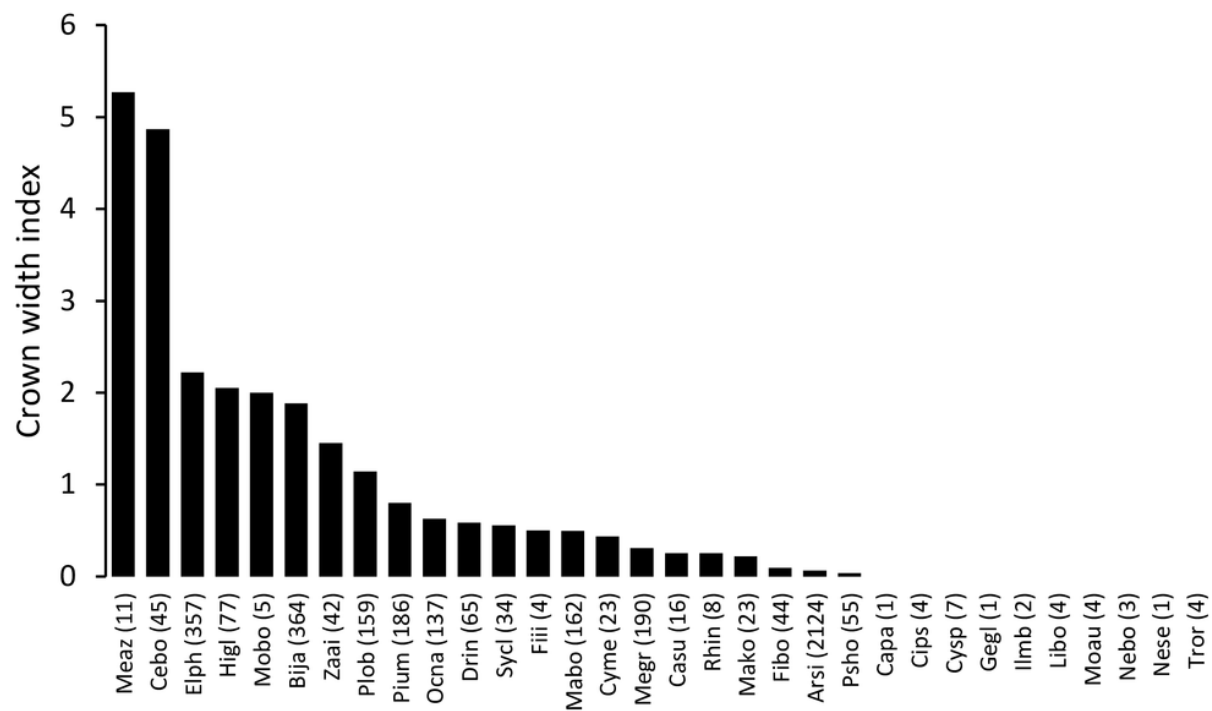Abbreviations of species name are defined in Table A.3.

Fig. 7

Figure 8

Predictions of the increase in *Bischofia javanica* population size.

Estimation of population size is based on (a) the number of stems (*N*) and (b) the total basal area (BA). Data points were predicted by logistic regressions based on data recorded in 1987 and 2006 in the Shimizu plot (filled circle). "West" and "East" refer to the two plots in Fig. A.1.
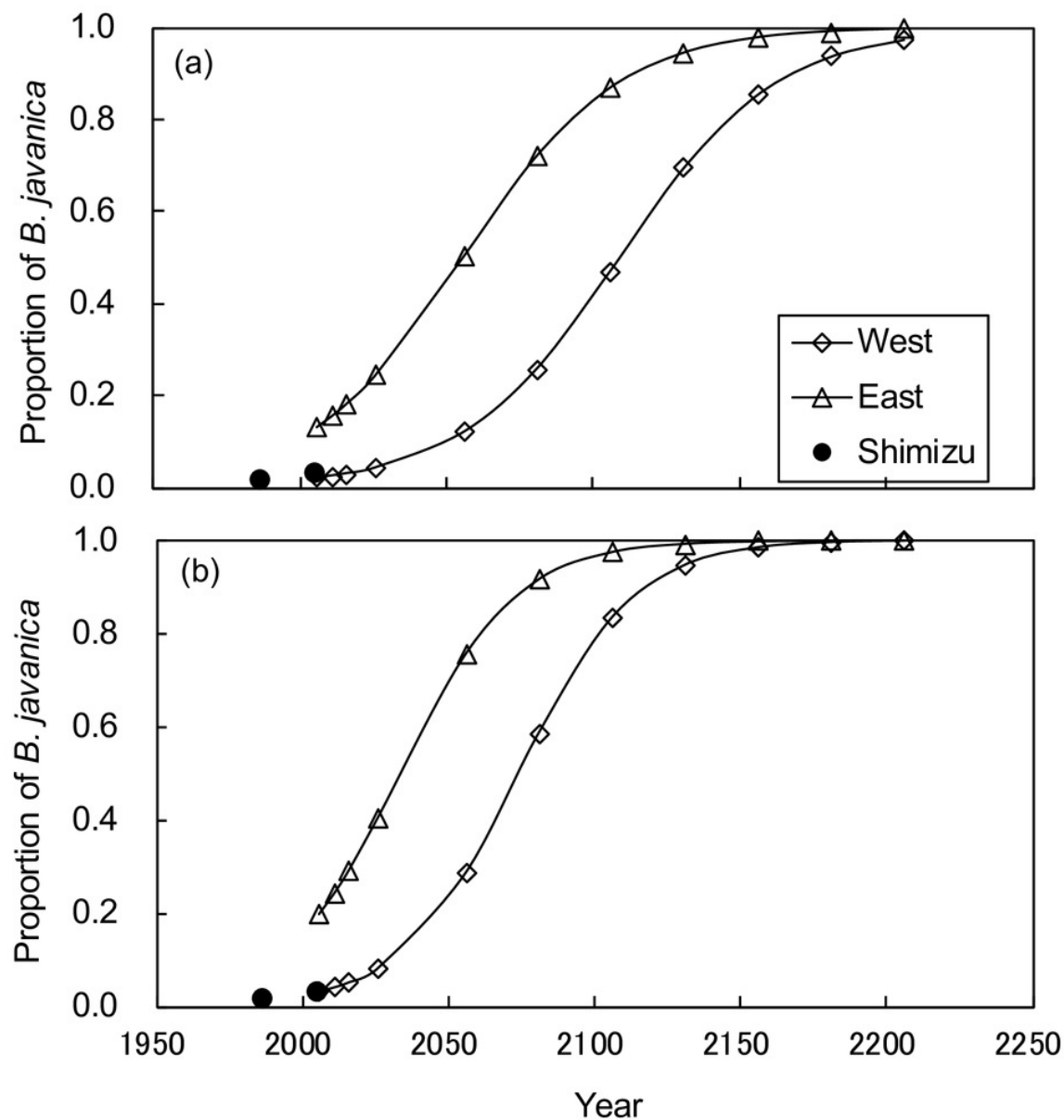
Fig. 8