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ORIGINAL ARTICLE

Clearcut areas aged 2–6 years in shelterbelts support high diversity of butterflies and flowering plants, including endangered grassland butterflies, in the Tokachi District of Hokkaido, northern Japan

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Abstract. Grassland butterflies are declining widely in temperate regions, and are thus a key target for conservation. Recent studies have shown that forest clearcuts can be temporary habitats for these species. Shelterbelts – rows of trees, planted to protect houses and crops from the winds – are periodically cleared. This clearing is necessary to prevent falling large branches from mature trees while maintaining their primary function. Consequently, recently cleared young shelterbelts have the potential to serve as habitats for grassland species. However, it remains unclear how long young shelterbelt plantations support grassland butterflies. In this study, we made a survey where the responses of flowering plants and butterflies to plantation age and environmental parameters were investigated during spring and summer in eight plantations aged 2–12 years. Plant richness, nectar abundance, as well as butterfly richness and abundance decreased with increasing plantation age. Butterflies, including endangered species, thrived in 2–6-year plantations, but declined dramatically thereafter. Age-related environmental variables, particularly canopy openness, explained the decline in plants and butterflies, with age being a more important factor than environmental variables. These results indicate that regenerated shelterbelts aged 2–6 years function as habitats for grassland butterflies, and that plantation age can be used as a simple indicator of habitat quality for such species, including endangered ones. Given that young plantations persist as grassland butterfly habitats for only 6 years since planting, a new clearcut needs to be created within the dispersal range for butterflies to help build metapopulations and ensure their conservation at a landscape scale.

INTRODUCTION

The conservation of biodiversity in human-modified landscapes is a pressing global issue (Kremen & Merenlender, 2018; Arroyo-Rodríguez et al., 2020). Semi-natural biotopes are the key elements in preserving biodiversity (Benton et al., 2003; Tscharntke et al., 2021) and maintaining ecosystem services (Thies & Tscharntke, 1999; Kremen et al., 2002). However, since the last century, natural and semi-natural grasslands within forest-dominated climates of East Asia and Europe have rapidly disappeared from agricultural landscapes because of abandonment, intensive agriculture, and conversion to different land uses (van Swaay et al., 2006; Schmitt & Rákosy, 2007; Babai & Molnár, 2014; Uchida & Ushimaru, 2014). In these regions, the majority of grasslands are semi-natural, and their maintenance via mowing, grazing and burning, is becoming increasingly rare (Eriksson et al., 2002; van Swaay, 2002; Ohwaki, 2018; Ushimaru et al., 2018). Consequently, the conservation of grassland species has become an urgent issue in many countries.

Temporary openings from forest harvesting can provide alternative habitats for grassland species, thus forest clearcuts are attracting increasing attention for conserving grassland species. As plantation forests are repeatedly harvested, clearcuts extend over substantial areas. Although secondary forests in many developed countries have sel-

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dom been harvested because of abandoned coppice management (Fukamachi et al., 2001; Ohwaki et al., 2013; Sebek et al., 2015; Kamp, 2022), plantation forests have been regularly managed in many countries (Brockerhoff et al., 2008), and the harvest has been gradually recovering since the 21st century in Japan (Japan Forestry Agency, 2025). Recently cleared, young (maximally 10 years) plantations are rich in species and offer temporary habitats for plants (Yamaura et al., 2012; Jonason et al., 2014, 2016; Ohwaki et al., 2018; Andersson et al., 2022), butterflies (Ibbe et al., 2011; Viljur & Teder, 2016; Ohwaki et al., 2018; Andersson et al., 2022), bees and wasps (Yamaura et al., 2012; Taki et al., 2013; Spake et al., 2019; Andersson et al., 2022), and birds (Yamaura et al., 2012; Kawamura et al., 2023, 2025) that prefer grasslands or early successional vegetation. However, although several studies in Europe have evaluated the effect of plantation age (up to 10 years) on plants and insects (Jonason et al., 2016; Viljur & Teder, 2016; Milberg et al., 2021), very few studies have examined the persistence of young plantations as alternative grassland habitats in East Asia (but Kawamura et al. (2023) investigated how long a Near Threatened bird species persists in clearcuts). This information is critically important for maintaining grassland species in plantation landscapes, particularly for less mobile organisms. By knowing how long young plantations offer refuge to grassland organisms, it is possible to determine when a new clearcut should be created.

Shelterbelts are rows of planted trees designed to protect houses and crops from the wind and to control wind erosion (Brandle et al., 2004). Furthermore, they provide plants, insects, and vertebrates with shelter (Thomson & Hoffmann, 2010), refuge (Hayamizu et al., 2019), and habitat (Hino, 1985; Heroldová et al., 2007; Bentrup et al., 2019). In eastern Hokkaido, northern Japan, shelterbelts are largely composed of coniferous monocultural plantations spanning tens of meters in width, and form rows or grids within agricultural landscapes (Tsuji et al., 2005). These shelterbelt areas are legally protected, and older forests have been periodically and partially cleared to prevent large branches from falling while maintaining their primary wind reduction function (Hokkaido Government, 2025). Consequently, young plantations of different ages are scattered throughout the landscape, which makes shelterbelts an excellent place for testing how plantations of different ages function as habitats for grassland species. Nakahama et al. (2022) found high butterfly diversity and abundant insect-pollinated flowers in young Japanese larch (*Larix kaempferi*; hereafter simply referred to as "larch") shelterbelt plantations in an agricultural landscape in Hokkaido. Although endangered butterflies did not utilize young plantations in their study, because the study was limited to early summer, research in other seasons would determine the contribution of young plantations to year-round biodiversity conservation. Indeed, studies performed in other regions of Japan found endangered butterflies in spring or mid-summer in young plantations or coppices (Inoue, 2003; Ohwaki et al., 2018).

Here, we conducted a survey in which butterfly and insect-pollinated flowering plants were investigated in young shelterbelt plantations of different ages during spring and summer in eastern Hokkaido, which has the same landscape as that studied by Nakahama et al. (2022). Butterflies are among the organisms most sensitive to human-driven environmental changes (Thomas, 2005) and have declined severely in recent decades (Warren et al., 2021; Edwards et al., 2025). Insect-pollinated flowers are an essential resource for butterflies and other pollinators, but they have been steadily declining, too (Potts et al., 2010). The objectives of this study were threefold. First of all, we examined how butterflies and flowering plants changed with plantation age; that is, how many years young plantations persisted as habitats for flowering plants and butterflies. Second, we assessed whether endangered butterfly species utilized young plantations as habitats. Third, we aimed to determine whether forest age alone can serve as a reliable basis for conservation of grassland species, thereby eliminating the need for labor-intensive surveys of environmental and biological variables. To achieve this, we identified how environmental factors varied with plantation age and then tested whether plantation age or environmental variables better explained changes in flowering plants and butterflies. We discuss appropriate management measures to reconcile the primary function of shelterbelts and biodiversity conservation.

MATERIAL AND METHODS

Study site

The study sites were located on the Tokachi Plain, Hokkaido, which has a hemiboreal climate. Shelterbelts of 30–50 m in width were scattered across the agricultural landscape in the plain, interspersed with clumps of plantations, shrub swamps, and riparian forest belts (Fig. 1). The shelterbelts were developed alongside the modernization at the Tokachi Plain (Umezawa, 2011), and were likely established in the early 20th century at the study sites. Japanese larch and Sakhalin spruce (*Picea glehnii*) are commonly planted in shelterbelts; whereas Manchurian Ash (*Fraxinus mandshurica*), white birch (*Betula pendula*), and deciduous oaks (*Quercus crispula* and *Q. dentata*) are rare or naturally regenerated. Before reclamation, the Tokachi Plain was subject to frequent flooding, and possibly burning as well, so vast grasslands and wetlands had stretched across the plain at least until the mid-19th century (Hashimoto et al., 2017). Reclamation of the open natural vegetation into agricultural lands at the study sites began around the 1920s (Sarabetsu Village, 2020), and most of the original grasslands and wetlands have already been lost.

We selected eight young shelterbelt larch plantations aged 2–12 years (one year means the current year of afforestation) as the study sites within a radius of 3 km in an agricultural landscape with shelterbelts. We focused on young larch plantations because they were the most common (Tsuji et al., 2005). The study area was flat at altitudes of 165–185 m and dominated by improved meadows and potato fields. The annual average temperature and total precipitation in the last three decades (1995–2024) recorded by the nearest meteorological station was 6.0°C and 1113 mm, respectively (Japan Meteorological Agency, 2025). The studied young plantations (i.e., the logged areas when cleared) ranged from 0.89 to 3.07 ha. In this region, herbaceous vegetation was mowed twice a year (early June and late August) during the first

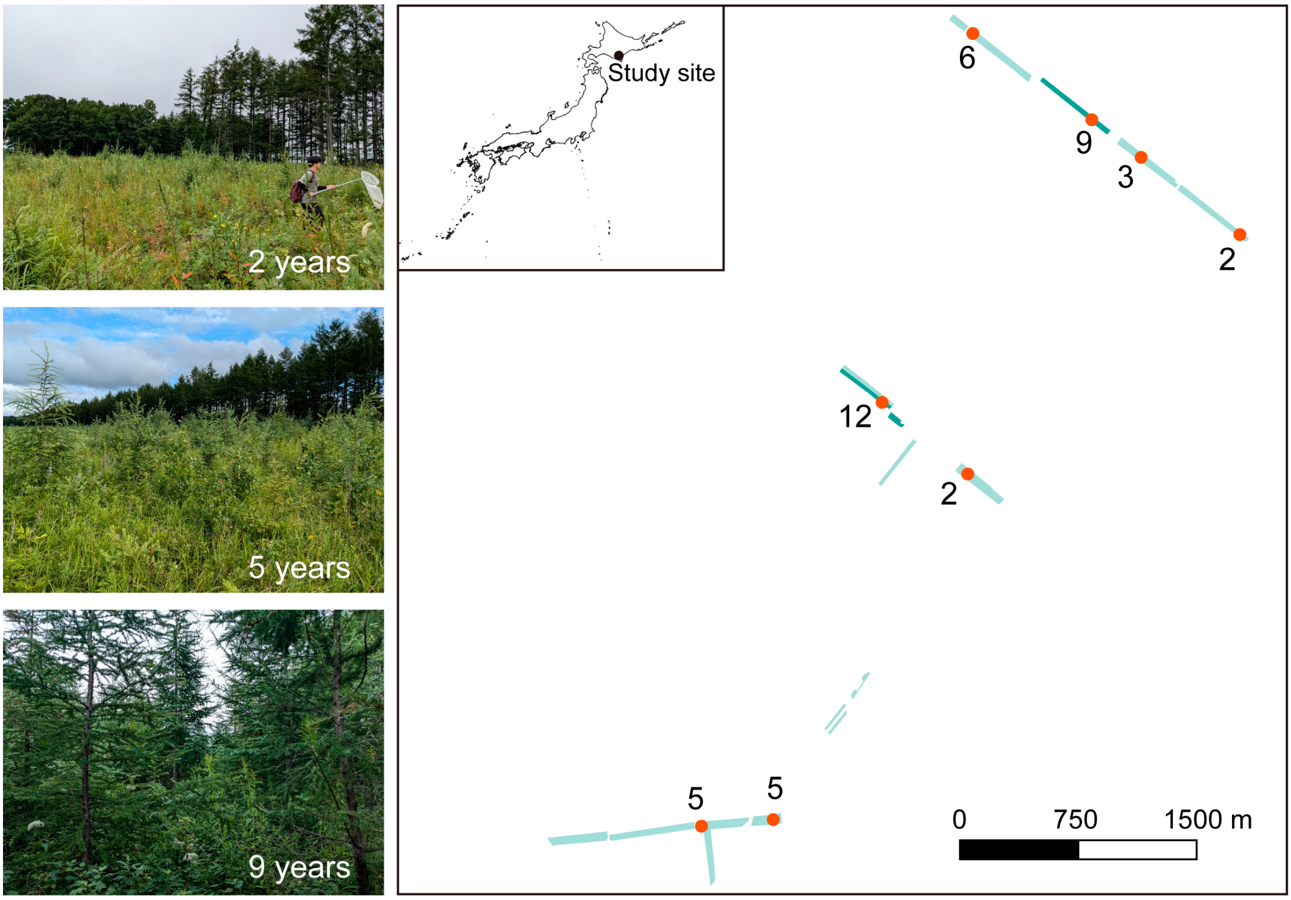

Fig. 1. Location of the study sites with pictures representing different plantation ages. The numbers beside the plots indicate plantation ages. Pale and dark green areas indicate young plantations aged 2–6 years and 7–12 years, respectively. Only young plantations aged 2–12 years are shown. The direction indicator is not included to avoid disclosing the exact position of the study sites and protect the endangered species.

4 years after planting (Nakagawa, 2012). Our study sites included 2-, 3-, 5-, 6-, 9-, and 12-year-old plantations, thus only 2- and 3-year plantations had been mowed in the study sites. Crucially, because the survey was conducted in mid-May and early August (as detailed below), no mowing disturbances occurred immediately prior to either survey.

Survey of plants, butterflies, and environmental variables

A 30 m × 3 m transect was established at each site. We surveyed the plants and butterflies, and measured several environmental variables in mid-May (spring) and early August (summer). For the butterfly survey, we walked along the transect at a steady pace, identified the species, and counted the number of individuals observed. Individuals that swiftly flew through the transect were not recorded. For the plant survey, insect-pollinated flowers were identified within the transects and the number of inflorescences was recorded for each species. We did not record other plant species such as wind-pollinated plants because we used plants as nectar sources.

We measured the tree (planted larch) height, canopy openness, and vegetation height in each transect. Five to 12 planted larch trees were selected within each transect, and their heights were measured in mid-May. Hemispherical photographs were taken 130 cm from the ground at 0, 10, 20, and 30 m of the transect (four points in each transect) in early August using a THETA SC2 360° camera (Ricoh Co., Ltd.). Canopy openness was then calculated from these photographs using CanopOn 2 software (http://takenaka-akio.org/etc/canopon2/index.html). Vegetation height was measured at 0, 10, 20, and 30 m on both sides of each transect (eight points/transect) in both seasons. For each environmental variable, the values were averaged at each site and then used to represent the corresponding environmental conditions.

Focal endangered butterfly species

Given the high conservation priority of endangered species, we focused on two endangered butterflies, *Pyrgus maculatus* and *Phengaris teleius*, which were relatively abundant in this study (see Results). The former is listed as Endangered (EN), while the Hokkaido population of the latter is listed as Near Threatened (NT) in the Japanese National Red List (Ministry of the Environment Japan, 2020). These species have undergone severe declines due to habitat destruction, cessation of grassland management, and the decline in forestry practices (Nakamura, 2011). *Pyrgus maculatus* is a skipper whose adults fly from mid-May to mid-June. It inhabits short vegetation grasslands and clearcuts. Its larvae feed on several herbaceous Rosaceae but depend almost exclusively on *Potentilla fragarioides* and *P. freyniana* (Japan Butterfly Conservation Society, 2017). At our study site, only *P. fragarioides* was observed as the host plant for this species. *Phengaris teleius* is an obligate myrmecophilous lycaenid butterfly whose adults fly from mid-July to August. It inhabits humid grasslands and its larvae depend on both host plants (*Sanguisorba* species: in our study site, only *S. tenuifolia* was present) and a particular lineage of the ant *Myrmica kotokui* (Ueda et al., 2016; Japan Butterfly Conservation Society, 2017). Consequently, these two butterfly species are habitat and larval host specialists.

Data analysis

We drew the abundance-based rarefaction and extrapolation curve of species richness and calculated sample coverage and estimated species richness (Chao 1 estimator) to assess whether sufficient samples were obtained during the entire survey (Chao et al., 2014).

We pooled data from May and August for both plants and butterflies in each transect throughout the analysis. Differences in species composition were described by Principal Coordinate Analysis (PCoA) based on the Bray-Curtis dissimilarity index for both flowering plants and butterflies. Singletons were excluded from PCoA to avoid undue effects of rare species (Borcard et al., 2011). We also checked whether the spatial location of plots affected species composition among flowering plants and butterflies by testing the correlations between the Bray-Curtis dissimilarity matrix of species composition and the distance matrix using Mantel tests.

We analyzed the relationships between stand age and three environmental factors (tree height, canopy openness, and average vegetation height of May and August), flowering plant richness (number of flowering insect-pollinated plant species), nectar abundance for butterflies (number of inflorescences), butterfly richness (number of butterfly species), butterfly abundance (number of butterfly individuals), number of individuals of two endangered butterfly species, *Pyrgus maculatus* and *Phengaris teleius*, and their host plants (*Potentilla fragarioides* and *Sanguisorba tenuifolia*), using generalized linear models (GLMs). In these GLMs, age and its square terms were explanatory variables, whereas environmental, plant, and butterfly parameters were response variables ("age-based model"). For nectar resources, insect-pollinated plants seldom visited by butterflies were excluded (Table S1). *Potentilla fragarioides* has an extraordinarily high number of inflorescences, and accounted for 96% of the observed inflorescences throughout the two seasons (Table S1). Therefore, we analyzed the relationship between stand age and nectar abundance with and without *P. fragarioides*. For the three environmental variables, GLMs were built with a Gaussian distribution; for butterfly and plant variables, GLMs were built with Poisson (plant and butterfly richness and abundances of *P. maculatus* and *P. teleius*), quasi-Poisson (butterfly abundance), or negative binomial (nectar abundance) distributions, depending on the dispersion (Zuur et al., 2009). Upon first assessment of dispersion parameters (residual deviance/residual d.f.) using age-based Poisson GLMs, the Poisson, quasi-Poisson, and negative binomial GLMs were adopted if the dispersion parameters were < 1.61, < 1.8–2.3, and > 10, respectively (Zuur et al., 2009). The models with the lowest Akaike Information Criterion corrected for small sample sizes (AICc for Poisson and negative binomial GLMs; QAICc for quasi-Poisson GLMs) were selected as the most parsimonious. We also considered other models if the differences in AICc/QAICc values between the most parsimonious model and the other models were < 2.

To evaluate which environmental variables affected changes in plants and butterflies in relation to plantation age, we built GLMs with environmental variables only ("environment-based model"). For plant GLMs, plant richness and nectar abundance were the response variables, whereas canopy openness and average vegetation height were the explanatory variables. Because tree height and canopy openness were highly correlated ($r = -0.929$, $P < 0.001$), canopy openness was consistently used. For butterfly GLMs, butterfly richness and abundance were the response variables, and canopy openness, vegetation height, plant species richness, and square-rooted nectar abundance were the explanatory variables. We also analyzed the responses of the two endangered butterflies (*P. maculatus* and *P. teleius*), using explanatory variables that included canopy openness, vegetation height during their flight period (May for the former and August for the latter), and the square-rooted abundance of their host plants (*P. fragarioides* and *S. tenuifolia*, respectively) and other nectar flower abundance during their flight periods. For environment-based models, the error distribution structure and model selection procedures were basically consistent with those of age-based models. That is, if a response variable followed a Poisson distribution and an AICc-based selection procedure in the age-based model, the same distribution and model selection procedure were applied in the environment-based model.

Finally, AICc/QAICc values of age- and environment-based models were compared to determine which models were more suitable for predicting plants and butterflies.

All statistical analyses were performed using R v4.4.1. Rarefaction and extrapolation of species richness, sample coverage, and estimated species richness were calculated using iNEXT

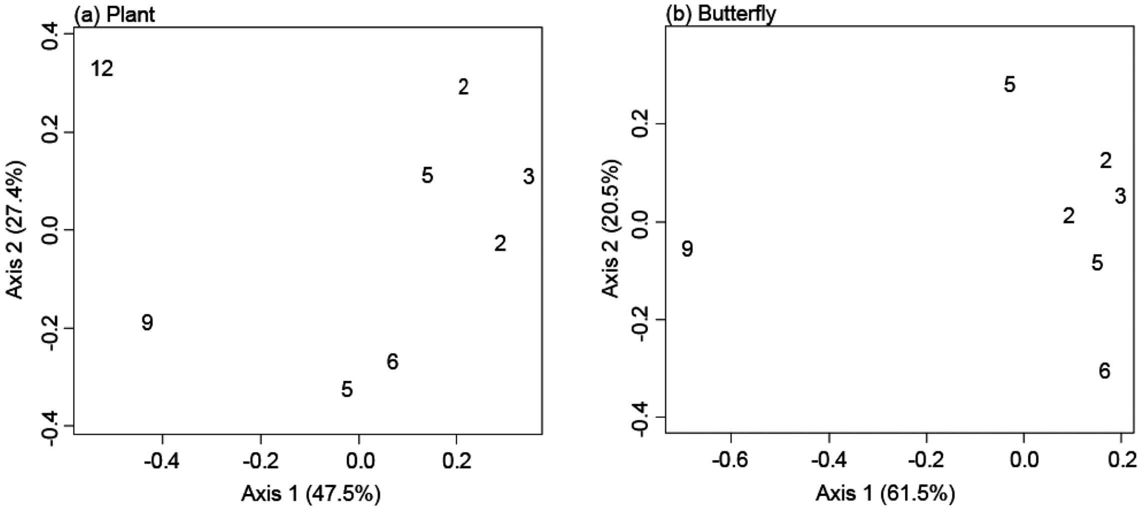

Fig. 2. Two-dimensional diagrams of Principal Coordinate Analyses of flowering plants (left) and butterflies (right) using Bray-Curtis dissimilarity index. The numbers in the panels indicated the plantation age. The first and second axis collectively explained more than 70% of the total variability for both plants and butterflies. For butterflies, 12-year plantation was not shown because of no observation of butterflies. The singletons were excluded from the analyses.

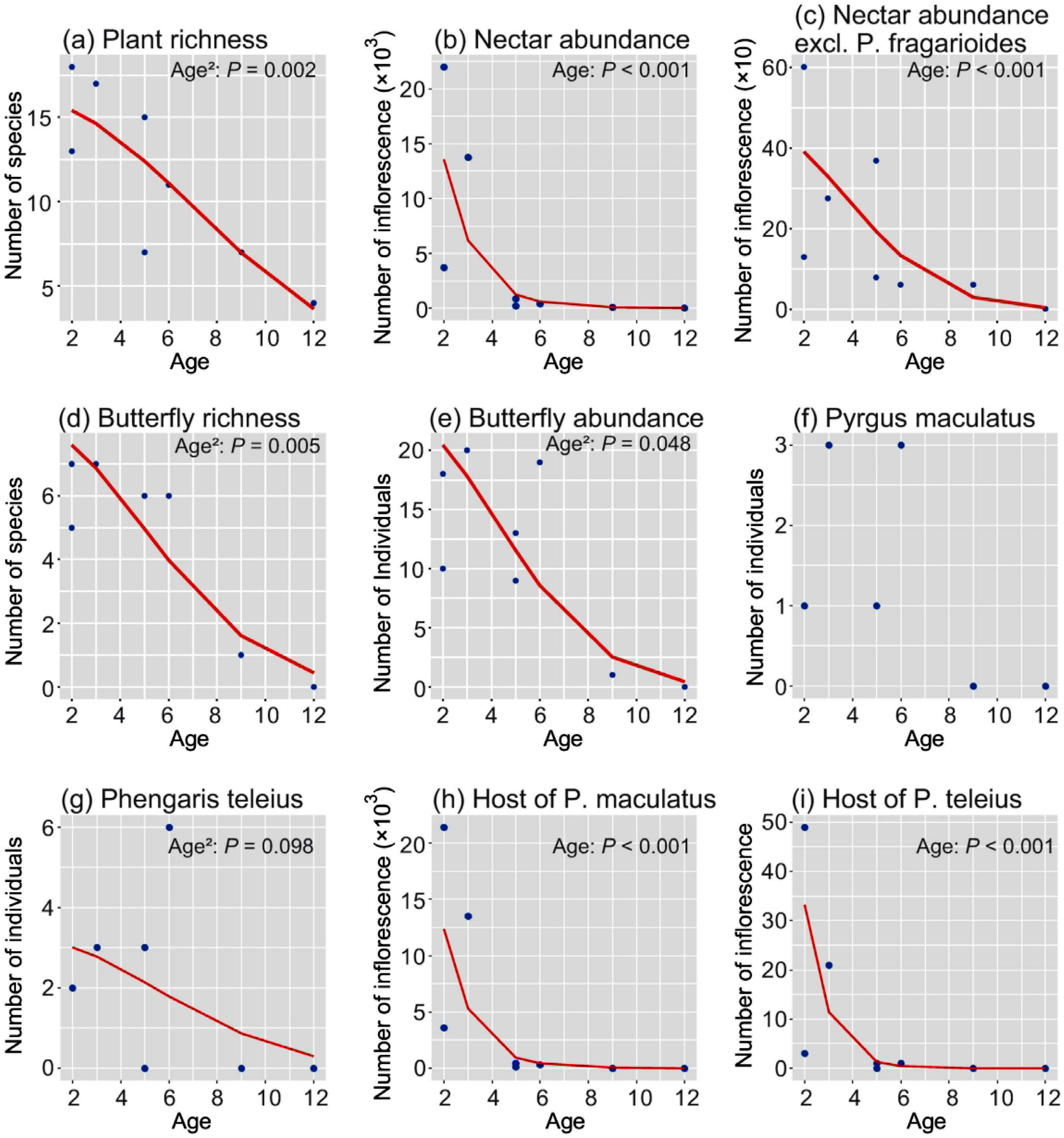

Fig. 3. Relationships between plantation age and plant and butterfly variables. (a) Plant richness, (b) nectar abundance represented by number of inflorescences, (c) nectar abundance excluding the superabundant species, *P. fragarioides*, (d) butterfly richness, (e) number of butterflies, (f) number of *P. maculatus*, and (g) number of *P. teleius*, (h) abundance of host plant of *P. maculatus* (*P. fragarioides*), and (i) abundance of host plant of *P. teleius* (*S. tenuifolia*). The regression lines of the most parsimonious models are indicated in red.

(Hsieh et al., 2016). Model selection was conducted in MuMIn v1.48.4 package (Bartoń, 2024). PCoA and Mantel tests were performed using the vegan v.2.6-8 package (Oksanen et al., 2024).

RESULTS

For insect-pollinated flowers, 35 species were observed during the survey. No plant species bloomed in either season. Only one plant species is indicated in red-listed (*Clematis fusca*; ranked as vulnerable). Nine blooming plant species were considered unsuitable nectar resources for butterflies during the survey (Table S1).

Among butterflies, 90 individuals from 10 species were observed during both seasons. Four of the ten butterfly species were red-listed, including *P. maculatus* (observed only in May) and *P. teleius* (observed only in August), which were relatively abundant (Table S2).

Chao 1 estimators for plant and butterfly species richness were 10.99 and 37, respectively, and the corresponding sample coverages were 0.999 and 0.978. These high

Table 1. Results of the model selection of the age-based GLMs based on (Q)AICc. Only the most parsimonious models were shown.

	Age		Age^2	
	Coeff.	*P* value	Coeff.	*P* value
Tree height^1	66.915	<0.001	–	–
Canopy openness^1	−0.473	<0.001	–	–
Average vegetation height^1	Null	–	Null	–
Plant richness^2	–	–	−0.010	0.002
Nectar abundance^3	−0.791	<0.001	–	–
Nectar abundance without *P. fragarioides*^{3}	–	–	−0.034	<0.001
Butterfly richness^2	–	–	−0.020	0.005
Butterfly abundance^4	–	–	−0.022	0.048
Pyrgus maculatus^2	Null	–	Null	–
Phengaris teleius^2	–	–	−0.016	0.098
Host plant of *P. maculatus*^{3}	−0.848	<0.001	–	–
Host plant of *P. teleius* and *Brenthis* sp.^{3}	−1.073	<0.001	–	–

Model selection: ^{1}AICc based on GLMs with a gaussian distribution; ^{2}AICc based on GLMs with a Poisson distribution; ^{3}AICc based on GLMs with a negative binomial distribution; ^{4}QAICc based on GLMs with a quasi-Poisson distribution.

coverage values indicated that our survey adequately represented both the plant and butterfly assemblages of the clearcuts in the studied seasons (Fig. S1).

Species compositions of both plant and butterfly assemblages were clearly separated between 2- to 6-year plantations and 9- to 12-year plantations (Fig. 2). The first and second axis explained more than 70% of the variability for both plants and butterflies. There were no correlations between the Bray-Curtis dissimilarity matrix and the distance matrix for either flowering plants (Mantel test: $r = -0.282$, $P = 0.949$) or butterflies (Mantel test: $r = -0.271$, $P = 0.942$).

Age-based models

Plantation age was significantly positively correlated with tree height, but significantly negatively correlated with canopy openness (Table 1, Fig. S2). The relationship between plantation age and average vegetation height was not significant (Table 1, Fig. S2).

Flowering plant richness gradually decreased with increasing age, whereas nectar abundance rapidly decreased 3 years or more after planting (Fig. 3a, b). Even when the superabundant species *P. fragarioides* was excluded, nectar abundance was low in 6-year or older plantations (Fig. 3c).

Butterfly richness and abundance, along with *P. teleius* numbers, decreased with increasing plantation age, but these values were stable in 2- to 6-year plantations (Fig. 3d, e, g). Although *P. maculatus* abundance did not correlate with plantation age, the species was not observed in the two oldest stands (Fig. 3f). The host plants of the two endangered butterfly species (*P. fragarioides* and *S. tenuifolia*) also declined with increasing plantation age, showing low abundance in 5–6-year sites and complete absence in the two oldest sites (Fig. 3h, i). Most of the responses of both plants and butterflies to age were statistically significant (Table 1). For plant richness and host plant of *P. teleius*, a candidate model was selected with ΔAICc < 2 ("Age" for the former (ΔAICc: 0.1) and "Age^2" for the latter (ΔAICc: 0.47)). These variables were significant in both cases ($P < 0.001$ for plant richness and $P = 0.001$ for host plant of *P. teleius*).

Environment-based models

The most parsimonious environment-based models of almost all plant parameters (except for host plant of *P. teleius*) and butterfly richness included only canopy openness, which was a positive and significant predictor (Table 2). For butterfly abundance, the most parsimonious models included three variables, i.e., canopy openness, plant species richness, and vegetation height, which were all positive and significant (Table 2). For the two endangered butterfly species, the null models were selected as the most parsimonious. Host plants and nectar resources were not significant for most butterfly analyses. Although the two endangered species had candidate models with ΔAICc < 2 (canopy openness for *P. maculatus* and canopy openness and vegetation height for *P. teleius*), none of these variables were significant. By contrast, the most parsimonious model of the host plant of *P. teleius* (*S. tenuifolia*) was the null model. However, the second model (ΔAICc: 2.6) included only canopy openness, and this variable was significant ($P = 0.028$).

Comparison between age-based and environment-based models

Comparisons of AICc values between age-based and environment-based models indicated that the former always performed better (Table 3). The large difference in apparent AICc values for total butterfly abundance stemmed

Table 2. The most parsimonious models explaining plant richness, nectar abundance, butterfly richness and abundance, endangered butterflies, and their host plants in environment-based models.

Response variables	Distribution	Parsimonious models	*P* value	AICc
Plant richness	Poisson	Openness (+)	0.002	46.2
Nectar abundance	Negative binomial	Openness (+)	<0.001	141.9
Nectar abundance without *P. fragarioides*	Negative binomial	Openness (+)	<0.001	103.5
Butterfly richness	Poisson	Openness (+)	0.004	34.7
Butterfly abundance	Poisson	Openness (+) Plant sp rich (+) Vegetation height (+)	<0.001 <0.001 <0.001	55.6
Pyrgus maculatus	Poisson	Null	–	25.4
Phengaris teleius	Poisson	Null	–	35.6
Host plant of *P. maculatus*	Negative binomial	Openness (+)	<0.001	134.9
Host plant of *P. teleius* and *Brenthis* sp.	Negative binomial	Null	–	50.3

Table 3. Comparison of (Q)AICc values between the most parsimonious age-based and environment-based models, explaining the variations in plants and butterflies. The (Q)AICc values corresponding to the best models are underlined.

Response variables	Age-based models	Environment--based models	(Q)AICc
Plant richness	44.4	46.2	AICc
Nectar abundance	134.9	141.9	AICc
Nectar abundance without *P. fragarioides*	101.6	103.5	AICc
Butterfly richness	34.0	34.7	AICc
Butterfly abundance	33.3 (53.7*)	55.6	QAICc/AICc
Pyrgus maculatus	25.4 (Null)	25.4 (Null)	AICc
Phengaris teleius	35.1	35.6 (Null)	AICc
Host plant of *P. maculatus*	134.8	134.9	AICc
Host plant of *P. teleius* and *Brenthis* sp.	45.4	50.3 (Null)	AICc

*Because QAICc value was calculated for the age-based model of butterfly abundance, AICc value was also calculated to compare that of the environment-based model.

from the fact that the age-based model utilized QAICc, whereas the environment-model utilized AICc. Even when the AICc value was calculated for the age-based model, it was still lower than that of the environment-based model.

DISCUSSION

The present study found that open young larch plantations (2–6 years since planting), with nectar resources and host plants, were suitable habitats for butterflies, including some red-listed species. Instead, in older plantations, habitat quality for grassland organisms rapidly deteriorated as vegetation succession proceeded, resulting in increased tree cover, reduced canopy openness and light availability, and a decline in butterfly resources, such as nectar flowers and host plants. Several studies have shown that plants and insects decrease as forest age increases in young plantations or coppice wood. In northern Europe, flower resources and bee pollinators decline with increasing age between 2–8 years after planting (Jonason et al., 2016; Milberg et al., 2021). In contrast, Viljur & Teder (2016) found that there were no differences in butterfly species composition in the plantations that were 2 to 10 years after planting. In coppice woods in northeastern France, butterfly richness, including of endangered species, was high for 2–7 years after logging, but declined thereafter (Fartmann et al., 2013). In Japan, meta-analysis showed that a high diversity of ground layer plants, butterflies, and bees was maintained in younger stands (approximately until 5–15 years after planting, depending on taxa), compared to older stands in both plantation and secondary forests (Spake et al., 2019). Therefore, our findings that butterfly richness and abundance remain high for up to 6 years post-plantation and decline thereafter are largely consistent with those of previous studies. These results provide greater insight into the habitat suitability of clearcuts for butterflies and plants.

Tree height of planted larches grew linearly, whereas canopy openness remained stable at 70–80% until 5 years after afforestation, but dropped to approximately 30% at 9 years (Fig. S2a, b). Therefore, good light conditions are maintained in plantations for up to 5–6 years. However, mowing was stopped after 5 years post-planting. Mowing is a well-known management practice to maintain grassland biodiversity and endangered grassland butterflies (Tälle et al., 2016; Hayamizu et al., 2024). Thus, both reduced light availability owing to planted tree growth and the cessation of mowing may have contributed to declining plant and butterfly diversity. Consequently, extended mowing may prolong the longevity of clearcuts as alternative grassland habitats. Interestingly, there was a discrepancy in the responses of butterflies and plants to plantation age. Flowering plant species and nectar abundance declined earlier than butterflies. Specifically, butterfly richness and abundance were stable during the first 6 years of planting, whereas nectar abundance dropped after 3 years post-planting. The sudden decrease in nectar abundance after 3 years post-planting was mostly caused by the superabundant flowering species, *P. fragarioides* (Fig. 3b, h). When this species was excluded, the decrease in nectar abundance became moderate (Fig. 3c). Vegetation succession proceeds rapidly during the first 2–3 years after clearcutting (Buckley et al., 1997; Palviainen et al., 2005), whereas the changes in butterfly assemblages are generally slower (Fartmann et al., 2013; Viljur & Teder, 2016). In this study, plant richness, nectar abundance, and the host plants of endangered butterfly species generally showed no correlation with butterfly assemblages or endangered butterflies. Even though host plants are essential resources for butterflies, several studies found a lack of explanatory power of host plants (Hardy & Dennis, 1999; Ohwaki, 2019). This might be because butterflies usually have preferences for the conditions of host plants (Gutiérrez et al., 1999; Zhang & Miyashita, 2018), or butterflies cannot utilize all of the host plants if they are very abundant. In this study, the host plants of the endangered butterflies were very abundant in 2–3-year plantations, but their abundance became scarce (though still present) in 5- to 6-year plantations, and disappeared in 9-year or older plantations. Our study surveyed only 90 m^2 within each stand, but the cleared stands ranged from 0.9 to 3.1 ha in size; thus, the 5- to 6-year-old stands are likely to contain enough host plants for butterflies. We observed a mating pair of *P. teleius* in the 6-year stand, suggesting suitable reproductive habitats. For these reasons, it is likely that plants changed drastically during 3 to 5 years, but butterflies responded more slowly, allowing 5- to 6-year plantations to support similar butterfly assemblages as 2- to 3-year plantations.

This study found that plantation age, rather than environmental variables, were always better predictors of plant and butterfly assemblages in young plantations. Plantation age is a composite indicator of light availability, as measured from tree height and canopy openness, and butterfly resource availability, such as plant richness, nectar abundance, and host plant availability. Further, while plantation age is inherently related to vegetation succession, it cannot be fully captured by environmental variables and simple plant measures because it is a complex outcome of biological process. In addition, as mentioned above, butterfly richness and abundance were not necessarily correlated with the abundance of host plants and nectar resources. For the endangered species, *Pyrgus maculatus* utilizes only host plants surrounded by bare ground (Tashita, 1989); consequently, high host abundance does not necessarily guarantee the availability of host plants for the butterflies. Furthermore, some young plantations may have been too isolated from the source populations. Since *Phengaris teleius* is known to be highly sedentary (Gao et al., 2016), landscape connectivity rather than habitat quality, measured by abundances of host plants and nectar resources, may primarily influence the abundance of these endangered butterflies (Nowicki et al., 2005). Furthermore, because *P. teleius* is tightly associated with a particular ant species throughout its life history (Ueda et al., 2016), the distribution of the host ant likely constrains the occurrence of the butterfly. These factors likely mask positive correlations between butterflies and floral resources. For these reasons, plantation age alone was a better predictor than the combination of environmental variables for both plants and butterflies. Assessing the suitability of young plantations as habitats by measuring environmental variables is labor intensive and requires expert knowledge of the target species or assemblages. Because land managers may not always have extensive ecological knowledge, simple measures that contribute to the conservation of biodiversity and endangered species are essential for advancing nature-positive goals (Lindenmayer et al., 2000). The use of plantation age as an indicator of habitat quality will help landowners and managers align the primary function of shelterbelts with biodiversity conservation. Nevertheless, previous land use history has affected vegetation and butterflies in plantations (Ibbe et al., 2011; Jonason et al., 2016). In plantation clearcuts with a previous grassland history, grassland plants can recover because some grassland plants are surviving on the forest floor (Milberg et al., 2019), and because seeds and vegetative propagules persist in the soil (Koyama & Uchida, 2022). In the Tokachi Plain, where the study sites were located, grasslands were widespread before reclamation (Hashimoto et al., 2017). Therefore, most of the clearcuts in the plain may have a grassland land use history. Grassland vegetation, including barochorous plants such as *Adenophora triphylla*, *P. fragarioides*, and *S. tenuifolia*, thus tended to recover here. This suggests that clearcuts could function as suitable habitats for grassland butterflies not only within the studied area but also more widely throughout the Tokachi plain.

This study had several limitations. First, because it had a small sample size and plantations of 7–8 years were not studied, the quality of young plantations during these years remains uncertain. Thus, our estimates for 2–6 years may be slightly conservative. Secondly, an exotic plant species, *Solidago gigantea*, often flourishes in various open vegetation areas throughout Hokkaido, including some clearcuts in the study area (Miyazaki & Hirata, 2024). Due to negative impacts on the native flora, including decreased plant richness and diversity and alteration of soil properties (Wang et al., 2019; Goossens et al., 2024), this exotic plant will cause an inevitable decline in butterfly resource diversity and stability, potentially leading to decreased butterfly diversity. We need to know which factors favor its dominance in clearcuts and how they affect the fauna of the clearcuts. Third, although we focused on young larch plantations, other tree species were planted in some clearcuts in the studied region. Because early growth rates differ among tree species, the longevity of young plantations as grassland habitats is expected to vary depending on the tree species planted. Finally, this study was conducted in a boreal area of Hokkaido, northern Japan, whereas most of the land area in Japan has intermediate to warm temperate climates and different biota (Fukushima & Iwase, 2005). Other studies focusing on plantation clearcuts have been performed at relatively high elevations in similarly cool temperate climates (Taki et al., 2013; Ohwaki et al., 2018). In the clearcuts in the warm temperate regions, pioneer trees flourish more rapidly than in northern Japan (Sakai et al., 2010). Thus, it is unclear whether the longevity of plantations as grassland habitats found in Hokkaido applies also to warmer regions of Japan. Further research should be conducted to evaluate the ecological functions of plantation clearcuts in more temperate regions.

Implications for conservation

This study demonstrates the importance of young plantations as a habitat for grassland butterflies, to whom they provide nectar resources and host plants. In spite of several natural grassland remnants in the studied landscape, most were fragmented, isolated, and small (Nakahama et al., 2022). Accordingly, remnant grasslands alone may not be able to support grassland butterflies at the landscape scale. Given that young plantations are temporary and persist for only 5 years (2–6 years) as a grassland habitat, a new clearcut needs to be created within the dispersal range for butterflies to help build metapopulations and ensure their conservation at a landscape scale (Hanski, 1991; Thomas et al., 1992). Mid- to late-stage plantations can harbor forest species, particularly if broadleaved trees are maintained (Kawamura et al., 2025), and the entire course of forest succession can support high biodiversity, with community turnover occurring among successional stages (Hilmers et al., 2018). In this agricultural landscape, spatially adequate management of shelterbelts at the landscape scale will help preserve both grassland and forest species, while ensuring the functionality of shelterbelts.

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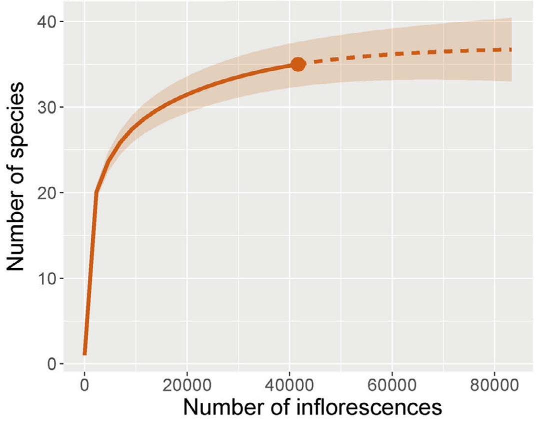
Table S1. A list of plant species observed in this study with reference to their origin (native/exotic), butterfly use, and number of inflorescences in May and August. Nomenclature followed YList (Yonekura & Kajita, 2023).

Scientific name	Family	Origin	Nectar for butterflies	Number of inflorescences	
				May	August
Angelica pubescens	Apiaceae	Native	Yes	–	3
Cynanchum caudatum	Apocynaceae	Native	Yes	–	12
Anaphalis margaritacea	Asteraceae	Native	Yes	–	1
Aster scaber	Asteraceae	Native	Yes	–	5
Aster yomena	Asteraceae	Native	Yes	–	3
Cirsium pectinellum	Asteraceae	Native	Yes	–	2
Erigeron annuus	Asteraceae	Exotic	Yes	–	250
Erigeron canadensis	Asteraceae	Exotic	Yes	–	14
Eupatorium glehnii	Asteraceae	Native	Yes	–	63
Picris hieracioides	Asteraceae	Native	Yes	–	85
Pterocypsela elata	Asteraceae	Native	Yes	–	12
Rudbeckia laciniata	Asteraceae	Exotic	Yes	–	15
Solidago gigantea	Asteraceae	Exotic	Yes	–	131
Solidago virgaurea	Asteraceae	Native	Yes	–	1
Taraxacum officinale	Asteraceae	Exotic	Yes	600	–
Patrinia villosa	Caprifoliaceae	Native	Yes	–	29
Hylotelephium erythrostictum	Crassulaceae	Native	Yes	–	2
Lespedeza bicolor	Fabaceae	Native	Yes	–	67
Trifolium lupinaster	Fabaceae	Native	Yes	–	9
Trifolium pratense	Fabaceae	Exotic	Yes	–	1
Vicia unijuga	Fabaceae	Native	Yes	–	5
Clinopodium coreanum	Lamiaceae	Native	Yes	–	67
Galeopsis bifida	Lamiaceae	Exotic	Yes	–	2
Potentilla fragarioides[1]	Rosaceae	Native	Yes	39423	–
Sanguisorba tenuifolia[2]	Rosaceae	Native	Yes	–	75
Viola mandshurica	Violaceae	Native	Yes	121	–
Convallaria majalis	Asparagaceae	Native	No	278	–
Adenophora triphylla	Campanulaceae	Native	No	–	150
Gentiana zollingeri	Gentianaceae	Native	No	2	–
Hypericum erectum	Hypericaceae	Native	No	–	18
Isodon trichocarpus	Lamiaceae	Native	No	8	–
Oenothera biennis	Onagraceae	Exotic	No	–	94
Thalictrum minus	Ranunculaceae	Native	No	–	90
Agrimonia pilosa	Rosaceae	Native	No	–	8
Galium verum	Rubiaceae	Native	No	–	1

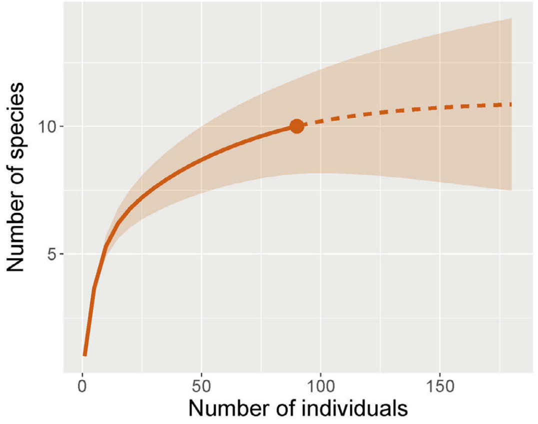
[1]Host plant of a red-listed butterfly, *Pyrgus maculatus*; [2]Host plant of two red-listed butterflies, *Phengaris teleius* and *Brenthis* sp.

Table S2. A list of butterfly species observed in this study with reference to their habitats and number of individuals in May and August. Butterfly habitats and nomenclatures follow Ohwaki (2018) and Japan Butterfly Conservation Society (2017), respectively.

Scientific name	Family	Habitat	Endangered status	Number of individuals	
				May	August
Pyrgus maculatus	Hesperiidae	Grassland	EN	10	–
Erynnis montanus	Hesperiidae	Forest		1	–
Phengaris teleius	Lycaenidae	Grassland	NT	–	16
Callophrys ferrea	Lycaenidae	Forest		1	–
Everes argiades	Lycaenidae	Ruderal		19	1
Minois dryas	Nymphalidae	Grassland		–	20
Brenthis sp.	Nymphalidae	Grassland	NT	–	2
Argyronome laodice	Nymphalidae	Grassland	VU	–	2
Colias erate	Pieridae	Ruderal		4	–
Pieris rapae	Pieridae	Ruderal		8	6

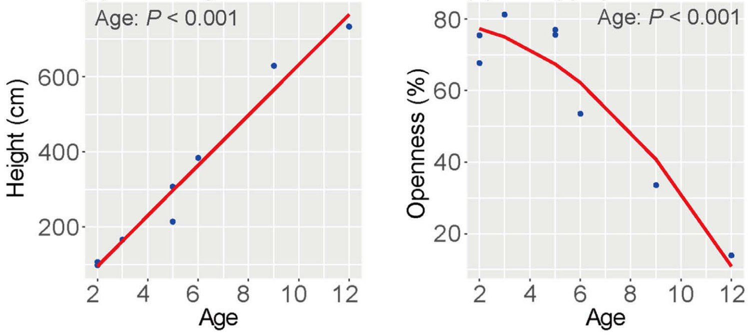


(a) Plant



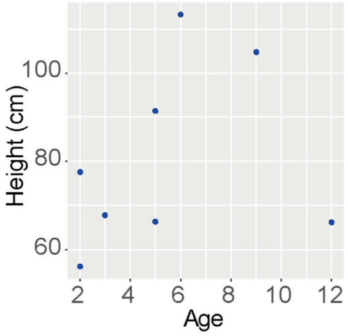
(b) Butterfly

Fig. S1. Rarefaction and extrapolation curves of the entire survey of (a) plants and (b) butterflies.



(a) Tree height

(b) Canopy openness



(c) Average vegetation height

Fig. S2. Relationships between the plantation age and (a) tree height, (b) canopy openness, (c), and average vegetation height.