Influence of clear-cutting, strip-cutting, and logging to construct strip roads on necrophagous silphid and dung beetle assemblages in a conifer plantation

AKIRA UEDA[1,2]*, HIROKI ITÔ[2], SEIICHI KANETANI[1]

[1]Kyushu Research Center, Forestry and Forest Products Research Institute (FFPRI), Kurokami 4-11-16, Chuo-ku, Kumamoto 860-0862, Japan

[2]Hokkaido Research Center, FFPRI, Hitsujigaoka 7, Toyohira-ku, Sapporo 062-8516, Japan

**Author for correspondence (e-mail: akira@ffpri affrc go.jp; fax: +81-96-344-5054)*

Abstract

To mitigate the impact of clear-cutting, strip-cutting has been prescribed in Japan. When harvesting trees, logging to construct strip roads is often conducted in adjacent forests. To evaluate the impacts of these logging practices, we collected necrophagous silphid and dung beetles in conifer plantation stands that were connected and partly harvested by strip-cuttings and clear-cuttings, with the construction of strip roads a few months before trapping. The abundances of two of the five species abundant in the uncut forests and the total beetle biomass (dry weight) were higher at the centers of 40-m-wide strip-cuts than near edges and/or at the centers of clear-cuts (≥ 60-m-wide). The beetle assemblages differed between the uncut forests and the uncut strips (unharvested areas of strip-cuttings). However, the abundances of four species abundant in the uncut forests ant the biomass were higher in the uncut strips than the strip-cuts. Therefore, we concluded that strip-cutting is a better harvesting method than clear-cutting because strip-cutting mitigated the impact on the beetle assemblages in forests and the ecosystem service estimated from biomass, and the uncut strips retained the beetle assemblages and ecosystem services observed in the uncut forests. The abundances of four species abundant in the uncut forests and the biomass were lower beside the ~2.5-m-wide strip roads than in the uncut forests but were higher than in the strip-cuts, indicating that logging to construct strip roads negatively affected to the forest species and the services, but the negative effect was lower than that of 40-m-wide logging.

Keywords: biomass, carrion-baited pitfall trap, coprophagous group of Scarabaeoidea, harvesting method, Silphidae, uncut strip

Introduction

In Japan, conifer plantations that were primarily established from the 1960s to the 1980s have matured and become ready for harvesting. As such, the amount of domestic wood production has increased since 2002 (Forestry Agency of Japan 2018). In areas with tree felling, standard large-scale clear-cuttings may have substantial negative impacts on forest ecosystems by causing excess sedimentation, deterioration of water quality and quantity, and degradation of biodiversity (e.g., Nakano

1971; Aiura et al. 1996; Pawson et al. 2006). To mitigate the impacts of logging and to maintain multi-aged forest stands, strip-cutting (i.e., a series of narrow clear-cuttings between 20 and 40 m in width) has been introduced in many conifer plantations, especially those that are nationally owned (Kinki-Chugoku Forest Management Bureau 2017). In these forests, the area of strip-cutting increased twofold during the past ten years (2005–2015) and reached one-third of the total logging area harvested (Forestry Agency of Japan 2019).

In associated studies of biodiversity, Ito et al. (2006) compared understory vegetation in the harvested area between strip-cuttings and clear-cuttings and suggested that strip-cutting may be more effective than clear-cutting in conserving plant species associated with natural forests. Some studies have been conducted to clarify the assemblages of carabid beetles, ants, collembolans, ground surface-wandering spiders, phalangiid harvestmen, and snails in strip-cutting areas (Jennings et al. 1984, 1986a, b, 1988; Moore et al. 2002, 2004). However, since these studies did not compare the assemblages directly using data collected in areas harvested with strip-cutting and clear-cutting, we cannot evaluate the effects of strip-cutting compared with those of clear-cutting on the mitigation of logging impacts.

Strip-cutting leaves narrow unharvested areas (uncut strips). If the biodiversity in uncut strips largely deteriorates compared to that in uncut forests, the advantages of strip-cutting must be de-emphasized. The species richness and abundances of carabid beetles in uncut strips were found to be higher than those in uncut forests, and carabid beetle species that were abundant in uncut forests were also abundant in uncut strips (Jennings et al. 1986a). Conversely, the species richness and abundances of ants in uncut strips were lower than those in uncut forests, and some ant species that were abundant in uncut forests were rare in uncut strips (Jennings et al. 1986b). The species richness and abundances of phalangiid harvestmen and ground surface-wandering spiders in uncut strips did not differ from those in uncut forests (Jennings et al. 1984, 1988).

When harvesting trees, logging is often carried out to construct strip roads ~2.5 m wide when stands are prepared for clear-cutting. This process allows entry of the forestry machinery used for harvesting and transportation. Such road construction will create long and narrow continuous canopy gaps (Sakai et al. 2002) and may affect forest biodiversity. It is known that the construction of strip roads enhances planted tree growth rates on roadsides because of improved access to light (Bembenek et al. 2013). Another study showed that enhanced damage by weevils on stumps on strip roads may also be associated with microclimatic factors, such as stump insolation, temperature, and humidity (Korczynski et al. 2007). Kotani and Ogura (2014) showed that the diversity of understory vegetation along strip roads peaked three years after construction. Some studies have clearly shown the influence of relatively wide roads (~3 m) on the diversity of insects. Hosaka et al. (2014a, b) showed that 4–5-m-wide temporary skid trails allowing entry of forestry machinery reduced the abundance, species richness, and biomass of dung beetles in selectively cut tropical rainforests. In contrast, Koivula (2005) found that the species richness of carabid beetles was higher on forest roadsides (3–7 m wide) than in adjacent forests. It is also known that some insects use roads as corridors connecting habitats (Munguira and Thomas 1992; Vermaulen 1994).

Necrophagous silphid beetles (Silphidae) are highly sensitive to variations in forest habitat quality factors such as the species, age, size, and density of the trees as well as the area and location of the forest (e.g., Katakura et al. 1986; Trumbo and Bloch 2000). Ito (1994) and Suzuki (2005) showed that silphid beetles are a useful indicator of forest habitat quality. Dung beetles (a coprophagous group of Scarabaeoidea; e.g., Troidae, Geotrupidae, Scarabaeinae, and Aphodiinae) are known to be important indicators of forest habitat quality and environmental changes due to logging, fire, windthrow, and drought (e.g., Davis et al. 2001; McGeoch et al. 2002). Some studies have indicated that dung beetles that have a habit of being attracted to carrion (necrophagous dung beetles) respond strongly to forest habitat quality in Japan (Ito and Aoki 1983; Shimada 1985; Shimada et al. 1991; Ueda 2016).

Necrophagous silphid and dung beetles serve important ecological functions, such as facilitating carcass decomposition and nutrient release, bioturbation, and plant growth enhancement (Barton et al. 2013). In addition, these beetles can control necrophagous flies (e.g., Springett 1968; Satou et al. 2000). Gibbs and Stanton (2001) showed that the low abundance of necrophagous silphid beetles increased the abundance of muscoid flies. Moreover, Amézqutta and Favila (2011) showed that a low biomass of necrophagous dung beetles led to a reduced carrion removal rate. Thus, a higher abundance and biomass of these beetles may indicate more robust ecological functions.

The purpose of this study was to evaluate the impact of logging practices, including logging for clear-cutting, strip-cutting, and to construct strip roads, on necrophagous silphid and dung beetle assemblages in a conifer plantation forest. 1) We evaluated the beetle assemblages in the harvested area of strip-cuttings (strip-cut) and compared beetle assemblages between strip-cuts and clear-cuts. 2) We evaluated the beetle assemblages in the unharvested area of strip-cuttings (uncut strip) and compared the beetle assemblages between uncut strips and uncut forests or strip-cuts. From the results of 1) and 2), we evaluated the impact of logging on the beetle assemblages in strip-cuttings. To evaluate the impacts of logging to construct strip roads, we compared the beetle assemblages between strip roads and uncut forests or 40-m-wide strip-cuts. From the results, we evaluated the influences of logging to construct strip roads on the beetle assemblages.

Materials and Methods

Study site: This study was conducted in a 60- to 70-year-old mixed Japanese cedar (*Cryptomeria japonica*) and Japanese cypress (*Chamaecyparis obtusa*) plantation forest in the national forest at Kigo, Kikuchi city, Kumamoto Prefecture (33°02’07”N, 130°56’01”E, 625 m asl–33°02’23”N, 130°56’24”E, 692 m asl). This forest consisted of 15 small stands connected to each other and mainly included planted conifers but contained naturally growing broad-leaved trees. This forest also contained five old-growth Japanese cedars with diameters at breast height (DBHs) of more than 99 cm. This forest faces southeast and is nearly rectangular (ca. 100 x 760 m) (Fig. 1). Its short sides are from valley to ridge. We set an 800-m-long trapping transect starting from 20 m inside of an adjacent 18-year-old Japanese cypress forest stand and extending 20 m into an adjacent broad-leaved secondary natural forest stand in 2012, before logging operations took place. The transect ran through the center of the short sides of the conifer plantation forest. In January and February 2013, logging operations occurred in the forest. Before logging for harvest, several ~2.5-m-wide strip roads were constructed by logging (Fig. 1). After that, logging for harvest took place in 6 areas with 40-120-m-widths. The width of the strip-cuts is double the mean tree height and must be less than 40 m (Kinki-Chugoku Forest Management Bureau 2017). Therefore, we treated four 40-m-wide areas of logging for harvest as strip-cutting and the 60- and 120-

m-wide logging areas as clear-cutting (Fig. 1). Just after the logging operations, young Japanese cypress trees were planted in the 40- and 60-m-wide cut areas, and young Japanese cedar trees were planted in the 120-m-wide cut area. Weeding was not performed during the study period. The mean DBH and mean height of the Japanese cedars in the 120-m-wide clear-cut area (1.2 ha) that were measured in August 2012 before cutting were 23.8 cm (range: 6.9–124.8 cm) and 16.9 m (9.0–33.3 m) (n = 1038), and those of the Japanese cypress were 23.4 cm (5.1–63.6 cm) and 17.5 m (9.9–26.5 m) (n = 408), respectively (Dr. Makoto Araki, FFPRI, unpubl. data). All five of the old-growth Japanese cedars were distributed in the 120-m-wide clear-cut area and harvested.

Trap: Pitfall traps baited with fish meat were used to collect beetles (Ueda 2015). At each trap site, a 20-cm-long grey vinyl chloride pipe (inner diameter: 94 mm; outer diameter: 114 mm) was driven into the ground until the opening was level with the ground surface. A plastic cup (95 mm in open diameter and 170 mm high) with four 2-mm-diameter holes for drainage on the sides (50 mm from the top) was used as the trap and inserted into the pipe. The trap contained 100 ml propylene glycol mixed with red pepper powder to kill and preserve the beetles collected and to repel animals. The cup also contained a small plastic cup fixed with steel wire on its upper lip (Ueda 2015). Another small plastic cup contained 15 g mackerel meat (*Scomber* spp.) and had a perforated lid (having 25 holes, each 1 mm in diameter); this cup was inserted into the suspended cup to attract beetles after 4 days of storage at 25°C to allow the fish meat to rot. To prevent rain water and animals from disturbing the traps, a concrete block (390 x 190 mm, 120 mm high, 11.3 kg) was laid over the trap and a steel rack (405 x 250 mm, 30 mm high) was inserted between the trap and the block so that the beetles were able to enter the trap through the spaces in the steel rack (Ueda et al. 2016; Ueda 2020).

Field trapping: We set up 41 trapping sites at 20-m intervals along the trapping transect in April 2012 (before logging operations) and buried the pipe in the ground at each site. Baited pitfall traps need to be set more than 50 m from one another to limit trap interference because baited pitfall traps can attract some dung beetles from as far as 50 m away (Larsen and Forsyth 2005). However, we had to set traps with a distance of 20 m between them to compare the effect of distances from forest edges on the beetle assemblages between 40-m-wide strip-cuttings and wider clear-cuttings. To solve this problem, we elongated the trapping transect into adjacent stands and set 2 “adjustment” traps on both ends of the trapping transect (Fig. 1). The “adjustment” traps were set to make their conditions (i.e., trap interference) equal to the conditions for the traps from which data were analyzed; that is, there were four traps equally spaced within a range of 50 m (Fig. 1). Logging operations were mostly performed as planned, although the second uncut strip area on the left in Fig. 1 was irregularly over-logged. Thus, data from trap nos. 7 and 8 in the over-logged area were not used in the analyses (Fig. 1).

Trapping sites were categorized along with logging operations (Fig. 1). Four uncut forest (UF) sites were in a large uncut area (> 180 m width) and were located at least 20 m inside the edge of the cut area and 20 m away from the strip road (trap nos. 27 and 28) or without strip roads nearby (trap nos. 36 and 37). Four uncut strip (US) sites were located in the 20- or 40-m-wide strips of uncut areas and 20 m inside the strip-cut areas. Trap no. 27 was 20 m from the strip road, while the other US traps were 30 m from the strip road. Six strip road (SR) sites were on the side of the strip road in the uncut forest. Ten forest edge (FE) sites were located on the borders of the uncut and cut areas. Four strip-cut (SC) sites were located in the centers of 40-m-wide strip-cuts. Four sites were located near the forest in clear-cuts (CCNF) and were 20 m into the clear-cuts from the forest edge. Three sites were located in the center of the clear-cut (CCCT) and were more than 40 m away from the forest edges on both the right and left sides of the 120-m-wide clear-cut.

We inserted the baited trap into the pipe on 17 April 2013 and collected beetles for 14 days. After the 14-day interval, we set the traps again, and collections were made at approximately 14-day intervals (every 13–15 days) up to 14 November 2013. All the captured beetles were dried on absorbent cotton and identified using a binocular microscope (Nikon SMZ 1500). We referred to Kurosawa (1985) and Kawai et al. (2005) for identification. All the beetles were stored at Kyushu Research Center, Forestry and Forest Products Research Institute.

Biomass of the collected beetles: As it is known that the biomass of dung beetles can be a good indicator of their ecological functions, such as carrion or dung removal and seed burial (Davis 1996; Larsen et al. 2005; Horgan 2005; Amézquita and Favila 2011; Slade et al. 2011), we evaluated the total biomass of the collected beetles. To obtain the total biomass at each site, beetles of each species were dried for six days at 70°C and for four additional days at 80°C. Almost all the specimens (i.e., the unbroken specimens) were weighed for species with < 50 individuals. We randomly selected and weighed 40 to 140 specimens for species with > 50 individuals. Total biomass was estimated as the product of the total number of individuals collected and the mean individual weight for each species.

Environmental conditions: To identify the environmental conditions at the trapping sites, we measured several environmental variables. To investigate the sizes, densities, and basal areas of the trees at the trapping sites, we made 10-m square plots, each of which was centered on a trap. We measured the DBH of all the trunks with DBHs above 30 mm and identified the tree species on 18 and 19 July and 3 and 9 August 2012 before logging operations. We calculated the basal areas of the trees at breast height (BA) from the measured DBH values. If a tree had several trunks, we calculated the BA of the tree by accumulating the BA of all measured trunks of the tree. On 10 and 11 October 2013, we checked logged, dead, or naturally fallen trunks and measured trunks that had reached the 30-mm DBH class. Data for these trunks were deleted from or added to the data for 2012. We also determined the degree of ground vegetation cover for each trapping site on 26 August 2013. The degrees of ground vegetation cover were categorized as follows: 0, no vegetation; 0.5, vegetation coverage less than 1%; 1, from 1 to 10%; 2, from 10 to 25%; 3, from 25 to 50%; 4, from 50 to 75%; and 5, more than 75% (Braun-Blanquet 1964). To obtain canopy openness at the trapping sites, we took hemispherical photographs at a height of 120 cm right over the traps using a digital camera (Nikon Coolpix 4500) with a fisheye lens (Nikon FC-E8) on 26 August 2013. We calculated the canopy openness from the hemispherical photographs using LIA32 software ver. 0.378 (Yamamoto 2008).

Data analysis: Nonmetric multidimensional scaling (NMS) was used to ordinate species composition at each site and analyze the similarities among the site categories. Sorensen distance was used for the analysis. Multivariate response permutation procedures (MRPPs) were applied to evaluate the effects of the categories on species composition. In this analysis, when the chance-corrected within-group agreement (A) was unity, all the assemblages in the respective groups were identical; if A was larger than 0.3, the identical level was fairly high, and the grouping was sufficiently reliable (McCune and Grace 2002).

To evaluate the beetle assemblages in the harvested areas of strip-cuttings, the beetle assemblages (i.e., species richness, total abundance, Simpson's diversity index (1/D), total biomass, and abundances of dominant species (species with > 100 individuals collected throughout this study)) in the strip-cuts were compared to those near the forest in the clear-cuts and those in the centers of the clear-cuts. A linear mixed model (LMM) was used to analyze Simpson's diversity index and total biomass. A generalized linear mixed model (GLMM) was used for the other variables with negative binomial error structures linked with logarithmic functions. The cut site numbers (Fig. 1) were used as a random effect in both models. To evaluate the beetle assemblages in the unharvested areas of the strip-cuttings, the beetle assemblages in the uncut strips were compared to those in the uncut forests and strip-cuts. To evaluate the impacts of logging to construct strip roads, the beetle assemblages beside the strip roads were compared to those in the uncut forests and the strip-cuts produced by 40-m-wide cuttings. A linear model (LM) was used to analyze Simpson's diversity index and total biomass. A generalized linear model (GLM) with negative binomial error structures linked with logarithmic functions was used to analyze the other variables.

PC-ORD ver. 6.07 (MJM Software Design 2011) was used for the NMS and MRPP analyses. For the LMM, the lmer function in the lme4 package (Bates et al. 2015) and the lmerTest package (Kuznetsova et al. 2017) for R 4.1.1 (R Core Team 2021) were used. For the GLMM and GLM, the glmer.nb function in the lme4 package and the glm.nb function in the MASS package (Venables and Ripley 2002) for R 4.1.1 (R Core Team 2021) were used, respectively. For the LM, the built-in lm function in R 4.1.1 (R Core Team 2021) was used.

Results

Environmental conditions: The density, total BA, mean BA, and maximum BA of the trees and the mean BA of the planted conifers were not largely different among the uncut forest, uncut strip, strip road, and forest edge sites, except for the high tree density at the uncut forest sites (Table 1). The degrees of ground vegetation cover did not differ greatly, including at the harvested sites (i.e., the strip-cut sites, sites located near the forest in clear-cuts, and sites in the center of the clear-cut), except for the low degree at the uncut forest sites (Table 1). Canopy openness increased with an increasing area of logging around a trap (Fig. 2).

Necrophagous silphid and dung beetle assemblages: A total of 11,232 individuals belonging to 17 species were collected in this study (Table 2). The NMS of necrophagous silphid and dung beetle assemblages resulted in a two-dimensional solution from the analysis using 6 axes and 10 runs, and the value of final stress (= 7.3%) from the analysis using 2 axes and 1 run indicated that the result was sufficiently reliable (generally a final stress value of 5–10% represents a good ordination with no risk of drawing false inferences (Clarke 1993)). The coordinates in each site category were grouped, and the groups were well separated from each other (Fig. 3). The MRPP results (A = 0.334, P = 0.000) indicated that categorization was sufficiently reliable; the compositions of beetle species from different site categories were different from one another. The coordinates of the uncut forest and uncut strip sites (i.e., the uncut sites) were distributed on the lower right and right sides of the graph, respectively, and those of the strip road, forest edge, and strip-cut sites and the sites located near the forest in clear-cuts and in the centers of the clear-cuts (i.e., the logged sites) were clustered in this order towards the upper left of the graph along with increasing area of logging around the trap (Fig. 3).

Species richness tended to decrease with increasing logging area around the trap except for the high species richness at one of the three sites in the centers of the clear-cuts (Fig. 4). Total abundance and total biomass tended to be much higher at the uncut strip sites and relatively higher at the uncut forest sites than at the other sites. These values decreased at the logged sites along with an increasing area of logging around the trap. Simpson’s diversity index tended to be higher at the uncut forest sites than at the other sites.

Among the 8 dominant species, 5 species, *Pheletrupes laevistriatus*, *Nicrophorus quadripunctatus*, *Onthophagus atripennis*, *Panelus parvulus*, and *O. ater* tended to be more abundant at the uncut forest sites than at the harvested sites (i.e., the strip-cut sites, sites located near the forest in clear-cuts and sites in the centers of clear-cuts) (Fig. 5). *Pheletrupes laevistriatus* also tended to be more abundant at the uncut strip sites. *Onthophagus fodiens* tended to be extremely more abundant at the uncut strip sites than the other sites. *Onthophagus nitidus* tended to be more abundant at the strip road sites than at the other sites. *Onthophagus lenzii* was absent at the uncut forest sites and tended to be extremely more abundant at the strip-cut sites than at the other sites.

A comparison between the sites in the strip-cuts and the clear-cuts (sites located near the forest in clear-cuts and in the centers of clear-cuts) showed that total abundance, total biomass, and the abundances of *O. nitidus* and *O. lenzii* were significantly higher at the sites in the strip-cuts than at the sites in the clear-cuts (Table 3). Two of the five species that were abundant in the uncut forests, *N. quadripunctatus* and *O. atripennis*, were significantly more abundant at the strip-cut sites than in the centers of the clear-cut sites and sites near forest in clear-cuts, respectively.

In the comparison between the uncut strips and the uncut forests or the strip-cuts, the Simpson's index and the abundances of two species abundant in the uncut forests, *N. quadripunctatus* and *P. parvulus*, were significantly higher at the sites in the uncut forests than in the uncut strips (Table 4). The total abundance and the abundance of *O. fodiens* were significantly higher at the sites in the uncut strips than at the sites in the uncut forests or the strip-cuts. The total biomass and the abundances of four species abundant in the uncut forests were significantly higher at the sites in the uncut strips than in the strip-cuts. Conversely, the abundances of *O. nitidus* and *O. lenzii* were significantly higher at the sites in the strip-cuts than in the uncut strips.

Regarding the logging to construct strip roads, Simpson's index, total biomass, and the abundances of three species abundant in the uncut forests were significantly lower at the strip road sites than at the uncut forest sites but higher than those at the strip-cut sites (Table 5). The abundance of *O. nitidus* was significantly higher at the strip road sites than at the uncut forest sites or the strip-cut sites.

Discussion

Mitigation of logging impacts by strip-cutting: The comparison among three logging operation categories in areas cut for harvest (strip-cuts, sites located near the forest in clear-cuts, and sites in the centers of clear-cuts) in our study allowed us to evaluate whether the width of cuttings affects necrophagous silphid and dung beetle assemblages. The similarity of the beetle species compositions in the cut areas to those in the uncut forest sites followed the order of the categories shown above, indicating that the strip-cuts slightly maintained a beetle species composition similar to that in the uncut forests to a greater extent than the clear-cuts, and the species composition of sites at the centers of the clear-cut areas was more degraded than that of sites in clear-cuts near the forest edges. Strip-cut areas were used by two species abundant in the uncut forests more frequently than areas near forest edges or the centers of clear-cut areas, suggesting that strip-cutting was effective in conserving the forest species. The higher biomass in the strip-cuts than in the clear-cuts suggested that the ecosystem service of beetles estimated from the total biomass of beetles was higher in the strip-cuts than in the clear-cuts; this resulted in strip-cutting mitigating the impact of logging on the beetle assemblages in forests and their functions to a greater extent than clear-cutting. This conclusion is consistent with a past study on understory vegetation that suggested that strip-cutting offers advantages over clear-cutting to conserving plant species associated with natural forests (Ito et al. 2006).

Onthophagus lenzii more frequently used strip-cuts than clear-cuts. This species is known to be most commonly found in open land (Kawai et al. 2005). *Onthophagus lenzii* may prefer open land near forests as its habitat to those far from forests, and strip-cuts might provide more suitable habitats than clear-cuts for nonforest species.

Beetle assemblages in uncut strips: In the comparison between the uncut forest sites and uncut strip sites, the significantly higher abundances of *N. quadripunctatus* and *P. parvulus* in the uncut forest sites than in the uncut strip sites and the extremely high abundance of *O. fodiens* in the uncut strip sites affected the different species composition, total abundance, and diversity index. These results indicated that the neighboring strip-cutting operations degraded the beetle assemblages in the uncut strips. This result was consistent with the findings of Jennings et al. (1986b) but not with those of Jennings et al. (1984, 1986a, 1988), who showed that the total abundance and the abundances of forest species were low in the uncut strips for ants and did not differ for phalangiid harvestmen or surface-wandering spiders, while they were higher in the uncut strips than in the uncut forests for carabid beetles. *Nicrophorus quadripunctatus* and *P. parvulus* may prefer closed forests as their habitats, whereas *O. fodiens* may prefer relatively disturbed forests. Indeed, *N. quadripunctatus* and *P. parvulus* are known to be more abundant in closed forests than in young forests and/or open lands (Katakura and Ueno 1985; Katakura et al. 1986; Suzuki 2001; Nagano and Suzuki 2003; Ueda 2020; Ueda and Sato 2020). However, Ueda (2016) showed that *P. parvulus* was an indicator species of young forest. Further study is needed to clarify the habitat preference of *P. parvulus*. Despite the differences mentioned above between the uncut forest sites and uncut strip sites, the abundances of the other species abundant in the uncut forests and total biomass did not significantly differ between these sites (Table 4).

The comparison between the uncut strip sites and the strip-cut sites indicated that there were significantly higher abundances of four species that were abundant in the uncut forests and of *O. fodiens* in the uncut strip sites than in the strip-cut sites and high abundance of *O. lenzii* in the strip-cut sites, affecting the species composition, total abundance, and total biomass in those sites. The higher abundances of the species abundant in the uncut forests and the higher biomass in the uncut strips than in the strip-cuts indicated that the uncut strips provided habitats suitable for forest species and maintained the estimated ecosystem services provided by beetles to a greater extent than the strip-cuts. This result was consistent with that of Jennings et al. (1984, 1986a), who showed that for phalangiid harvestmen and carabid beetles, total abundance and the abundances of species abundant in uncut forests were higher in uncut strips than in strip-cuts. However, Jennings et al. (1988) also showed higher abundance and species richness of surface-wandering spiders in strip-cuts than in uncut strips.

Influence of logging to construct strip roads: In the comparison between the uncut forest sites and strip road sites, there were significantly higher abundances of *P. laevistriatus*, *N. quadripunctatus*, *P. parvulus* and *O. ater* in the uncut forest sites than in the strip road sites, and the high abundance of *O. nitidus* in the strip road sites influenced the species composition, total abundance, diversity index, and total biomass in those sites. However, four species that were abundant in the uncut forest sites were more abundant in the strip road sites than in the strip-cut sites, with logging widths of 40 m. The high abundances of these four species and *O. nitidus* in the strip road sites affected the species composition, total abundance, diversity index, and total biomass in those sites. These results indicated that logging to construct strip roads negatively affected the forest species and the estimated ecosystem service of beetles, but the negative effect was lower for the strip roads than for the 40-m-wide logging areas.

Hosaka et al. (2014a, b) showed that the construction of temporary skid trails negatively affected dung beetle diversity in tropical forests in Malaysia. Koivula (2005) found that a dominant forest carabid beetle species was less abundant in the 3–7-m-wide roadside forest than in adjacent forests. These findings are consistent with those of this study. When not limited to forest species, Kotani and Ogura (2014) found that strip road openings increased the diversity of understory vegetation. Koivula (2005) found that the dominant generalists of carabid beetles that prefer open forests were more abundant on roadsides than in adjacent forests, which caused higher species richness on roadsides than in adjacent forests. The finding in this study that the abundance of *O. nitidus* was highest in the strip road sites might have occurred through the same mechanism that allowed generalist carabids to be dominant in Kouivula (2005) because *O. nitidus* is generally collected in all sorts of forest environments but prefers forests with low tree densities or young forests (Shimada et al. 1991; Ueda 2016).

Conclusion

We conclude that strip-cutting is a better harvesting method than clear-cutting because of the two following results: 1) strip-cutting mitigates the impact of logging on beetle assemblages in forests and the ecosystem services provided by beetles estimated from biomass to a greater extent than clear-cutting, and 2) the residual uncut strips generally retain beetle assemblages found in forests and maintain the estimated ecosystem services more than logged areas. We also conclude that logging to construct strip roads negatively affected the forest species and their estimated ecosystem services, but the negative effect was lower than that observed in 40-m-wide logging areas. However, since this study was conducted for only one insect group in one forest, more studies are needed to determine the advantages of strip-cutting and the influences of logging to construct strip roads on other insect groups and/or in other forest types.

Acknowledgments

We thank the late Masato Ito, Kenichi Ozaki, Masahiro Kon for their suggestions for the study, Hideaki Goto and Masahiro Sueyoshi for the field support, Rob Johns for editing the manuscript, and the anonymous referees who made comments that led to a considerable improvement in the text. We also thank the Kyushu Regional Forest Office and Kumamoto District Forest Office for offering the study site. This study was supported by research grant 201106 of FFPRI.

References

Aiura H, Kato A, Hasegawa M (1996) Occurrence process of shallow landslides after clear-cutting beech and planting conifers on heavy-snow mountain slopes. J Jpn For Soc 78:398-403 (in Japanese with English summary)

Amézquita S, Favila ME (2011) Carrion removal rates and diel activity of necrophagous beetles (Coleoptera: Scarabaeinae) in a fragmented tropical rain forest. Environ Entmol 40: 239-246

Barton PS, Cunningham SA, Macdonald BCT, McIntyre S, Lindenmayer DB, Manning AD (2013) Species traits predict assemblage dynamics at ephemeral resource patches created by carrion. PLOS ONE 8: e53961, 9 pp

Bates D, Maechler M, Bolker B, Walker, S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67(1): 1-48

Bembenek M, Giefing DF, Karaszewski Z, Lacka A, Mederski PS (2013) Strip road impact on selected wood defects of Norway spruce (*Picea abies* (L.) H. Karst). Drewno 56: 63-76

Braun-Blanquet J (1964) Pflanzensoziologie. 3 Aufl. Springer, Wien, 865 pp

Clarke KR (1993) Non-parametric multivariate analyzes of changes in community structure. Austral J Ecol 18: 117-143

Davis AJ, Holloway JD, Huijbregts H, Krikken J, Kirk-Spriggs AH, Sutton SL (2001) Dung beetles as indicators of change in the forests of northern Borneo. J Appl Ecol 38:593–616

Davis ALV (1996) Seasonal dung beetle activity and dung dispersal in selected South African habitats: implications for pasture improvement in Australia. Agri eco environ 58:157-169

Forestry Agency of Japan (2018) Annual report on forest and forestry in Japan fiscal year 2018. The annual report group of the Forestry Agency, Tokyo, 40pp, URL: http://www.maff.go.jp/e/data/publish/attach/pdf/index-176.pdf (accessed 2021-3-19)

Forestry Agency of Japan (2019) Work survey of Forestry Agency. e-stat, URL: https://www.e-stat.go.jp/stat-search (accessed 2019-3-5) (in Japanese)

Gibbs JP, Stanton EJ (2001) Habitat fragmentation and arthropod community change: carrion beetles, phoretic mites, and flies. Ecol Appl 11:79-85

Horgan FG (2005) Effects of deforestation on diversity, biomass and function of dung beetles on the eastern slopes of the Peruvian Andes. For Ecol Manage 216:117-133

Hosaka T, Niino M, Kon M, Ochi T, Yamada T, Fletcher CD, Okuda T (2014a) Impacts of small-scale clearings due to selective logging on dung beetle communities. Biotropica 46:720-731

Hosaka T, Niino M, Kon M, Ochi T, Yamada T, Fletcher C, Okuda T (2014b) Effects of logging road networks on the ecological functions of dung beetles in Peninsular Malaysia. For Ecol Manage 326:18-24

Ito M (1994) Silphid beetles. In: Nature Conservation Society of Japan (ed) Field guide series 3 indicator species, Heibonsha Co, Tokyo, pp 264-269 (in Japanese)

Ito M, Aoki J (1983) Urban environment of Yokohama City and soil animal communities I. Coleopteran fauna surveyed by baited pitfall trap. Bull Environ Sci Tech Yokohama Nat Univ 9:183-196 (in Japanese with English summary)

Ito S, Ishigamo S, Mizoue N, Buckley GP (2006) Maintaining plant species composition and diversity of understory vegetation under strip-clearcutting forestry in conifer plantations in Kyushu, southern Japan. For Ecol Manage 231:234-241

Jennings DT, Houseweart MW, Cokendolpher JC (1984) Phalangids (Arachnida: Opiliones) associated with strip clearcut and dense spruce-fir forests of Maine. Environ Entomol 13:1306-1311

Jennings DT, Houseweart MW, Dunn GA (1986a) Carabid beetles (Coleoptera: Carabidae) associated with strip clearcut and dense spruce-fir forests of Maine. Coleo Bull 40:251-263

Jennings DT, Houseweart MW, Francoeur A (1986b) Ants (Hymenoptera: Formicidae) associated with strip-clearcut and dense spruce-fir forests of Maine. Can Ent 118:43-50

Jennings DT, Houseweart MW, Dondale CD, Redner JH (1988) Spiders (Araneae) associated with strip-clearcut and dense spruce-fir forests of Maine. J Arachnol 16:55-70

Katakura H, Ueno R (1985) A preliminary study on the faunal make-up and spatio-temporal distribution of carrion beetles (Coleoptera: Silphidae) on the Ishikari coast, northern Japan. Jap J Ecol 35:461-468

Katakura H, Sonoda M, Yoshida N (1986) Carrion beetle (Coleoptera, Silphidae) fauna of Hokkaido University Tomakomai experiment forest, Northern Japan, with a note on the habitat preference of a geotrupine species, *Geotrupes laevistriatus* (Coleoptera, Scarabaeidae). Bull Col Exp For Hokkaido Univ 43:43-55

Kawai N, Hori S, Kawahara M, Inagaki M (2005) Atlas of Japanese Scrabaeoidea vol 1 coprophagous group, Roppon-ashi Entomological Books, Tokyo, 189pp (in Japanese)

Kinki-Chugoku Forest Management Bureau (2017) Guideline for management. Kinki-Chugoku Forest Management Bureau, Osaka, 27pp, URL: http://www.rinya.maff.go.jp › for_planning-3 (accessed 2021-3-22) (in Japanese)

Koivula MJ (2005) Effects of forest roads on spatial distribution of boreal carabid beetles (Coleoptera: Carabidae). Coleo Bull 59:465-487

Korczynski I, Kuzminski R, Mazur A (2007) The effect of strip roads in pine stands on the population size of large weevil – *Hylobius abietis* (L.). Acta Sci Pol Silv Colendar Rat Ind Lignar 6(2):11-14

Kotani J, Ogura A (2014) Vegetation recovery since establishment of spur roads for thinning in coniferous plantations. J Jpn For Soc 96:261-266 (in Japanese with English summary)

Kurosawa Y (1985) Silphidae. In: Ueno S, Kurosawa Y, Sato M (eds) The Coleoptera of Japan in color vol II, Hoikusha Co, Osaka, pp 246-252 (in Japanese)

Kuznetsova A, Brockhoff PB, Christensen RHB (2017) lmerTest package: tests in linear mixed effects models. J Stat Softw 82(13):1-26

Larsen TH, Forsyth A (2005) Trap spacing and transect design for dung beetle biodiversity studies. Biotropica 37:322-325

Larsen TH, Williams NM, Kremen C. (2005) Extinction order and altered community structure rapidly disrupt ecosystem functioning. Ecol Lett 8:538-547.

McCune B, Grace JB (2002) Analysis of ecological communities. MjM Software Design, Gleneden Beach, 300pp.

McGeoch MA, Rensburg BJV, Botes A (2002) The verification and application of bioindicators: a case study of dung beetles in a savanna ecosystem. J Appl Ecol 39:661–672

MJM Software Design (2011) PC-ORD ver 6.07, Greneden Beach, Oregon

Moore JD, Ouimet R, Camiré C, Houle D (2002) Effects of two silvicultural practice on soil fauna abundance in a northern hardwood forest, Québec, Canada. Can J Soil Sci 82:105-113

Moore JD, Ouimet R, Houle D, Camiré C (2004) Effects of two silvicultural practice on ground beetles (Coleoptera: Carabidae) in a northern hardwood forest, Quebec, Canada. Can J For Res 34:959-968

Munguira ML, Thomas JA (1992) Use of road verges by butterfly and burnet populations, and the effect of roads on adult dispersal and mortality. J Appl Ecol 29:316-329

Nagano M, Suzuki S (2003) Phenology and habitat use among *Nicrophorine* beetles of the genus *Nicrophorus* and *Ptomascopus* (Coleoptera: Silphidae). Edaphologia 73:1-9

Nakano H (1971) Effect on streamflow of forest cutting and change in regrowth on cut-over area. Bull Gov For Exp Sta 240:1-251 (in Japanese with English summary)

Pawson SM, Brockerhoff EG, Norton DA, Didham RK (2006) Clear-fell harvest impacts on biodiversity: past research and the search for harvest size thresholds. Can J For Res 36:1035-1046

R Core Team (2021) R: A language and environment for statistical computing, R Foundation for Statistical Computing, Vienna, Austria, URL https://www.R-project.org/. (accessed 2021-12-15)

Sakai H, Aruga K, Watanabe S (2002) Environmental conservation effects of forest strip roads and promotion of infrastructure. J Jpn For Soc 84:125-129 (in Japanese with English summary)

Satou A, Nisimura T, Numata H (2000) Reproductive competition between the burying beetle *Nicrophorus quadripunctatus* without phoretic mites and the blow fly *Chrysomya pinguis.* Entomol Sci 3:265-268

Shimada M (1985) Studies on inhabitant of insects in parks and open spaces of the urban area.

Zouenzasshi 48(5):187-191 (in Japanese with English summary)

Shimada M, Takahashi T, Maruta Y (1991) Studies on inhabitant environment of insects in parks and open spaces in urban area. Zouenzasshi 54(5):287-292 (in Japanese with English summary)

Slade EM, Mann DJ and Lewis OT (2011) Biodiversity and ecosystem function of tropical forest dung beetles under contrasting logging regimes. Biol Conserv 144:166-174

Springett BP (1968) Aspects of the relationship between burying beetles, *Nicrophorus* spp. and the mite, *Poecilochirus necrophori* Vitz. J Animal Ecol 37:417-424

Suzuki S (2001) Effects of the thinning of a fir forest on the fauna of carrion beetle. New Entomol 50(3,4):51-54 (in Japanese with English summary)

Suzuki S (2005) Potential for Nicrophorinid beetle (Silphidae: Coleoptera) as environmental indicator and the effectiveness of baited hanging traps to collecting Nicrophorinid beetles. J Environ Edu 8:111-116 (in Japanese with English summary)

Trumbo ST, Bloch PL (2000) Habitat fragmentation and burying beetle abundance and success. J Insect Conserv 4:245-252

Ueda A (2015) Tools for evaluating forest habitat using carrion silphid (Silphidae) and scarabaeoid dung beetles (coprophagous group of Scarabaeoidea) as indicators: Effects of bait type, trap type, and trap number on beetle captures. Bull For Forest Prod Res Inst 14:1-14 (in Japanese with English summary)

Ueda A (2016) Response of assemblages of carrion beetles (carrion silphid and scarabaeoid dung beetles) in a forest consisting of small, different-aged stands. J Jpn For Soc 98:207-213 (in Japanese with English summary)

Ueda A (2020) Silphid and dung beetle assemblages lured by carrion in old-growth evergreen broad-leaved forests and other forest environments. Bull For Forest Prod Res Inst 19:105-114 (in Japanese with English summary)

Ueda A and Sato S (2020) Preliminary study of assemblages of carrion silphid and dung beetles in a forest consisting of small, different-aged, different-tree species stands in Sapporo. Boreal For Res 68:11-15 (in Japanese)

Ueda A, Tone K, Sano M (2016) Assemblages of carrion beetles (Silphidae and coprophagous group of Scarabaeoidea) in Okinawa City and Nago City and their seasonal changes. Kyushu J For Res 69:53-57 (in Japanese)

Venables WN, Ripley BD (2002) Modern applied statistics with S. Fourth edition. Springer, New York.

Vermeulen HJW (1994) Corridor function of a road verge for dispersal of stenotopic heathland ground beetles Carabidae. Biol Conserv 69:339-349

Yamamoto K (2008) LIA32 ver.0.378. URL: http://www.agr.nagoya-u.ac.jp/~shinkan/LIA32/ (accessed 2014-9-12) (in Japanese)

Figure legend

Fig. 1. Aerial photograph of the study site (upper) and the condition of the study site as well as the logging operation categories of the traps along the trapping transect (lower)

The photograph was taken on 12 March 2013. The dotted parts of the trapping transect in the photograph indicate where "adjustment traps" were placed. The "adjustment" traps were set to make the trap interferences within a 50-m range identical to those of the traps for which data were analyzed (see 'data analysis' in materials and methods). Data from the "adjustment" traps and the traps in the over-logged area were omitted. UF: uncut forest, US: uncut strip, SR: strip road, FE: forest edge, SC: strip-cut, CCNF: near forest in the clear-cut, and CCCT: center of the clear-cut.

Fig. 2 Canopy openness in each site category obtained from hemispherical photographs (left) and hemispherical photographs at a site in each site category (right)

Boxes and thick horizontal lines illustrate the interquartile range (lower limit: 25th percentile; upper limit: 75th percentile) and the median value (50th percentile), respectively. The bottom and top whiskers depict the lowest and highest values. The numbers and percentages above the photographs indicate trap No. in Fig. 1 and canopy openness, respectively. The abbreviations of the site categories are the same as in Fig. 1.

Fig. 3 NMS ordination of necrophagous silphid and dung beetle assemblages (final stress = 7.3%). Abbreviations of the site categories are the same as in Fig. 1. Parenthesized percentages on the titles of the axes indicate the proportion of the variance represented by each axis, based on the r^2 between the distance in the ordination space and the distance in the original space. The solid line indicates the range of coordinates of each site category.

Fig. 4 Species richness, total abundance, diversity index, and total biomass in each site category
a: species richness (the number of species collected per trap), b: total abundance (the total number of beetles collected per trap), c: diversity index (the value of Simpson's diversity index (1/D) for each trap), and d: total biomass (the total dry weight of beetles per trap). The boxes, horizontal lines, and whiskers represent the same information as in Fig. 2. The abbreviations of the site categories are the same as in Fig. 1.

Fig. 5 Number of beetles collected in each trap in each site category
Data are shown for only the beetle species for which we collected >100 individuals throughout this study (i.e., the dominant species). The beetles are categorized as species abundant in the uncut forest sites, species abundant in the uncut strip or strip road sites other sites, and species absent in the uncut forest sites. Next, the beetles are arranged by their total abundances from left to right. The boxes, horizontal lines, and whiskers represent the same information as in Fig. 2. The abbreviations of the site categories are the same as in Fig. 1.

Table 1 Mean ± SE of tree data and degree of ground vegetation cover for each trap site category

	Uncut forest (UF)	Uncut strip (US)	Strip road (SR)	Forest edge (FE)	Strip-cut (SC)	Near forest in clear-cut (CCNF)	Center of clear-cut (CCCT)
Number of sites	4	4	6	10	4	4	3
Tree density (ha^{-1})	1,925 ± 386	750 ± 222	767 ± 263	620 ± 77	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Total of trunk basal area (BA) (m^2 ha^{-1})	61.7 ± 4.1	56.3 ± 17.3	40.6 ± 6.7	42.8 ± 7.9	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Mean BA of trees (cm^2)	331 ± 81	812 ± 126	501 ± 165	663 ± 86	-	-	-
Maximum BA of trees (cm^2)	1219 ± 343	1353 ± 285	803 ± 230	1281 ± 242	-	-	-
Mean BA of planted conifers (cm^2)	521 ± 118	1140 ± 354	568 ± 156	644 ± 94	-	-	-
Degree of ground vegetation cover	0.8 ± 0.1	3.0 ± 0.9	1.7 ± 0.5	2.9 ± 0.5	3.3 ± 0.5	3.7 ± 1.1	1.7 ± 1.2

Table 2 Total number of individuals of silphid and dung beetles collected throughout this study

Family and species name	No. captured
Silphidae	
Nicrophorus concolor	79
Nicrophorus maculifrons	14
Nicrophorus quadripunctatus	897
Ptmascopus morio	20
Oiceoptoma nigropunctatum	3
Eusilpha japonica	3
Calosilpha brunneicollis	8
Geotrupidae	
Phelotrupes laevistriatus	1,250
Scrabaeidae	
Panelus parvulus	281
Copris acutidens	1
Liatogus minutus	1
Onthophagus lenzii	110
Onthophagus nitidus	566
Onthophagus atripennis	457
Onthophagus ater	110
Onthophagus fodiens	7,431
Aphodius rectus	1
Total	11,232
Species richness	17

Table 3 Results of the comparison between strip-cutting and clear-cutting

	Applied distribution	Model	Strip-cut (SC) vs.			
			Near forest in clear-cut (CCNF)		Center of clear-cut (CCCT)	
			z (t)	*P*	z (t)	*P*
Species richness	nb	GLMM	-0.395	0.693	-0.040	0.968
Total abundance	nb	GLMM	-2.164	*0.030*	-4.411	< *0.0001*
Simpson's diversity index (1/D)	normal	LMM	0.896	0.389	0.660	0.523
Total biomass	normal	LMM	-2.549	*0.027*	-4.767	*0.0006*
Phelotrupes laevistriatus (F)	nb	GLMM	0.011	0.991	-0.882	0.378
Nicrophorus quadripunctatus (F)	nb	GLMM	0.216	0.829	-2.513	*0.012*
Onthophagus atripennis (F)	nb	GLMM	-2.448	*0.014*	-1.738	0.082
Panelus parvulus (F)	nb	GLMM	-0.215	0.830	-0.778	0.437
Onthophagus ater (F)	nb	GLMM	0.571	0.568	0.201	0.841
Onthophagus fodiens (G)	nb	GLMM	-2.031	*0.042*	-3.885	*0.0001*
Onthophagus nitidus (G)	nb	GLMM	1.098	0.272	-0.298	0.766
Onthophagus lenzii (O)	nb	GLMM	-4.486	< *0.0001*	-3.245	*0.001*

nb means negative binomial distribution. The t value was used for normal distribution.

F: species abundant in the uncut forest sites, G: species abundant in the uncut strip or the strip road sites, O: species absent in the uncut forest sites

Table 4 Results of the comparison for the beetle assemblages of the uncut strip sites

	Applied distribution	Model	Uncut strip (US) vs.			
			Uncut forest (UF)		Strip-cut (SC)	
			z (t)	P	z (t)	P
Species richness	nb	GLM	-0.11	0.913	-1.283	0.200
Total abundance	nb	GLM	-5.454	*<0.0001*	-9.131	*<0.0001*
Simpson's diversity index (1/D)	normal	LM	5.298	*0.0005*	-0.342	0.740
Total biomass	normal	LM	-2.101	0.065	-6.495	*0.0001*
Phelotrupes laevistriatus (F)	nb	GLM	-0.507	0.612	-8.878	*<0.0001*
Nicrophorus quadripunctatus (F)	nb	GLM	2.904	*0.004*	-2.982	*0.003*
Onthophagus atripennis (F)	nb	GLM	1.418	0.156	-2.966	*0.003*
Panelus parvulus (F)	nb	GLM	3.396	*0.0007*	0.327	0.743
Onthophagus ater (F)	nb	GLM	1.007	0.314	-3.405	*0.0007*
Onthophagus fodiens (G)	nb	GLM	-4.539	*<0.0001*	-3.435	*0.0006*
Onthophagus nitidus (G)	nb	GLM	0.61	0.542	3.396	*0.0007*
Onthophagus lenzii (O)	nb	GLM	-0.004	0.997	4.912	*<0.0001*

nb means negative binomial distribution. The t value was used for normal distribution.

F: species abundant in the uncut forest sites, G: species abundant in the uncut strip or the strip road sites, O: species absent in the uncut fores

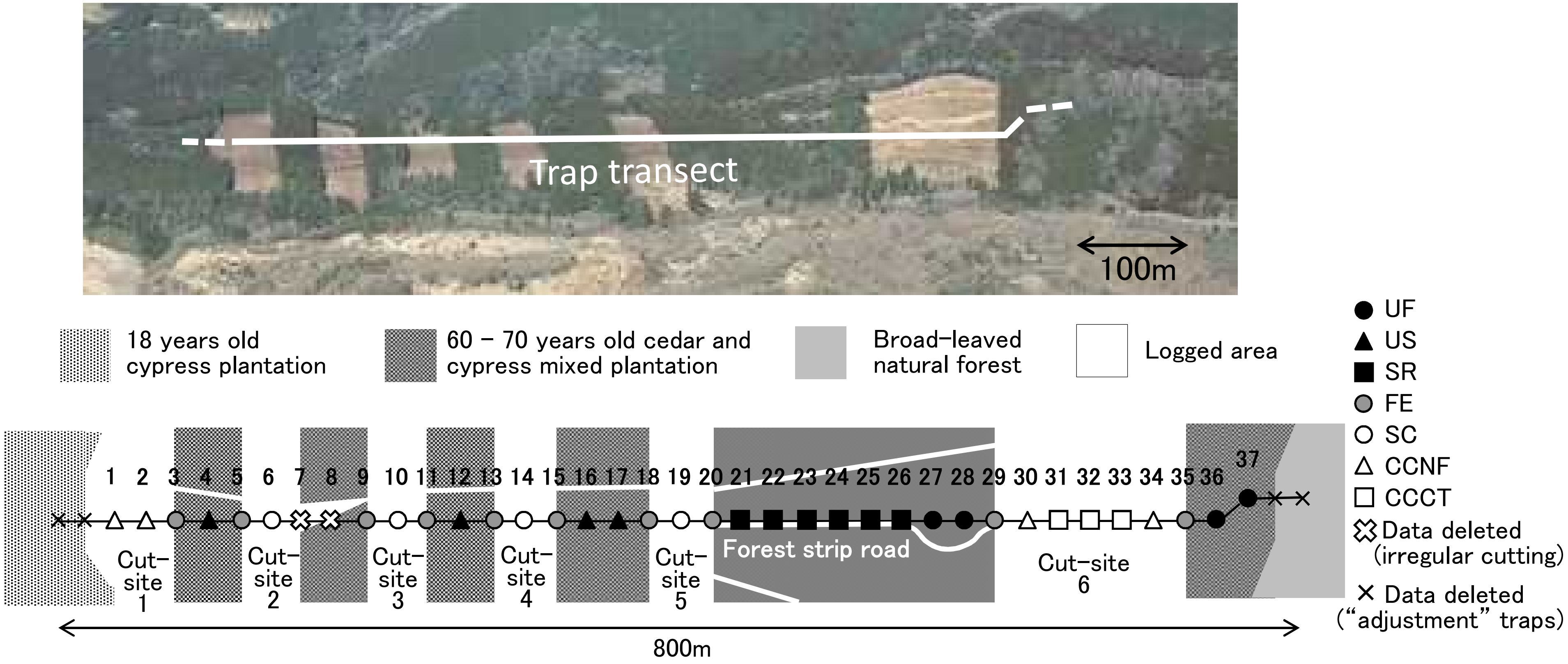
Table 5 Results of the comparison for the beetle assemblages of the strip road sites

	Applied distribution	Model	Strip road (SR) vs.			
			Uncut forest (UF)		Strip-cut (SC)	
			z (t)	*P*	z (t)	*P*
Species richness	nb	GLM	0.628	0.530	-0.664	0.507
Total abundance	nb	GLM	0.577	0.563	-2.521	*0.012*
Simpson's diversity index (1/D)	normal	LM	2.653	*0.022*	-3.249	*0.008*
Total biomass	normal	LM	3.512	*0.005*	-3.035	*0.011*
Phelotrupes laevistriatus (F)	nb	GLM	2.930	*0.004*	-5.117	*<0.0001*
Nicrophorus quadripunctatus (F)	nb	GLM	1.993	*0.046*	-4.582	*<0.0001*
Onthophagus atripennis (F)	nb	GLM	0.412	0.680	-3.567	*0.0004*
Panelus parvulus (F)	nb	GLM	4.367	*<0.0001*	1.511	0.131
Onthophagus ater (F)	nb	GLM	3.502	*0.0005*	-2.659	*0.008*
Onthophagus fodiens (G)	nb	GLM	-1.401	0.161	-0.229	0.819
Onthophagus nitidus (G)	nb	GLM	-7.657	*<0.0001*	-4.918	*<0.0001*
Onthophagus lenzii (O)	nb	GLM	-0.003	0.998	5.654	*<0.0001*

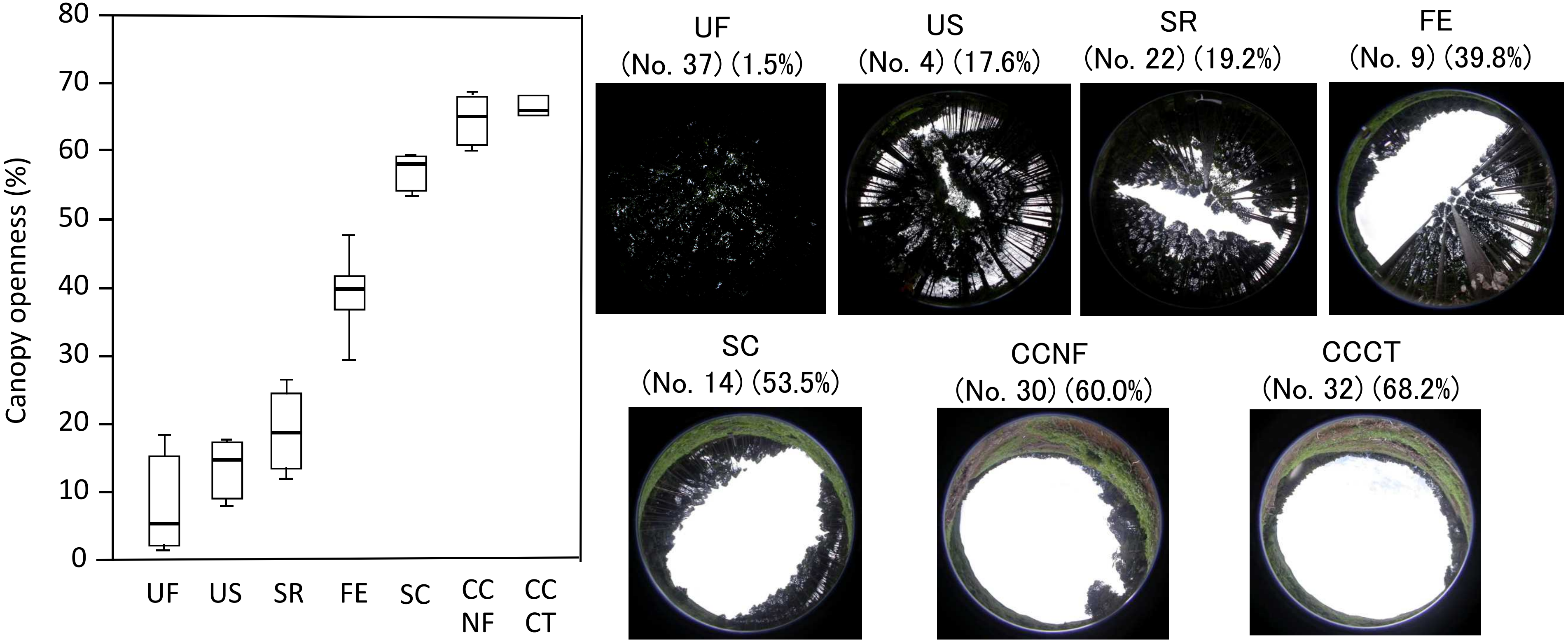
nb means negative binomial distribution. The t value was used for normal distribution.

F: species abundant in the uncut forest sites, G: species abundant in the uncut strip or the strip road sites, O: species absent in the uncut forest si

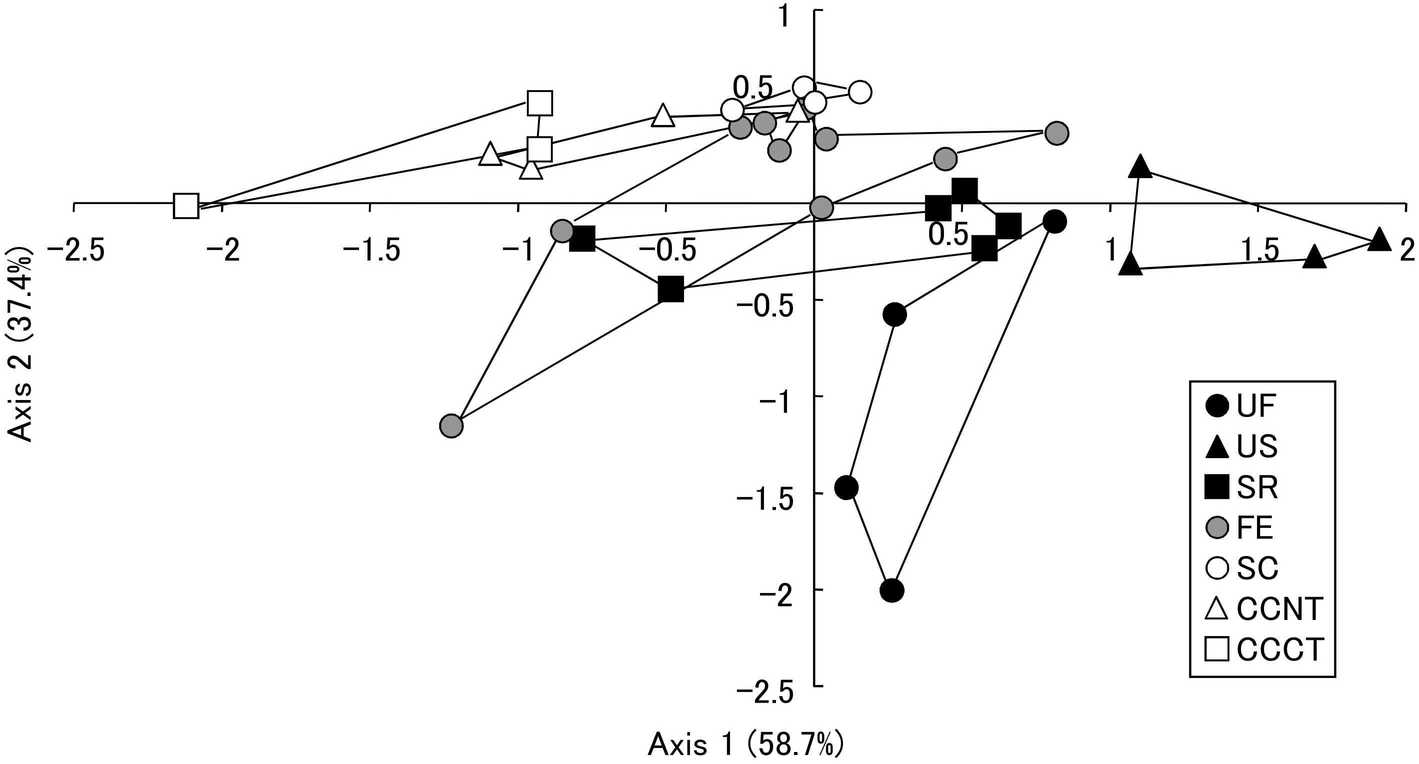
Ueda Fig. 1


Trap transect
100m
18 years old cypress plantation
60 – 70 years old cedar and cypress mixed plantation
Broad-leaved natural forest
Logged area
● UF
▲ US
■ SR
● FE
○ SC
△ CCNF
□ CCCT
Data deleted (irregular cutting)
× Data deleted ("adjustment" traps)
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37
Cut-site 1
Cut-site 2
Cut-site 3
Cut-site 4
Cut-site 5
Forest strip road
Cut-site 6
800m

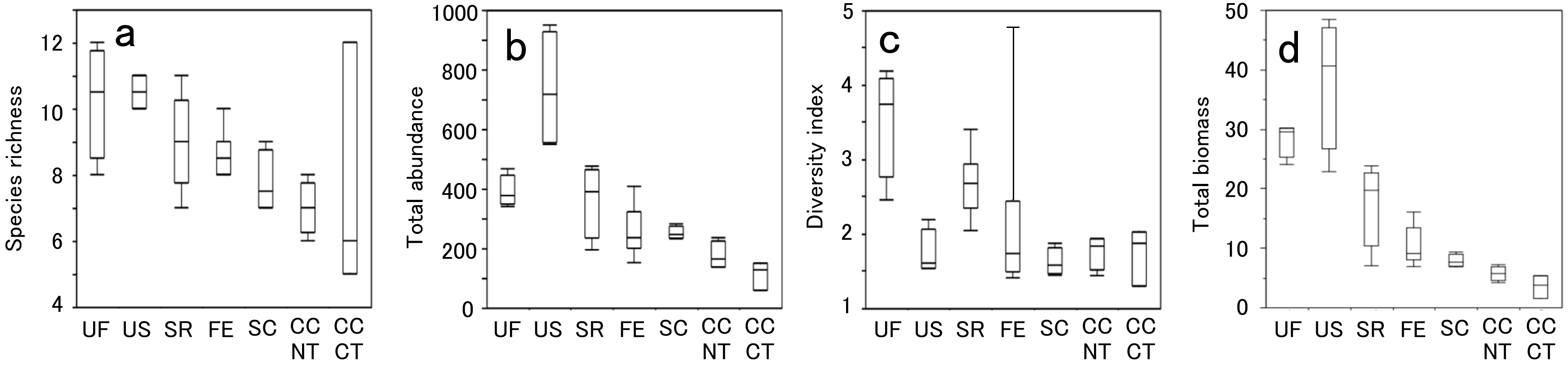
Ueda Fig. 2


80
70
60
50
40
30
20
10
0
Canopy openness (%)
UF
US
SR
FE
SC
CC NF
CC CT
UF (No. 37) (1.5%)
US (No. 4) (17.6%)
SR (No. 22) (19.2%)
FE (No. 9) (39.8%)
SC (No. 14) (53.5%)
CCNF (No. 30) (60.0%)
CCCT (No. 32) (68.2%)

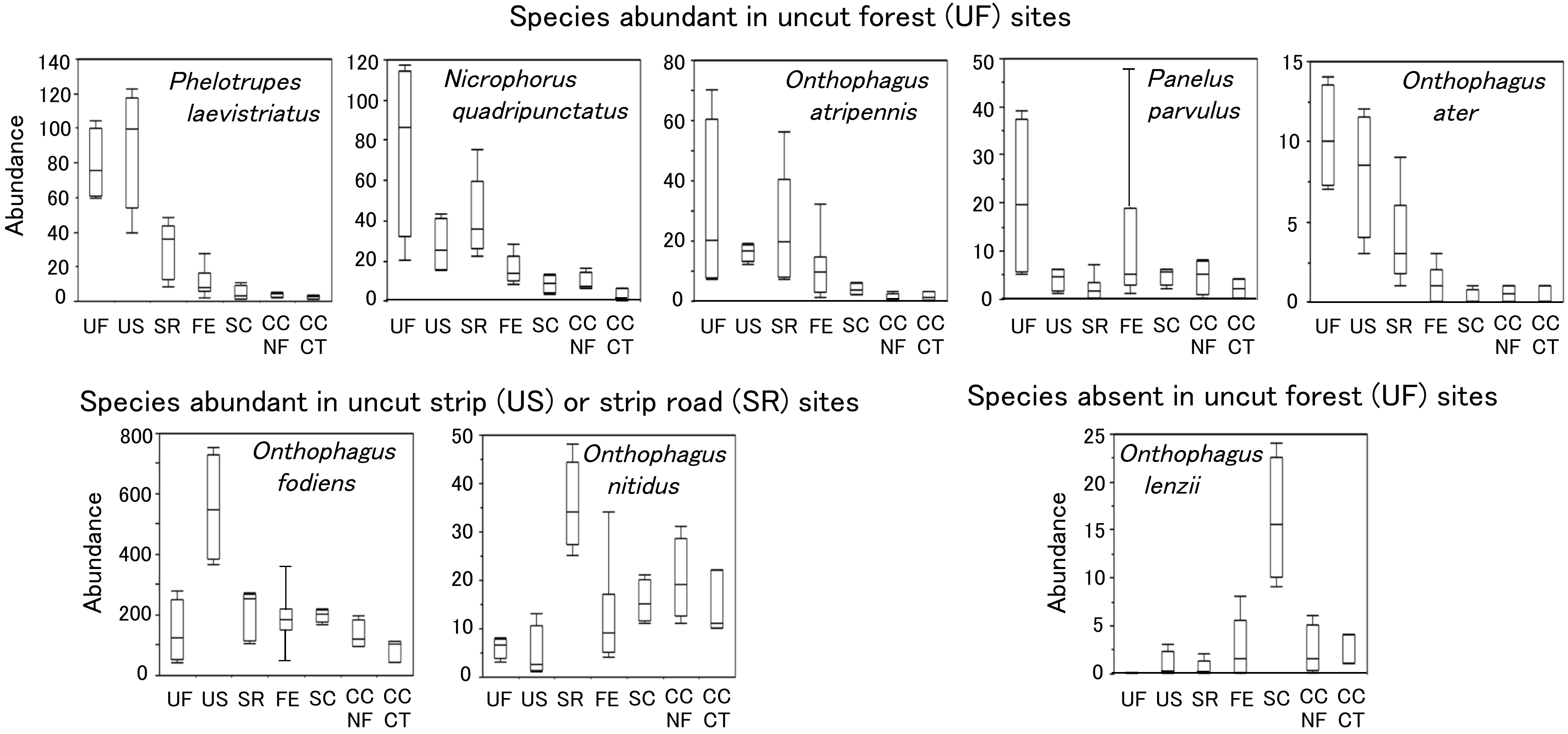
Ueda Fig. 3


1
0.5
−0.5
−1
−1.5
−2
−2.5
−2.5
−2
−1.5
−1
−0.5
0.5
1
1.5
2
Axis 2 (37.4%)
Axis 1 (58.7%)
● UF
▲ US
■ SR
● FE
○ SC
△ CCNT
□ CCCT

Ueda Fig. 4


a
Species richness
4
6
8
10
12
b
Total abundance
0
200
400
600
800
1000
c
Diversity index
1
2
3
4
5
d
Total biomass
0
10
20
30
40
50
UF
US
SR
FE
SC
CC NT
CC CT

Ueda Fig. 5


Species abundant in uncut forest (UF) sites
Phelotrupes laevistriatus
Nicrophorus quadripunctatus
Onthophagus atripennis
Panelus parvulus
Onthophagus ater
Abundance
0
20
40
60
80
100
120
140
UF US SR FE SC CC NF CC CT
Species abundant in uncut strip (US) or strip road (SR) sites
Onthophagus fodiens
Onthophagus nitidus
0
200
400
600
800
Species absent in uncut forest (UF) sites
Onthophagus lenzii
0
5
10
15
20
25