



HOKKAIDO UNIVERSITY

Title	Early successional habitats created through plantation harvesting benefit the Gray Nightjar (<i>Caprimulgus jotaka</i>) : An 8-year survey in central Hokkaido, northern Japan
Author(s)	Kawamura, Kazuhiro; Yamaura, Yuichi; Nakamura, Futoshi
Citation	Journal of Forest Research, 28(4), 289-296 https://doi.org/10.1080/13416979.2023.2195038
Issue Date	2023-03-30
Doc URL	https://hdl.handle.net/2115/91439
Rights	This is an Accepted Manuscript of an article published by Taylor & Francis in Journal of Forest Research on 30 Mar 2023, available online: http://www.tandfonline.com/10.1080/13416979.2023.2195038 .
Type	journal article
File Information	Nightjar_Draft_230216_final.pdf



Title

Early successional habitats created through plantation harvesting benefit the Gray Nightjar (*Caprimulgus jotaka*): An 8-year survey in central Hokkaido, northern Japan

Authors

Kazuhiro Kawamura^{1,2*}, Yuichi Yamaura³, Futoshi Nakamura²

Affiliations

1. Department of Wildlife Biology, Forestry and Forest Products Research Institute, Matsunosato 1, Tsukuba, Ibaraki 305-8687, Japan
2. Department of Forest Science, Graduate School of Agriculture, Hokkaido University, Kitaku Kita 9 Nishi 9, Sapporo, Hokkaido 060-8589, Japan
3. Shikoku Research Center, Forestry and Forest Products Research Institute, 2-915 Asakuranishimachi, Kochi-shi, Kochi 780-8077, Japan

***Corresponding author:** Kazuhiro Kawamura, Email: kawamurak@ffpri.affrc.go.jp, phone: +81-29-928-8259

Abstract (204/250 words)

Early successional habitats and their associated species have been decreasing globally. In contrast, plantations have been expanding and their young stages (stand age ≤ 10 years) can serve as early successional habitats. The Gray Nightjar (*Caprimulgus jotaka*), a nocturnal bird species, breeds and forages in early successional habitats surrounded by forests; its populations have declined since the 1970s in Japan. Because nightjars are more abundant in warmer areas across Hokkaido, northern Japan, habitat creation through plantation harvesting was expected to promote nightjar abundance or occupancy in this region. To explore the effects of plantation harvesting on nightjar occupancy, we conducted an 8-year playback survey in a plantation landscape in central Hokkaido. We considered the effects of elevation as a surrogate for temperature. The results indicated that increasing young forest cover within 500 m of the centroid of each site enhanced nightjar occupancy, whereas elevation negatively affected occupancy. Therefore, at lower elevations, we predict a larger increase in occupancy probability with increasing young forest cover following plantation harvesting. Our results suggest that young forest creation in landscapes can contribute to Gray Nightjar conservation. To effectively create early successional species habitats through plantation harvesting, it is important to consider climate and elevation in the target area.

Keywords (5/5 words): *Abies sachalinensis*, clear-cut, disturbance-dependent species, forest management, retention forestry

Main text

Introduction

Plantations have been expanding worldwide (FAO 2020), many replacing natural forests (Puyravaud et al. 2010; Hua et al. 2018). Compared with natural forests, plantations have simpler composition and structure, leading to lower species richness and abundance of organisms (Brockerhoff et al. 2008; Chaudhary et al. 2016). Plantations are sometimes converted from open lands (Lindenmayer et al. 2019; Iezzi et al. 2020; Ueno et al. 2022), and their young stages (stand age ≤ 10 years) can serve as alternative or superior habitats for species that prefer early successional habitats created by disturbances (Schlossberg and King 2009; Yamaura et al. 2012a; Ohwaki et al. 2018; Ram et al. 2020). As early successional species have decreased globally (Swanson et al. 2011; King and Schlossberg 2014), plantation harvesting has been expected to contribute to their conservation (Yamaura et al. 2012a, 2012b; Iezzi et al. 2020).

However, the effects of harvesting on early successional species vary spatially. For example, biological responses to habitat management can be contingent on climate (Amano et al. 2011; Betts et al. 2019; Spake et al. 2020), which affects organisms directly via physiological processes (such as maintaining body temperature for animals: Cooper et al. 2006; Camacho 2013), and indirectly via prey resources, vegetation, or land uses (Huston and Wolverton 2009; Yamaura et al. 2011). Temperature can be critical for determining species distributions in mountainous regions, because it changes greatly with elevation (Sergio and Pedrini 2007; Jarzyna et al. 2021). Large-scale, rapid changes in climate due to global warming, coupled with land use change, have threatened many species (Oliver and Morecroft 2014; Díaz et al. 2019). Therefore, it is important to consider the effects of climate or elevation on the distribution or habitat selection of target species for effective conservation by managing habitats.

In Japan, conifer plantations largely replaced natural forests and grasslands from the 1950s to the 1980s (Yamaura et al. 2012b; Ueno et al. 2022), and now account for 41% of the total forest area (Forestry Agency 2017). In the decades following plantation expansion, this forestry decline prevented the creation of young forests (Yamaura et al. 2012b). Semi-natural grasslands and farmlands have been degraded or lost as a result of agricultural intensification and forest transition

68 from abandoned farmland (Koshida and Katayama 2018; Ushimaru et al. 2018). Furthermore, natural
69 disturbances such as wildfires, landslides, floods, and avalanches are suppressed by humans
70 (Ushimaru et al. 2018; Ohwaki 2018). These land-use changes cause population declines in early
71 successional species (Yamaura et al. 2009; Nakamura 2011; Ohwaki 2018). Recently, large-scale
72 clear-cutting of mature plantations has been conducted to increase the domestic wood supply in
73 Japan (Forestry Agency 2021), potentially enhancing the recovery of early successional species
74 (Yamaura et al. 2012a, 2012b).

75 The Gray Nightjar (*Caprimulgus jotaka*) is a nocturnal bird species that breeds in open lands
76 surrounded by forests, including young plantations after harvesting and planting (Fujimaki 1973;
77 Tada 2022). The breeding range of this species across Japan contracted by 57% between 1978 and
78 2002 (Amano and Yamaura 2007). In a previous study, we reported that nightjars were more
79 abundant in warm areas across Hokkaido, northern Japan (Kawamura et al. 2016), where plantation
80 harvesting was anticipated to promote nightjar abundance or occupancy. In this study, we conducted
81 an 8-year playback survey for the Gray Nightjar in 18 plantations, 15 of which were harvested before
82 or during the study period, and three natural forests, for a total of 21 stands in central Hokkaido. We
83 analyzed the effects of stand harvesting and surrounding young forest cover on nightjar occupancy,
84 as well as the effects of elevation as a surrogate of temperature.

85

86

87 **Materials and Methods**

88 **Study area and sites**

89 This study was conducted from 2015 to 2022 at sites established in the Retention Experiment for
90 Plantation Forestry in Sorachi, Hokkaido (REFRESH project: 43°34'37"–43°39'26"N, 142°05'27"–
91 142°09'33"E). In this experiment, we have been investigating whether retaining some canopy trees in
92 harvested Todo fir (*Abies sachalinensis*) plantations might enhance the multifunctionality of the
93 plantations, including the habitat functions of plants, insects, and birds (Yamaura et al. 2018). The
94 study sites were located at the foot to mid-slope of Mt. Irumukeppu (864 m a.s.l.) in landscapes
95 dominated by Todo fir plantations (Fig. 1). Sites were selected in five harvesting types: clear-cutting
96 (CC); small (SS), medium (SM), and large (SL) amounts of single-tree retention; and group retention

97 (GR). We also had two types of control site: unharvested mature plantation (PC) and natural forest
98 (NC). Each treatment had three replicates, for a total of 21 stands.

99 PC sites were dominated by planted Todo firs with stand ages of 48–51 years in 2015. NC sites
100 consisted mainly of linden (*Tilia japonica*), Mongolian oak (*Quercus crispula*), and painted maple
101 (*Acer pictum*). In the SS, SM, and SL sites, 10, 50, and 100 sparsely distributed broadleaved trees/ha
102 were retained, respectively; these mainly consisted of birch (*Betula platyphylla*, *Betula ermanii*, and
103 *Betula maximowicziana*), linden, and Mongolian oak. In each GR site, one unharvested patch of
104 Todo firs (60 m × 60 m: 0.36 ha) was retained at the center of the harvested area. From 2014 to 2016,
105 one site per harvesting type was harvested each year (Appendix S1). Todo fir seedlings had been
106 planted the next spring after harvesting, and weeding had been conducted once or twice annually
107 (Akashi et al. 2017; Yamaura et al. 2018).

108 We did not survey sites undergoing harvesting operations in 2015 and 2016 (Appendix S1).
109 Thereafter, we surveyed all sites in each year except 2021 (and except NC3 in 2022: Appendix S1).
110 For five plantation sites, we surveyed before and after harvesting. As unharvested sites, eight
111 plantations (CC3, GR3, SS3, SM3, SL3, PC1, PC2, and PC3) and three natural forests (NC1, NC2,
112 and NC3) were surveyed and only PC and NC sites were surveyed on multiple years (Appendix S1).
113 The area of each site was 5.0–8.2 ha (Appendix S1), and the distance between sites was at least 200
114 m, except for one pair (SM2 to SS3, Fig. 1; Akashi et al. 2017; Yamaura et al. 2018). The elevation
115 range for all sites was calculated by averaging the values in a 10 m digital elevation model, as 236–
116 506 m (Fig. 1).

117

118 **Bird survey**

119 To examine Gray Nightjar occupancy, we conducted a playback survey (Bibby et al. 2000). In each
120 survey year, we visited each site three times during the Gray Nightjar breeding season, from late
121 May to early August (Saiki 2016). Surveys were conducted between 19:30 and 03:30, when Gray
122 Nightjars are active, avoiding rain and strong winds (> 5 m/s). The male territorial call of the Gray
123 Nightjar was broadcast for 5 min at the edge of each site and any nightjar callbacks within the next 5
124 min were recorded (i.e., 10 min/survey). In 2022, the survey consisted of three repetitions of 2 min of
125 playback and 1 min of recording, plus an additional 1 min of recording at the end, for a total of 6 min

126 of playback and 4 min of recording, corresponding to the sampling method used in our ongoing
127 study. We recorded the number and location of any individual calling in each site and a 50 m buffer
128 zone around each site, and considered these individuals as users of the site.

129 Kawamura et al. (2016) used a similar survey method and found that the detection probability of
130 each territorial individual per survey was ~0.65 and remained constant regardless of the survey
131 season and time of day. We surveyed most sites within one night for each visit. Therefore, we judged
132 that differences among survey seasons or survey conditions were relatively small and that nearly all
133 individuals could be detected within three visits to each site. For playback, we used speakers [(2015–
134 2020) PDX-B11: Yamaha, Hamamatsu, Japan; (2022) SoundLink Revolve+ II: Bose Corporation,
135 Framingham, MA, USA] connected to players (iPhone 5s or iPhone SE: Apple, Cupertino, CA,
136 USA). Although speaker and player models varied, the nightjars responded similarly to playback
137 through different devices, and the amplitudes were nearly identical (66.8 dB for PDX-B11 and 66.7
138 dB for SoundLink Revolve+ II at 5 m from the speaker) and audible throughout each site (Kawamura
139 and Yamaura, personal observation).

140

141 **Environmental variables**

142 *Harvesting treatment and forest type*

143 As a categorical variable at the stand scale, we considered the harvesting treatment (i.e., harvested
144 vs. not harvested). Although retained trees may provide perches for nightjars (Winiger et al. 2018;
145 Camacho 2014) and different harvesting types (i.e., CC, SS, SM, SL, and GR) may have different
146 conservation roles, we treated all harvesting types as a single category. This was because the Gray
147 Nightjar prefers both sparse forests and clear-cut areas (Yamaguchi and Mitarai 2018; Tada 2022)
148 and nightjar occupancy or abundance was too low to examine the effects of harvesting types or the
149 proportion of retained trees. The other categorical variable at the stand scale was forest type
150 (plantation vs. natural forest).

151 *Young forest cover in landscapes*

152 We considered that the young forest cover (stand age ≤ 10) surrounding each site could affect
153 nightjar occupancy. This was because the Gray Nightjars observed in this study were expected to use

the areas surrounding the study sites, considering that the territories (i.e., defended areas for breeding) of the closely related European Nightjar (*Caprimulgus europaeus*) have a radius of approximately 200 m and their home range has a radius of several kilometers (Alexander and Cresswell 1990; Sharps et al. 2015). Furthermore, windthrow occurred in forests adjacent to some sites, immediately followed by harvesting and planting in these sites (Fig. 1, Appendix S1). Kawamura et al. (2016) detected the effects of forest cover within 4 km (home range scale) of each sampling site on nightjar abundance. However, since the large (e.g., 3.0 km radius) buffers of YFC overlapped well (Holland et al. 2004), we used YFC within 500 m (500 m YFC; i.e., territory scale) from the centroid of each site (Fig. 1). This was performed using the ArcGIS Desktop v10.6 software (ESRI, Redlands, CA, USA). Forest data were obtained from Hokkaido Government Opendata CC-BY4.0 (<https://www.pref.hokkaido.lg.jp/sr/dyr/DOP.html> [date of data acquisition: March 31, 2016, in Japanese] and <https://www.pref.hokkaido.lg.jp/sr/srk/98818.html> [date: December 31, 2019, in Japanese]). The 500 m YFC was calculated for each survey year, but the young forests created by harvesting or windthrow after the date of the original data acquisition were not reflected. Therefore, we revised the data when we found young forests in the field.

Elevation

We used elevation as a surrogate for temperature at the local scale (Fig. 1, Appendix S2). Elevation was calculated by averaging the 10 m digital elevation model provided by the Geospatial Information Authority of Japan (https://fgd.gsi.go.jp/download/ref_dem.html (in Japanese)). The 500 m YFC and elevation were standardized prior to model runs. The 500 m YFC, elevation, and the area of sites were not strongly correlated ($|r| < 0.5$).

Statistical analyses

We analyzed using the R v4.1.0 software (R Core Team 2021). To examine the effects of young forest creation through plantation harvesting on nightjar occupancy, we used generalized linear mixed models, using the ‘glmer’ function in the *lme4* package (Bates et al. 2015). Our analyses involved two steps: the harvest/non-harvest model, examining the effects of harvesting treatment (plantation harvesting at the stand scale); and the young forest cover model, analyzing the effects of

182 500 m YFC (young forests mainly created by plantation harvesting). Because the harvesting
183 treatment and 500 m YFC were not independent (i.e., harvested survey stands had more young forest
184 cover, they were not incorporated into the model simultaneously.

185 *Harvest/non-harvest model*

186 We constructed models, where the response variable was nightjar occurrence/non-occurrence in each
187 site in each year and the explanatory variables were the harvesting treatment and elevation. We
188 assumed that the response variable followed a binomial distribution, and used a complementary log-
189 log link function (cloglog). Thus, we modeled the probability that at least one individual occurs at
190 each site assuming that nightjar abundance followed a Poisson distribution (Kajihara et al. 2016).
191 This method allowed us to correct nightjar occupancy for site area differences by considering the
192 proportional increase in abundance with the area of site i [i.e., setting $\log(Area_i)$ as an offset term].
193 To account for pseudoreplication associated with repeatedly surveying the same sites, we used site
194 ID as a random intercept (i.e., random site effect). We constructed models for all possible
195 combinations of the explanatory variables and selected the model with the lowest AIC as the best
196 model (Burnham and Anderson 2002), using the ‘dredge’ function in the *MuMIn* package (Bartoń
197 2022). We calculated the 95% confidence intervals of the coefficients of each explanatory variable in
198 the best models using the ‘confint.merMod’ function (method = “profile”). We interpreted the effect
199 of an explanatory variable as significant when the interval did not overlap with zero. The effect of
200 forest type was confounded with that of harvesting treatment because most plantation sites were
201 harvested and all surveyed natural forests were unharvested controls. Forest type was therefore
202 excluded from the explanatory variables.

203 *Young forest cover model*

204 Using the same method, we also conducted the analysis with 500 m YFC, forest type, and elevation
205 as explanatory variables. In contrast to the harvest/non-harvest model, forest type was included as an
206 explanatory variable in this model because the VIFs of 500 m YFC and forest type were below 10
207 (5.10 for 500 m YFC and 6.22 for forest type: Dormann et al. 2013). We interpreted the effect of
208 young forest creation through harvesting on nightjar occupancy considering the results of both the
209 harvest/non-harvest model and the young forest cover model.

Consideration of the effect of site area and the annual variation in nightjar occupancy

Although we assumed that the nightjar abundance was directly proportional to the area of site i ($Area_i$) and set the offset term to $\log(Area_i)$ [i.e., the coefficient of $\log(Area_i)$ was fixed at 1], the coefficient of $\log(Area_i)$ could exceed 1 if Gray Nightjars preferred larger harvested areas. In our preliminary analysis, we extracted data only from harvested sites and constructed a model using $\log(Area_i)$ and elevation as explanatory variables. The results showed a coefficient of $\log(Area_i)$ of -0.40 , with a wide confidence interval (Appendix S3). Therefore, we used $\log(Area_i)$ only as an offset term in our analyses, assuming a small area effect of harvesting on nightjar occupancy.

In our preliminary analysis, we considered annual variation in nightjar occupancy in addition to the random site effect, by including the survey year as a random intercept (random year effect) in the models. However, the random year effect did not explain the variation in our data, and intercept and coefficient estimates were nearly identical to those for the model that did not include a random year effect (Appendix S4). Therefore, only the random site effect was considered in our analyses.

Results

During the 8-year study period, we detected Gray Nightjars in seven of the 21 sites (Fig. 1). Five of these sites were harvested, including one clear-cutting site (CC2), two single-tree retention sites (SS2 and SL1), and two group retention sites (GR1 and GR3). The earliest nightjar occurrence after harvesting was the following year (GR3), and the latest was 6 years later (CC2) (Appendix S1). Nightjars also occurred in two unharvested natural forest sites, although they only began to occupy NC2 after windthrows occurred in adjacent forest areas (the 500 m YFC was relatively low at both sites: Appendix S1, Fig. 2). Nightjars were detected in multiple years at four sites (GR3, SS2, SL1, and NC2) and in GR3 during four consecutive years after harvesting (Appendix S1). The only site where multiple individuals occurred during a single visit was SS2, where two individuals were detected in 2017; one of these individuals may have also called back in the neighboring site, GR3. Other occurrences in the same year were not considered to be in the territory of the same individual because the calling locations were >700 m apart.

Harvest/non-harvest model

In the best model, harvesting treatment and elevation were included as the explanatory variables (Appendix S5). There was a single competing model (i.e., the second-ranked model with $\Delta AIC < 2$) that had the elevation as an explanatory variable (Appendix S5). The coefficient of harvesting treatment in the best model was estimated to be positive, but the difference in nightjar occupancy between harvested and unharvested sites was not significant at the 5% level (Table 1a). Elevation negatively affected occupancy (Table 1a, Fig. 1).

Young forest cover model

The young forest cover model showed a positive effect of YFC and a negative effect of elevation. The best model contained 500 m YFC, elevation, and forest type as explanatory variables (Table 1b). Nightjar occupancy was higher in areas with higher 500 m YFC and lower elevation (Table 1b, Fig. 2). Occupancy tended to be low in plantation sites compared to natural forest sites (Table 1b). Although we did not use the interaction term between 500 m YFC and elevation, the absolute increment in occupancy probability at plantation sites with increasing 500 m YFC was predicted to differ greatly according to elevation (Fig. 2). In 5 ha plantation sites where the 500 m YFC was 0%, occupancy probability was almost zero across the elevation range. As the 500 m YFC increased to 25% (~20 ha increase in young forest), the occupancy probability increased to 0.94 and 0.25 in areas with low (236 m) and medium (383 m) elevation, respectively. In contrast, in high-elevation sites (506 m), occupancy probability increased only slightly (0.04).

Discussion

Positive effects of young forest cover within 500 m

Nightjar occupancy was enhanced by increasing young forest cover (mainly young plantations, including the harvested survey sites) within 500 m. These results indicate that young forest creation through plantation harvesting can contribute to Gray Nightjar conservation. The Gray Nightjar tends to nest in young plantations (Fujimaki 1973; Tada 2022), and assuming a similar territory range to the European Nightjar, its territory is likely contained within an area of 500 m (Bowden and Green

1994; Sharps et al. 2015). Open environments near forests are also suitable for the visual detection of insects flying from mature forests (e.g., large moths) and for catching these prey insects in the air (Sierro et al. 2001; Evens et al. 2018, 2020). Studies have shown that European Nightjars frequently forage near their nests during the incubation period (Alexander and Cresswell 1990; Cross et al. 2005) and that foraging sites near the nests are superior in terms of low commuting costs (Sharps et al. 2015; Evens et al. 2018). Therefore, forested areas with high young forest cover provide suitable nesting and foraging environments.

In western Tokyo, central Japan, Yamaguchi and Mitarai (2018) reported that nightjar occupancy within 250 m increased with increased clear-cutting area, exceeding 0.5 in sites with a clear-cut area of > 4.3 ha (0.5–27.9 ha). Young forest creation through clear-cutting also positively affects European Nightjar occupancy, although the minimum area for occupation differs among studies (0.7 ha: Wichmann 2004; 1 ha: Scott et al. 1998; 10 ha: Ravenscroft 1989). In this study, the maximum area of harvested survey stands was 8.2 ha and the effects of the stand harvesting treatment were not significant. However, nightjar occupancy increased more clearly in sites where young forest cover within 500 m exceeded 10% (7.9 ha). These results suggest that harvesting stands (5.8–8.2 ha in our case) only would not provide sufficient habitat and surrounding young forests also contribute to nightjar occupancy. Thus, in landscapes where forestry is active, multiple harvested stands would support nightjar occupancy.

Broadleaved natural forests and retention cutting stands as habitats

Natural forests tended to be preferred by nightjars over plantations, although only three natural forest sites were surveyed. Given that young forest cover, including harvested plantations, positively affected nightjar occupancy, our results indicate a poor habitat function of unharvested plantations. This finding is supported by those of a previous study conducted in eastern Hokkaido (Toyoshima et al. 2013), which occasionally detected early successional birds in stands older than 60 years in natural forests, but not in mature plantations. Nightjars did not prefer mature plantations with a high tree density. Nightjars were also found in harvested sites with retention rates of 10–100 broadleaved trees/ha and in a site with a retained Todo fir patch (0.36 ha). Retention cutting areas generally harbor fewer early successional species than clear-cutting areas because of their smaller open spaces

297 (Fedrowitz et al. 2014). However, both the Gray Nightjar and European Nightjar prefer sparse forests
298 as habitats (Sierro et al. 2001; Winiger et al. 2018; Tada 2022), and the Red-necked Nightjar
299 (*Caprimulgus ruficollis*) selects areas near tall vegetation as refuges from predators when descending
300 to the ground (Camacho 2014). Future studies should investigate the habitat function of natural and
301 sparse managed forests for early successional species. For nightjars with a large home range and
302 wide range of habitat uses, the interactive effects of forest type with landscape variables are also
303 needed for evaluation (Knight et al. 2021b).

304

305 **Negative effects of elevation**

306 Nightjars were more abundant in areas with lower elevation. By contrast, no elevation effect on
307 nightjar occupancy was detected in a previous study conducted in warmer regions of Japan
308 (Yamaguchi and Mitarai 2018); thus, our results were likely a reflection of temperature effects. The
309 negative impacts of cool conditions have been reported for nocturnal insectivores (European
310 Nightjar: Morris et al. 1994, bats: Rydell et al. 1996; Davy et al. 2022). There are two possible
311 explanations for this finding. First, the availability of flying insects (e.g., moths) as prey resources
312 tends to be lower under cooler conditions (Turner et al. 1987; McGeachie 1989; Roy et al. 2001). In
313 this area, elevation was the most important determinant of understory plant communities, with a
314 negative impact on their species richness (Akashi et al. 2022). Second, nocturnal flying vertebrates
315 may be physiologically sensitive to temperature; for example, the Red-necked Nightjar prefers warm
316 roads on cold nights (Camacho 2013; De Felipe et al. 2019). Although nightjar occupancy may also
317 be influenced by other environmental factors correlated to elevation, such as young forest cover at
318 larger scales (Kawamura et al. 2016), pastures, or farmlands (Evens et al. 2021), cool areas tend to
319 restrict the distributions of Caprimulgidae species, which evolved in the tropics and share similar
320 morphology and foraging ecology (Cleere and Nurney 1998).

321

322 **Implications for forest management and conservation**

323 Despite the moderate spatial extent of our study region (6×12 km), there were spatial differences in
324 the nightjar occupancy increment with increasing young forest cover. The absolute increment in
325 nightjar occupancy with young forest creation was predicted to be larger in areas with lower

elevation, according to nightjar distribution model results for Hokkaido. The determining factors of species distribution and the degree of these effects can vary regionally (Crosby et al. 2019; Knight et al. 2021a). For example, Knight et al. (2021b) demonstrated that the disturbance type and time since disturbance were important factors for determining the nesting habitat use of the Common Nighthawk (*Chordeiles minor*) and their habitat usage duration in disturbed areas was longer in landscapes with a higher proportion of pine forests. The area effects of harvesting itself and landscape/climate-dependent area effects on nightjar occupancy may be detected using sites with wider ranges of each environment. Nevertheless, our results provide valuable insights for designing conservation strategies for early successional species. Considering the effects of climate, elevation, and landscape on conservation target species is essential to implement plantation harvesting for effective habitat creation and promoting biodiversity conservation efforts in balance with timber production.

Acknowledgments

We thank the officials of the Fishery and Forestry Department of Hokkaido Prefecture and the local branch of the Sorachi Forest Office for their help with the REFRESH project. We greatly appreciated A. Unno for providing useful information on our study sites and surrounding stands. Two anonymous reviewers provided useful comments for the manuscript. This study was supported by the Japan Society for the Promotion of Science [17J01767, 21K20599] and the Research grant of the Forestry and Forest Products Research Institute [202110].

Declaration of interest statement

None declared.

References

- Akashi, N., Tsushima, T., Unno, A., Nagasaka, A., Nagasaka, Y., Ohno, Y., Nitta, N., Watanabe, I., Minamino, K., Yamada, K., Ishihama, N., Takiya, M., Tsuda, T., Takeuchi, F., Ishizuka, W., Fukuchi, M., Yamaura, Y., Ozaki, K., Hironaka, Y., Inari, N. 2017. Composition of trees before harvesting in the Retention Experiment for plantation FoREstry in Sorachi, Hokkaido (REFRESH) sites. *Bullet. Hokkaido Forestry Res. Inst.* 54, 31–45. In Japanese with English abstract. <https://agriknowledge.affrc.go.jp/RN/2010911825.pdf>.
- Akashi, N., Nitta, N., Ohno, Y. 2021. Effect of forest management on understory vascular plants in planted *Abies sachalinensis* forests. *For Ecol Manag.* 497:119521.
- Alexander I, Cresswell B. 1990. Foraging by nightjars *Caprimulgus europaeus* away from their nesting areas. *Ibis.* 132(4):568-574.
- Amano T, Yamaura Y. 2007. Ecological and life-history traits related to range contractions among breeding birds in Japan. *Biol Conserv.* 137(2):271-282.
- Amano T, Kusumoto Y, Okamura H, Baba YG, Hamasaki K, Tanaka K, Yamamoto S. 2011. A macro-scale perspective on within-farm management: how climate and topography alter the effect of farming practices. *Ecol Lett.* 14(12):1263-1272.
- Bartoń K. 2022. MuMIn: Multi-Model Inference. R package version 1.46.0. <https://CRAN.R-project.org/package=MuMIn>
- Bates D, Maechler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. *J Stat Softw.* 67(1):1-48. doi:10.18637/jss.v067.i01.
- Betts MG, Wolf C, Pfeifer M, Banks-Leite C, Arroyo-Rodríguez V, Ribeiro DB, Barlow J,

373 Eigenbrod F, Faria D, Fletcher RJ. 2019. Extinction filters mediate the global effects of
 374 habitat fragmentation on animals. *Science*. 366(6470):1236-1239.
 375 Bibby CJ, Burgess ND, Hill DA. 2000. Bird census techniques. 2nd ed. London: Academic Press.
 376 Bowden CGR, Green RE. 1994. The ecology of nightjars on pine plantations in Thetford forest.
 377 Sandy, Bedfordshire: Royal Society for the Protection of Birds.
 378 Brockerhoff EG, Jactel H, Parrotta JA, Quine CP, Sayer J. 2008. Plantation forests and biodiversity:
 379 oxymoron or opportunity? *Biodivers Conserv*. 17(5):925-951.
 380 Burnham KP, Anderson DR. 2002. Model selection and multimodel inference: a practical
 381 information-theoretic approach. 2nd ed. New York: Springer.
 382 Camacho C. 2013. Behavioural thermoregulation in man-made habitats: surface choice and mortality
 383 risk in red-necked nightjars. *Bird Study*. 60(1):124-130.
 384 Camacho C. 2014. 'bodyguard' plants: Predator-escape performance influences microhabitat choice
 385 by nightjars. *Behav Processes*. 103:145-149.
 386 Chaudhary A, Burivalova Z, Koh LP, Hellweg S. 2016. Impact of forest management on species
 387 richness: global meta-analysis and economic trade-offs. *Sci Rep*. 6:23954.
 388 Cleere N, Nurney D. 1998. Nightjars: a guide to nightjars and related nightbirds. East Sussex: Pica
 389 Press.
 390 Cooper CB, Hochachka WM, Phillips TB, Dhondt AA. 2006. Geographical and seasonal gradients in
 391 hatching failure in eastern bluebirds *Sialia sialis* reinforce clutch size trends. *Ibis*.
 392 148(2):221-230.
 393 Crosby AD, Bayne EM, Cumming SG, Schmiegelow FK, Dénes FV, Tremblay JA. 2019.
 394 Differential habitat selection in boreal songbirds influences estimates of population size and
 395 distribution. *Divers Distrib*. 25(12):1941-1953.
 396 Cross T, Lewis J, Lloyd J, Morgan C, Rees D. 2005. Science for conservation management:
 397 European nightjar *Caprimulgus europaeus* breeding success and foraging behaviour in
 398 upland coniferous forests in mid-wales. Countryside Council for Wales (unpublished report).
 399 Davy CM, von Zuben V, Kukka PM, Gerber BD, Slough BG, Jung TS. 2022. Rapidly declining
 400 body size in an insectivorous bat is associated with increased precipitation and decreased
 401 survival. *Ecol Appl*. 23(7):e2639.
 402 De Felipe M, Sáez-Gómez P, Camacho C. 2019. Environmental factors influencing road use in a
 403 nocturnal insectivorous bird. *European J Wildl Res*. 65(3):1-7.
 404 Díaz S, Settele J, Brondízio ES, Ngo HT, Agard J, Arneth A, Balvanera P, Brauman KA, Butchart
 405 SH, Chan KM Garibaldi LA. 2019. Pervasive human-driven decline of life on Earth points to
 406 the need for transformative change. *Science*. 366(6471):eaax3100.
 407 Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, Marquéz JRG, Gruber B, Lafourcade
 408 B, Leitão PJ, Münkemüller T. 2013. Collinearity: a review of methods to deal with it and a
 409 simulation study evaluating their performance. *Ecography*. 36(1): 27-46.
 410 Evens R, Beenaerts N, Neyens T, Witters N, Smeets K, Artois T. 2018. Proximity of breeding and

411 foraging areas affects foraging effort of a crepuscular, insectivorous bird. *Sci Rep.* 8(1):1-11.

412 Evens R, Conway G, Franklin K, Henderson I, Stockdale J, Beenaerts N, Smeets K, Neyens T,
 413 Ulenaers E, Artois T. 2020. DNA diet profiles with high-resolution animal tracking data
 414 reveal levels of prey selection relative to habitat choice in a crepuscular insectivorous bird.
 415 *Ecol Evol.* 10(23):13044-13056.

416 Evens R, Jacot A, Artois T, Ulenaers E, Neyens T, Rappaz L, Theux C, Pradervand JN. 2021.
 417 Improved ecological insights commission new conservation targets for a crepuscular bird
 418 species. *Anim Conserv.* 24(3):457-469.

419 FAO. 2020. Global Forest Resources Assessment 2020: Main report. Rome.

420 Fedrowitz K, Koricheva J, Baker SC, Lindenmayer DB, Palik B, Rosenvald R, Beese W, Franklin
 421 JF, Kouki J, Macdonald E. 2014. Can retention forestry help conserve biodiversity? A meta-
 422 analysis. *J Appl Ecol.* 51(6):1669-1679.

423 Forestry Agency. 2017. Proportion of forests to land area and of plantations to forest area in each
 424 prefecture in Japan (in Japanese).
 425 <https://www.rinya.maff.go.jp/j/keikaku/genkyou/h29/1.html>.

426 Forestry Agency. 2021. Annual reports on forest and forestry in Japan for fiscal year 2020. Tokyo:
 427 Forestry Agency. In Japanese. [https://www.maff.go.jp/e/data/publish/attach/pdf/index-](https://www.maff.go.jp/e/data/publish/attach/pdf/index-208.pdf)
 428 [208.pdf](https://www.maff.go.jp/e/data/publish/attach/pdf/index-208.pdf)

429 Fujimaki Y. 1973. *Yotaka no eisou 2 rei* (2 example of Jungle Nightjar nesting). *Tori* 22:30–32. In
 430 Japanese.

431 Holland JD, Bert DG, Fahrig L. 2004. Determining the spatial scale of species' response to habitat.
 432 *BioScience.* 54(3):227-233.

433 Hua F, Wang L, Fisher B, Zheng X, Wang X, Douglas WY, Tang Y, Zhu J, Wilcove DS. 2018. Tree
 434 plantations displacing native forests: the nature and drivers of apparent forest recovery on
 435 former croplands in southwestern china from 2000 to 2015. *Biol Conserv.* 222:113-124.

436 Huston MA, Wolverton S. 2009. The global distribution of net primary production: resolving the
 437 paradox. *Ecol Monogr.* 79(3):343-377.

438 Iezzi ME, De Angelo C, Di Bitetti MS. 2020. Tree plantations replacing natural grasslands in high
 439 biodiversity areas: how do they affect the mammal assemblage? *For Ecol Manag.*
 440 473:118303.

441 Jaeger B. 2017. r2glmm: computes R squared for mixed (multilevel) models. R package version
 442 0.1.2. <https://CRAN.R-project.org/package=r2glmm>

443 Jarzyna MA, Quintero I, Jetz W. 2021. Global functional and phylogenetic structure of avian
 444 assemblages across elevation and latitude. *Ecol Lett.* 24(2):196-207.

445 Kawamura K, Yamaura Y, Senzaki M, Yabuhara Y, Akasaka T, Nakamura F. 2016. Effects of land
 446 use and climate on the distribution of the Jungle Nightjar *Caprimulgus indicus* in Hokkaido,
 447 northern Japan. *Ornithol Sci.* 15(2):203-212.

448 King DI, Schlossberg S. 2014. Synthesis of the conservation value of the early-successional stage in

449 forests of eastern north America. For Ecol Manag. 324:186-195.

450 Knight EC, Smith AC, Brigham RM, Bayne EM. 2021a. Combination of targeted monitoring and
 451 breeding bird survey data improves population trend estimation and species distribution
 452 modeling for the common nighthawk. Condor. 123(2):duab005.

453 Knight EC, Brigham RM, Bayne EM. 2021b. Specialist or generalist? It depends. Context-dependent
 454 habitat relationships provide insight into forest disturbance effects for a boreal bird species.
 455 For Ecol Manag. 502:119720.

456 Koshida C, Katayama N. 2018. Meta-analysis of the effects of rice-field abandonment on
 457 biodiversity in Japan. Conserv Biol. 32(6):1392-1402.

458 Lindenmayer DB, Blanchard W, Westgate MJ, Foster C, Banks SC, Barton P, Crane M, Ikin K,
 459 Scheele BC. 2019. Novel bird responses to successive, large-scale, landscape
 460 transformations. Ecol. Monogr. 89(3):e01362.

461 McGeachie WJ. 1989. The effects of moonlight illuminance, temperature and wind speed on light-
 462 trap catches of moths. Bull Entomol Res. 79(02):185-192.

463 Morris A, Burges D, Fuller RJ. 1994. The status and distribution of nightjars *Caprimulgus europaeus*
 464 in Britain in 1992. A report to the British trust for ornithology. Bird Study. 41(3):181-191.

465 Nakamura Y. 2011. Conservation of butterflies in japan: status, actions and strategy. J Insect
 466 Conserv. 15(1):5-22.

467 Ohwaki A. 2018. How should we view temperate semi-natural grasslands? Insights from butterflies
 468 in japan. Glob Ecol Conserv. 16:e00482.

469 Ohwaki A, Koyanagi TF, Maeda S. 2018. Evaluating forest clear-cuts as alternative grassland
 470 habitats for plants and butterflies. For Ecol Manag. 430:337-345.

471 Oliver TH, Morecroft MD. 2014. Interactions between climate change and land use change on
 472 biodiversity: attribution problems, risks, and opportunities. Wiley Interdiscip Rev Clim
 473 Change. 5(3):317-335.

474 Puyravaud JP, Davidar P, Laurance WF. 2010. Cryptic destruction of india's native forests. Conserv
 475 Lett. 3(6):390-394.

476 R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for
 477 Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.

478 Ram D, Lindström Å, Pettersson LB, Caplat P. 2020. Forest clear-cuts as habitat for farmland birds
 479 and butterflies. For Ecol Manag. 473:118239.

480 Ravenscroft NOM. 1989. The status and habitat of the nightjar *Caprimulgus europaeus* in coastal
 481 suffolk. Bird Study. 36(3):161-169.

482 Roy DB, Rothery P, Moss D, Pollard E, Thomas JA. 2001. Butterfly numbers and weather:
 483 predicting historical trends in abundance and the future effects of climate change. J Anim
 484 Ecol. 70(2):201-217.

485 Rydell J, Entwistle A, Racey PA. 1996. Timing of foraging flights of three species of bats in relation
 486 to insect activity and predation risk. Oikos.243-252.

487 Saiki M. 2016. Seasonal change in the song frequency of Jungle Nightjar in the Chichibu Mountains.
 488 Jpn J Ornithol 65:31-35.

489 Schlossberg S, King DI. 2009. Postlogging succession and habitat usage of shrubland birds. J Wildl
 490 Manag. 73(2):226-231.

491 Scott GW, Jardine DC, Hills G, Sweeney B. 1998. Changes in nightjar *Caprimulgus europaeus*
 492 populations in upland forests in Vorkshire. Bird Study. 45(2):219-225.

493 Sergio F, Pedrini P. 2007. Biodiversity gradients in the alps: the overriding importance of elevation.
 494 Biodivers Conserv. 16(12):3243-3254.

495 Sharps K, Henderson IAN, Conway G, Armour-Chelu N, Dolman PM. 2015. Home-range size and
 496 habitat use of European Nightjars *Caprimulgus europaeus* nesting in a complex plantation-
 497 forest landscape. Ibis. 157(2):260-272.

498 Sierro A, Arlettaz R, Naef-Daenzer B, Strebel S, Zbinden N. 2001. Habitat use and foraging ecology
 499 of the nightjar (*Caprimulgus europaeus*) in the swiss alps: Towards a conservation scheme.
 500 Biol Conserv. 98(3):325-331.

501 Spake R, Soga M, Kawamura K, Cooke RS, Yamaura Y, Eigenbrod F. 2020. Regional variability in
 502 landscape effects on forest bird communities. Landsc Ecol. 35(5):1055-1071.

503 Swanson ME, Franklin JF, Beschta RL, Crisafulli CM, DellaSala DA, Hutto RL, Lindenmayer DB,
 504 Swanson FJ. 2011. The forgotten stage of forest succession: early-successional ecosystems
 505 on forest sites. Front Ecol Environ. 9(2):117-125.

506 Tada H. 2022. Nesting habitat characteristics of Jungle Nightjar in central Okayama Prefecture. Jpn J
 507 Ornithol 71:1-8. In Japanese with English abstract.

508 Toyoshima Y, Yamaura Y, Mitsuda Y, Yabuhara Y, Nakamura F. 2013. Reconciling wood
 509 production with bird conservation: A regional analysis using bird distribution models and
 510 forestry scenarios in Tokachi district, northern Japan. For Ecol Manag. 307:54-62.

511 Turner JRG, Gatehouse CM, Corey CA. 1987. Does solar energy control organic diversity?
 512 Butterflies, moths and the british climate. Oikos. 195-205.

513 Ueno R, Fujiwara T, Sato N, Fujioka Y. 2022. Where did people plant trees during the mass
 514 afforestation after WW 2 ? ~An analysis of the Kyushu area using the 1960 World Census of
 515 Agriculture and Forestry~. Kyushu J For Res. 75:97-100. In Japanese.

516 Ushimaru A, Uchida K, Suka T. 2018. Grassland biodiversity in Japan: threats, management and
 517 conservation. In *Grasslands of the World: Diversity, Management and Conservation*. pp. 211-
 518 232. Boca Raton, US: CRC press.

519 Wichmann G. 2004. Habitat use of nightjar (*Caprimulgus europaeus*) in an Austrian pine forest. J
 520 Ornithol. 145(1):69-73.

521 Winiger N, Korner P, Arlettaz R, Jacot A. 2018. Vegetation structure and decreased moth abundance
 522 limit the recolonisation of restored habitat by the European nightjar. Rethink Ecol. 3:25-39.

523 Yamaguchi T, Mitarai N. 2018 Distribution of the Jungle Nightjar in cutovers and quarries in
 524 western Tokyo, central Japan. Strix 34:17-25. In Japanese with English abstract.

525 Yamaura Y, Amano T, Koizumi T, Mitsuda Y, Taki H, Okabe K. 2009. Does land-use change affect
526 biodiversity dynamics at a macroecological scale? A case study of birds over the past 20
527 years in japan. *Anim Conserv*. 12(2):110-119.

528 Yamaura Y, Amano T, Kusumoto Y, Nagata H, Okabe K. 2011. Climate and topography drives
529 macroscale biodiversity through land-use change in a human-dominated world. *Oikos*.
530 120(3):427-451.

531 Yamaura Y, Royle JA, Shimada N, Asanuma S, Sato T, Taki H, Makino S. 2012a. Biodiversity of
532 man-made open habitats in an underused country: a class of multispecies abundance models
533 for count data. *Biodivers Conserv*. 21(6):1365-1380.

534 Yamaura Y, Oka H, Taki H, Ozaki K, Tanaka H. 2012b. Sustainable management of planted
535 landscapes: lessons from japan. *Biodivers Conserv*. 21(12):3107-3129.

536 Yamaura Y, Akashi N, Unno A, Tsushima T, Nagasaka A, Nagasaka Y, Ozaki K. 2018. Retention
537 experiment for plantation forestry in Sorachi, Hokkaido (REFRESH): a large-scale
538 experiment for retaining broad-leaved trees in conifer plantations. *Bull For For Prod Res Inst*.
539 17(1):91-109.

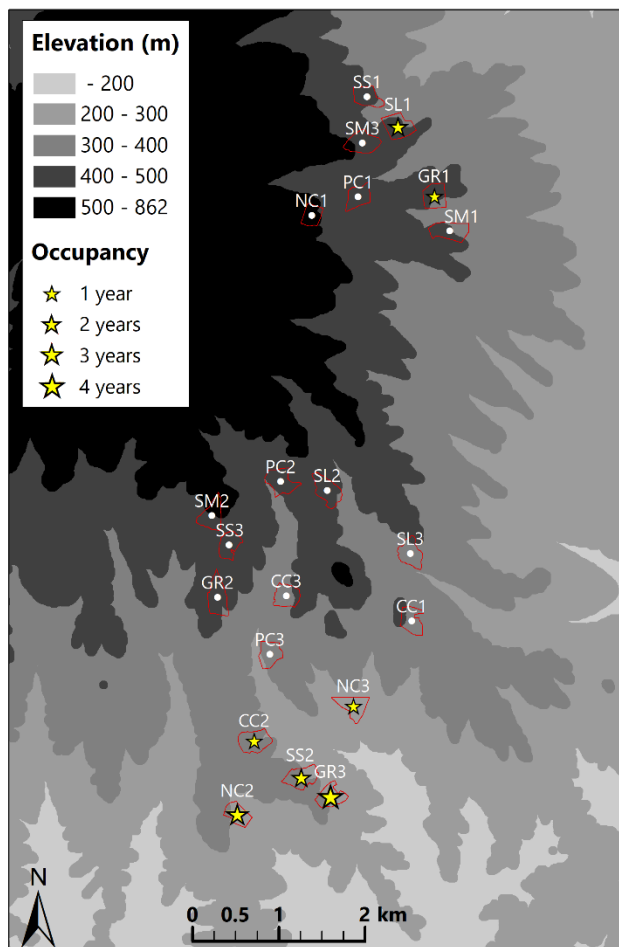
540

Table and Figures

Table 1. Parameter estimates of the best (a) harvest/non-harvest and (b) young forest cover models. For each model, R^2 was calculated using the ‘r2beta’ function in the package *r2glmm* (Jeager 2017). Abbreviations: Harvest, the categorical explanatory variable of harvested sites compared to non-harvested sites; 500-m YFC, young forest cover within 500 m; Plantation, the categorical explanatory variable of plantations compared to natural forests; 95%CI.l and 95%CI.u, lower and upper 95% confidence interval limits, respectively. The intercept represents (a) non-harvested forests and (b) natural forests. Bold indicates the significance of the explanatory variable at the 5% level. The Δ AIC (i.e., AIC difference from the best model) of the second-rank model was (a) 1.44 for the harvest/non-harvest model and (b) 2.02 for the young forest cover model. These second-rank models contained fewer explanatory variables (see details in Appendix S5).

	Variables	Estimates	SE	z value	Wald p	95%CI.l	95%CI.u
	R^2	0.21				0.10	0.36
(a)	Intercept	−6.37	1.12	−5.68	< 0.001		
	Harvest	1.47	0.86	1.70	0.089	−0.08	4.06
	Elevation	−1.83	0.51	−3.57	< 0.001	−3.38	−0.95
	R^2	0.16				0.07	0.31
(b)	Intercept	−3.07	1.45	−2.11	0.035		
	500-m YFC	1.96	0.92	2.13	0.033	0.66	4.65
	Elevation	−1.09	0.54	−2.02	0.044	−2.40	−0.04
	Plantation	−3.33	2.08	−1.60	0.110	−9.36	−0.07

(a)



(b)

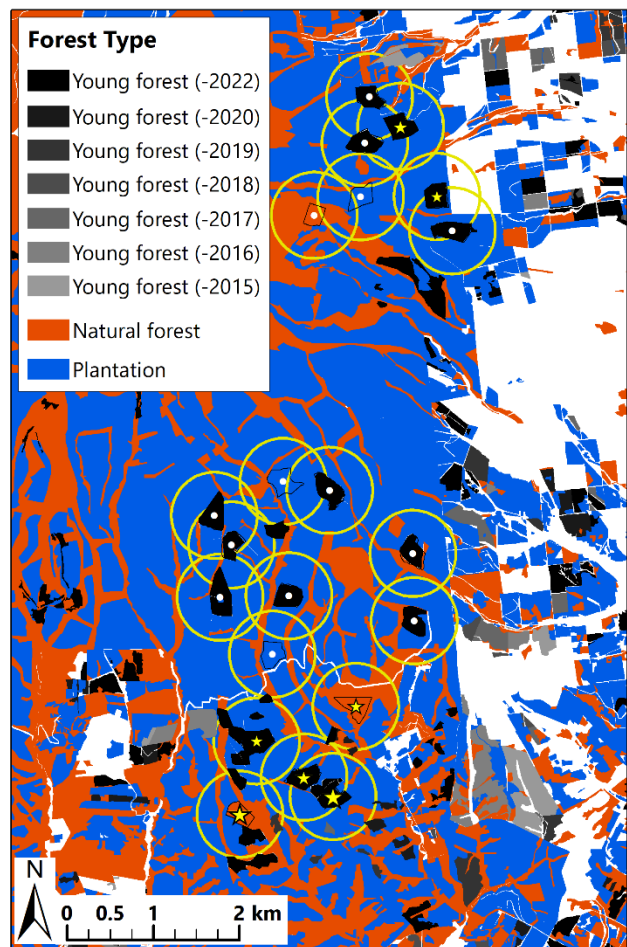
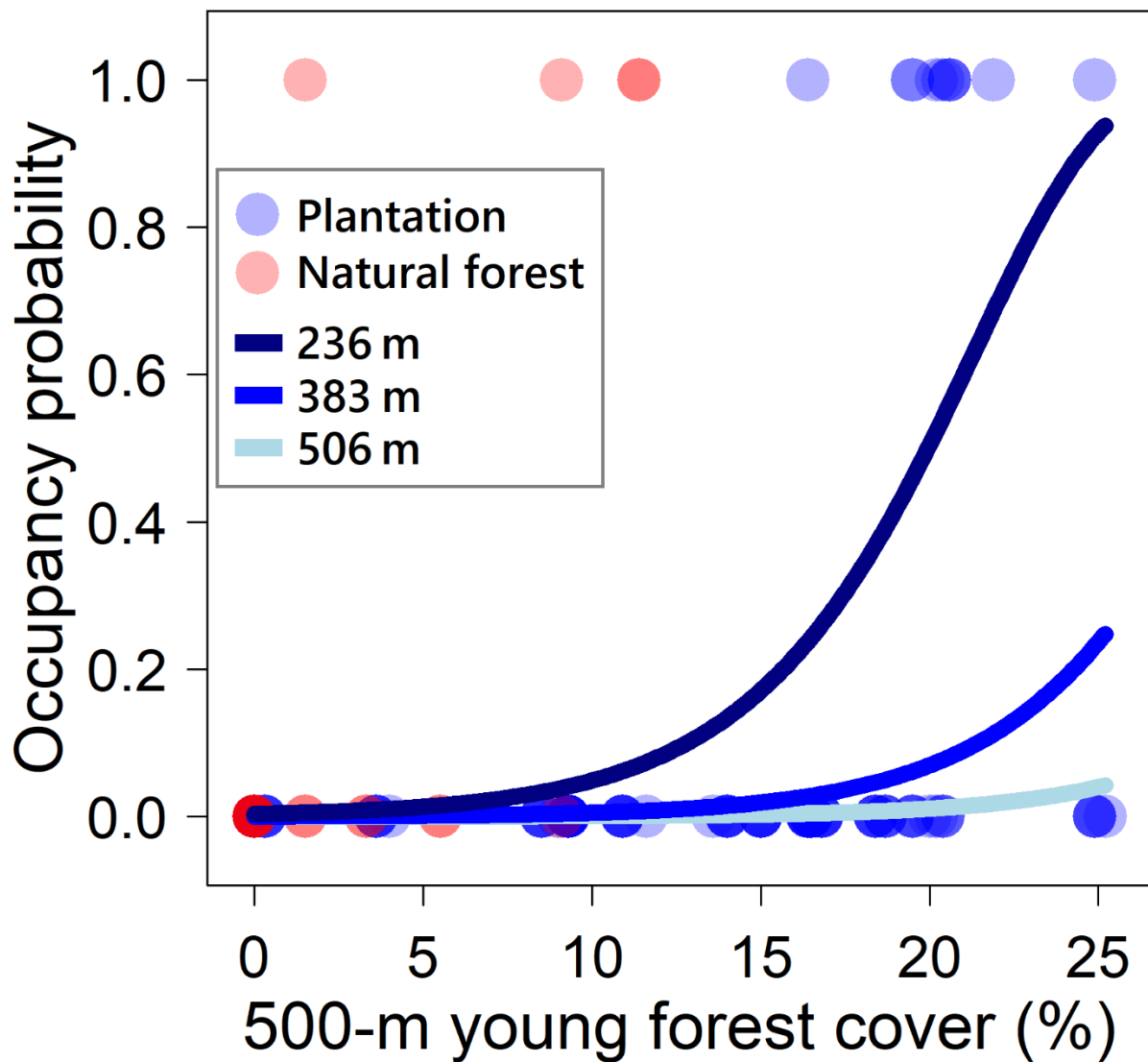


Fig. 1. Map of the study area. Symbols at the center of each site indicate nightjar occupancy status; the size of the star indicates the number of years in which nightjars occurred, and white circles indicate no occurrence. Shading represents differences in (a) elevation and (b) forest type. In young forests, lighter colors indicate higher stand age. For example, “Young forest (–2016)” indicates that these stands were treated as young forest stands until 2016 and thereafter as > 10-year-old stands. The yellow circles around each site represent 500-m radius zones.



562

563 **Fig. 2.** Estimated relationship between nightjar occupancy probability and explanatory variables in
 564 the young forest cover models. Solid lines are predictions by the best performing models; colors
 565 indicate different elevations. Blue and red translucent circles represent the observed values in
 566 plantation and natural forest sites, respectively. Site area differed among these observed values, and
 567 was fixed to 5 ha for predictions.

568 The English in this document has been checked by at least two professional editors, both native
569 speakers of English. For a certificate, please see:

570 <http://www.textcheck.com/certificate/7FvXyn>

571