Effects of dispersed and aggregated retention-cuttings and differently sized clear-cuttings in conifer plantations on necrophagous silphid and dung beetle assemblages

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Abstract

Retention forestry and small-sized clear-cuttings are thought to partially mitigate the impacts of logging. To evaluate the impacts of these two harvesting methods, a variety of logging operations were conducted in mature Sakhalin fir plantation forests in Hokkaido, northern Japan. The stands were logged with the following approaches: dispersed retention of naturally regenerated broad-leaved trees in large (100 trees/ha), medium (50), or small (10) amounts; 60×60 m aggregated retention;

quadrilateral small-sized (ca 1-ha) clear-cutting; and whole clear-cutting. We collected necrophagous silphid and dung beetles from these stands and from unharvested natural broad-leaved forests and plantation forests using carrion-baited pitfall traps. All logging operations clearly affected the beetle assemblages. The 0.36 ha unharvested forest patches under aggregated retention did not act as refugia for forest species because their assemblages were almost identical to those outside the forest patches and in the whole clear-cuts. However, the total abundance of forest species and, specifically, the abundances of two dominant forest species were significantly and positively related to the trunk basal area of retained trees in the dispersed retention sites. The total abundance of forest species was significantly higher in the small clear-cuts than in the whole clear-cuts. A dominant open-land species was abundant in the harvested areas irrespective of the type of logging operation. Thus, we concluded that dispersed retention and small-sized clear-cuttings were beneficial harvesting methods for the beetle conservation because they conserved forest species compared to whole clear-cuttings and preserved the habitats of open-land species as well as whole clear-cuttings.

Implications for insect conservation: Our results indicated that large areas of unharvested forest patches are needed to conserve the habitat of forest necrophagous silphid and dung beetles, most species of which are adept at flying. Our results also indicated that the higher density of retained trees in dispersed retention forestry and the smaller areas of clear-cuttings were better for conserving forest species. Our findings provide useful information for selecting methods and designs of logging

practices for species protection of flying insects in logged areas.

Keywords

Silphidae, coprophagous group of Scarabaeoidea, retention forestry, green-tree retention, group retention, necrophagous beetle

Introduction

In Japan, conifer plantations that were largely established from the 1960s to 1980s mature and become ready for harvesting. As such, the amount of domestic wood production started increasing in 2002 and is expected to increase more in the future (Forestry Agency of Japan 2018). In cases of tree felling, standard clear-cuttings may have some impacts on forest ecosystems by causing increases in landslides and debris flows and decreases in forest species (Imaizumi et al. 2008; Imaizumi and Sidle 2012; Aiura et al. 1996; Pawson et al. 2006). Retention forestry (i.e., a measure to retain unharvested live and/or dead trees at harvest time) has been performed in several parts of European, North American, Tasmanian, and Patagonian forests, and a variety of studies on biodiversity have been undertaken there (Gutafsson et al. 2012; Lindenmayer et al. 2012; Mori and Kitagawa 2014; Ozaki et al. 2018). Rosenvald and Lõhmus (2008) demonstrated that the species richness and abundances of birds and ectomycorrhizal fungi were larger in retention-cuts than in clear-cuts, but those of herbs, arthropods, and small mammals did not significantly differ between retention-cuts and clear-cuts. Fedrowitz et al. (2014) showed that the species richness and abundances of both forest and open-land species of most organism groups in the stands under retention forestry were intermediate between those of unharvested forests and clear-cut areas and concluded that retention forestry decreased the negative impacts of tree felling and functioned to conserve open-land species.

However, these practices have been examined only in natural forests, and no studies on retention forestry have been performed in plantation forests (Ozaki et al. 2018; Yamaura et al. 2018). Moreover, retention forestry with large experimental study sites has never been undertaken in Asia (Ozaki et al. 2018; Yamaura et al 2018). Thus, as the first attempt at retention forestry in both plantation forests and Asia, the sites of this study, “the Retention Experiment for plantation FoREstry in Sorachi, Hokkaido (REFRESH)”, were initiated in 2013 in conifer plantation forests in Hokkaido, Northern Japan (Akashi et al 2017; Ozaki et al. 2018; Yamaura et al 2018).

There are two approaches to retention forestry. Dispersed retention distributes the retained trees through the whole harvested stand. Aggregated (group) retention distributes unharvested areas in a harvested stand. Aggregated retention aims at unharvested areas functioning as refugia of forest species called ‘lifeboat’ (Matveinen-Huju et al. 2006). Aubry et al. (2009) demonstrated that the diversities of most organism groups did not significantly differ between dispersed and aggregated retentions in North America. Baker et al. (2009) showed that aggregated retention benefited ground-active beetles compared to dispersed retention in Tasmania. In the REFRESH, both dispersed and aggregated retentions were installed to compare their advantages (Akashi et al 2017; Ozaki et al. 2018; Yamaura et al 2018).

As another measure to mitigate logging impacts, the effects of small clear-cuttings on biodiversity have also been studied. Koivula (2002) showed that the abundances of habitat generalists of carabid beetles were low in small clear-cut areas compared to large clear-cut areas as well as unharvested forests. Ito et al. (2006) showed that strip-cutting (a series of narrow clear-cuts) was more effective in conserving plant species of natural forests than clear-cutting. In the REFRESH, both small-sized clear-cuttings and whole stand clear-cuttings were installed to determine whether small-sized clear-cuttings mitigated the logging impacts compared to standard clear-cuttings (Akashi et al 2017; Ozaki et al. 2018; Yamaura et al 2018). Currently, a variety of investigations, including not only biodiversity but also the commercial values of timber and river water conditions, have been performed in and around the stands of the REFRESH site (Yamaura et al 2018).

Necrophagous silphid beetles (Silphidae) and dung beetles (coprophagous group of Scarabaeoidea: Troidae, Geotrupidae, and a part of Scarabaeidae (Scarabaeinae) in this study) clearly respond to forest habitat quality (Ohkawara et al. 1998; Gibbs and Stanton 2001; Davis et al. 2001) and are treated as useful indicators of forest conditions such as tree species, forest age, and tree density (Suzuki 2005; Gardner et al. 2008; Nichols and Gardner 2011). It is also known that studies of necrophagous silphid and dung beetles are generally low cost because of the large collection of beetles by using carrion-baited pitfall traps. Setting only one trap per stand enables the collection of all dominant species in the stand, and the assemblage data are sufficient to compare stands because the trap catches are almost identical in a stand (Nichols and Gardner 2011; Ueda 2015).

Necrophagous silphid and dung beetles perform important ecological functions, such as promoting the rapid decomposition of carcasses and influencing nutrient cycling, bioturbation, and plant growth enhancement (Barton et al. 2013). Amézqutta and Favila (2011) showed that a low biomass of necrophagous dung beetles led to a reduced rate of carrion removal. Moreover, beetles also exhibit ecological functions to control necrophagous flies because the flies are in the same food guild as the beetles (Wilson 1983). Gibbs and Stanton (2001) showed that a low abundance of silphid beetles increased the abundance of muscoid flies.

As mentioned above, necrophagous silphid and dung beetles are highly sensitive indicators, low cost for study materials, and have important ecological functions. However, no studies on necrophagous silphid and dung beetle assemblages associated with retention forestry and small clear-cuttings have been performed. The purpose of this study was to evaluate the impact of logging practices in conifer plantation forests, including logging for dispersed retention, aggregated retention, small-sized clear-cutting, and whole clear-cutting, on necrophagous silphid and dung beetle assemblages in the REFRESH. We especially focused on whether logging for retention forestry and small-sized clear-cutting mitigated the impacts on beetle diversity compared to those of whole clear-cutting. For the evaluation, 1) we addressed the dominant beetle species to forest species and open-land species. 2) We tested the significance of relationships between the trunk basal area and the beetle assemblages in the dispersed retentions to understand the effects of dispersed retention. 3) We showed the beetle assemblages inside and outside the unharvested forest patch in the aggregated retentions in comparison with the unharvested stands and the whole clear-cuts to estimate the effects of aggregated retention. 4) We compared the beetle assemblages between the small-sized clear-cuts and the whole clear-cuts to understand the effects of small-sized clear-cuttings. Then, 5) we discussed whether retention forestry and small-sized clear-cuttings mitigate the logging impacts on beetle diversity.

Materials and Methods

Study site: This study was conducted at the REFRESH project sites located on the east and south slopes of Mt. Irumukeppu (864 m asl.), Sorachi District, Central Hokkaido, Northern Japan (43°34'37"-39'26"N, 142°05'27"-09'33"E) (Akashi et al 2017; Yamaura et al 2018). The study sites were 3 natural broad-leaved tree forest stands (NC) dominated by linden (*Tilia japonica*), mono maple (*Acer pictum*), and Mongolian oak (*Quercus crispula*) and 20 mature Sakhalin fir, *Abies sachalinensis*, plantation forest stands that were 56 years old on average (range 48-72 years) in 2014 (Akashi et al 2017; Yamaura et al 2018). The stands had edge-to-edge distances of more than 150 m from each other

(Akashi et al 2017; Yamaura et al 2018). The first set of 5 types of logging operations was conducted in spring-summer in 2014 at the different plantation stands, and the second and third sets of the 5 types of logging operations were conducted in 2015 and 2016, respectively (5 types × 3 replicates = 15 plantation stands) (Table 1). The 5 types of logging operations were as follows: 1) large-amount dispersed retention (SL): ca. one hundred broad-leaved trees that naturally regenerated in the plantation per ha were retained, 2) middle-amount dispersed retention (SM): ca. fifty broad-leaved trees per ha were retained, 3) small-amount dispersed retention (SS): ca. ten broad-leaved trees per ha were retained, 4) aggregated retention (GR): a 0.36 ha (60×60 m) unharvested forest patch was retained at the centre of the stand, and 5) whole clear-cutting (CC): no trees were retained (Table 1). Three and two quadrilateral small-sized (ca 1-ha) clear-cuttings (SC) were conducted in another 9.24 and 7.83 ha plantation stands in 2015 and 2016, respectively (5 replicates) (Table 1). The small clear-cuts had edge-to-edge distances of more than 10 m from each other. Sakhalin fir saplings were planted in spring the year following logging operations in the harvested areas. Three residual stands of the 20 fir plantations were used as unharvested controls (PC) (Table 1).

Field trapping: Two baited pitfall traps were set more than 50 m inside from the stand edge at each site except for the aggregated retention stands (GR) and the small clear-cutting sites (SC). These two traps were set more than 50 m apart from each other to prevent trap interference (Larsen and Forsyth 2005). In the GR stand, one trap was set near the centre of the 0.36 ha unharvested patch (GRR), and another 2 traps were set in the clear-cut area (GRC) more than 50 m apart from the edge of the unharvested patch (Table 1). At the SC site, one trap was set near the centre (Table 1). Each trap was set on 13-15 June 2017 (Table 1, Fig. 1). The trap frames were the same as those in Ueda et al. (2016) and Ueda (2020); a 20-cm-long grey vinyl chloride pipe was driven into the ground with the opening 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 side (50 mm from the top) was used as the trap and inserted into the pipe; the trap contained 100 ml propylene glycol and a small plastic cup (42 mm in open diameter and 35 mm high) were fixed with steel wire on its upper lip. Another small plastic cup containing 15 g meat of mackerel (*Scomber* spp.) with a perforated lid (having 25 holes, each 1 mm in diameter) was inserted into the suspended cup, and a steel rack (405×250 mm, 30-mm high) was laid over the trap to make slits for the beetles to enter. The steel rack was weighed down with a concrete block (390×190 mm, 120-mm high, 11.3 kg) to prevent rainwater and animals from disturbing the traps. Beetle collection and replacements of propylene glycol and bait were performed on 10-13 July, 8-10 August, and 1-4 September. Trapping was finished on 2-3 October (Table 1). The trapping period was 110 or 111 days in total for each trap (Table 1).

Investigation of site conditions: We used modified data on tree density, broad-leaved tree density, basal area (BA) of tree trunks, and BA of broad-leaved trees measured by Akashi et al. (2017), who measured the diameters at breast height (DBH) of tree trunks and identified tree species with DBHs above 5 cm. Since heavy wind throw occurred at the unharvested forest patch in the aggregated retention site of the third set (GRR3) before this study, we measured the DBH of trees above 5 cm in DBH in the 10×10 m plot on the trapping site on 28 August 2017. We determined the rate of vegetation ground cover in circles with a diameter of approximately 2 m surrounding each trap site on 28-31 August 2017. Degrees of ground cover were categorized as follows: 0: no vegetation, 0.5: covered less than approximately 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). Data of site conditions are shown in Table 1.

Identification and storage of specimens and calculation of beetle biomass: All 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 beetles are stored at the Hokkaido Research Center, Forestry and Forest Products Research Institute. Since it is known that the biomass of necrophagous dung beetles is consistent with the extent of carrion removal (Amézquita and Favila 2011), we calculated the total biomass of trapped beetles to estimate their ecological functions. To obtain biomass data for the beetles collected in each trap, beetles of each species were dried for three days at 70°C and 4 additional days at 80°C. Almost all specimens (i.e., unbroken specimens) were weighed for 9 minor species for which fewer than 17 individuals were collected (Appendix table 1). For 7 dominant species for which more than 164 individuals were collected (Appendix table 1), we weighed the beetles in two ways along with the numbers of beetles collected in a collection period. If more than 234 individuals in a collection period were collected, we randomly selected more than 100 specimens (102-137 specimens) in every collection period and weighed them. If fewer than 234 specimens (actually fewer than 91 individuals (Appendix table 1)) were collected in a collection period, almost all specimens were weighed. The biomass of minor species collected per trap was calculated from the products of the number of individuals collected and the mean dry weight of all seasons. The biomass of dominant species collected per trap was calculated from the accumulated weight of each collection period in considering the seasonal changes in beetle body weights. The weight of each collection period was calculated from the products of the numbers of individuals collected in the respective collection periods and the mean dry weights in the periods.

Data analysis: To collect data from one site, we applied the mean values of beetle capture data where two traps were set. To understand whether retention forestry and small clear-cutting mitigate the logging impacts, we need to evaluate the abundances divided into forest species and open-land species. However, there were no adequate references for the habitat preferences of necrophagous silphid and dung beetles in Japan. Then, we decided the habitat preferences of the dominant species in this study from the collection data of whole harvested stands and unharvested stands. It is known that some species prefer dense or sparse vegetation ground cover irrespective of the different light environments, such as in forests or grasslands (Ueda and Sato 2010). We illustrated the relationships among the trunk basal area, the level of vegetation ground cover, and the number of beetles captured. We addressed the species apparently abundant in unharvested stands to ‘forest species’ and those abundant in harvested stands to ‘open-land species’.

To illustrate the differences in beetle assemblages among sites, nonmetric multidimensional scaling (NMS) was used for the ordination of the species composition at each site to analyse the similarities among the site categories. Sorensen distance was used for the analysis. First, we analysed 6 axes and 10 runs using the autopilot system of the software to determine the appropriate dimension numbers. Next, we analysed the recommended numbers of axes and 1 run. Multivariate response permutation procedures (MRPPs) were applied to evaluate the effects of the categories on beetle assemblages. In this analysis, when the chance-corrected within-group agreement (*A*) is unity, all assemblages in the respective groups are identical, and if *A* is larger than 0.3, the identical level is fairly high, and the grouping is sufficiently reliable (McCune and Grace 2002). PC-ORD ver. 6.07 (MJM Software Design 2011) was used for these analyses.

To understand the effects of dispersed retention, we analysed the relationships between retention revels and beetle assemblages using data from dispersed retentions and whole clear-cuts. We used the trunk basal area as the explanatory variable and treated the year of harvest as the explanatory variable; the year of harvest could not be treated as a random effect because there were only three levels in this data set. We used the total abundances of all species, forest species, and each dominant species, species richness, and biomass for each site as objective variables. A linear model (LM) was used for biomass.

A generalized linear model (GLM) with negative binomial error structures linked with the logarithmic function was used for the other variables. We used the number of valid traps of each site as an offset term in the analyses.

To understand the effects of aggregated retention, we illustrated the total abundances of all species and forest species, species richness, and biomass along with the trunk basal area for the sites inside and outside of the 0.36 ha unharvested patch, in the unharvested plantations, and in the whole clear-cuts. We could not perform any statistical analyses for the effects of aggregated retention because of the short numbers of replicates. Then, we estimated the effects of aggregated retention from the figures.

To understand the effects of small-sized clear-cuttings, we compared the beetle assemblage data between the small clear-cuts and the whole clear-cuts. We used site categories and the year of harvest as explanatory variables. The objective variables, the models used, and the offset term were the same as the analyses for dispersed retention.

For these analyses, the glm.nb function of the MASS package (Venables and Ripley 2002) and the lm function were used in R 4.1.1 (R Core Team 2021).

Results

Since one of the two trap sets was broken by animals at SM3 and GRC2, data from these traps were deleted from analyses (Table 1). In total, 16 species and 21,579 individuals of necrophagous silphid and dung beetle were collected (Appendix tables 1 and 2). The most abundant species, *Onthophagus ater*, was addressed to the open-land species because of the apparent low collections in the unharvested stands (Fig. 2a). *Nicrophorus quadripunctatus*, *Geotrupes laevistriatus, Nicrophorus investigator*, and *Nicrophorus tenipes* were addressed to the forest species because of the apparent high collections in the unharvested stands (Fig. 2b, d, e, and g). In these forest species, *G. laevistriatus* was especially abundant in the natural brad-leaved forests (Fig. 2d). No species showed a clear response to the levels of vegetation ground cover (Fig. 2).

The NMS analysis of the beetle assemblages recommended a two-dimensional solution, and the value of final stress (= 8.3%) from the analysis using 2 axes and 1 run indicated that the result was sufficiently reliable. The MRPP results (A = 0.224, P = 0.0005) indicated that categorization was reliable and that categories were moderately separated overall. The coordinates were largely separated into unharvested stands and harvested stands along axis 1, which had a high contribution rate (Fig. 3).

In the analyses of the effects of dispersed retention, the total abundance, total biomass, and total abundance of forest species were significantly and positively related to trunk basal area (Table 2, Fig 4). The abundances of two forest species, *N. quadripunctutus* and *G. laevistriatus,* were also significantly and positively related to trunk basal area (Table 2; additionally, refer to the circle sizes of the harvested stands in Fig. 2b and d). The total abundance of forest species and the abundance of

N. quadripunctatus were significantly and negatively related to both 2015 and 2016, but the p values for the years were larger than those for the trunk basal area (Table 2). Species richness and the abundances of an open-land species, *O. ater*, and of two forest species, *N. investigator* and *N. tenuipes*, did not significantly relate to any variables (Table 2, Additionally, refer the circle sizes of the harvested stands in Fig. 2a, e and g).

In the figures for the effects of aggregated retention, total abundance did not clearly differ among site categories (Fig. 5a). Species richness, total biomass, and total abundance of forest species were high at the sites in the unharvested plantations but did not differ among the sites in and outside the unharvested patch and the sites in the whole clear-cuts (Fig. 5b, c, and d). The abundance of an open-land species, *O. ater*, did not differ among sites except for the unharvested plantation sites where this species had low abundances at two of the three sites (Fig 5e).

In the analyses of the effects of small-sized clear-cutting, the total abundance of forest species was significantly and negatively related to whole clear-cutting (Table 3, Fig 6). No significant relationships occurred in the analyses for the effects of small-sized clear-cutting other than this (Table 3).

Discussion

Mitigation of logging impacts by retention forestry

Different coordinates of the NMS analysis between unharvested stands and harvested stands indicated that logging operations strongly affected necrophagous silphid and dung beetle assemblages. This was supported by the MRPP results, which showed relatively identical beetle assemblages in each site category and significant differences among the site categories. However, the results on the forest species in this study indicated that dispersed retention mitigated the logging impacts for the forest species. This was identical to the result on the carabid beetle assemblages conducted at the same sites as this study (Yamanaka et al. 2021) and the results on most organism groups (Fedrowitz et al. 2014). The results for the open-land species in this study indicated that dispersed retention did not affect its abundance. This was not identical to the result on the carabid beetle assemblages conducted at the same sites as this study (Yamanaka et al. 2021) and the results on most organism groups (Fedrowitz et al. 2014). The levels of dispersed retention in this study might have been too low to reveal a decrease in the open-land species. Further study needs to be conducted at higher levels of dispersed retention to clarify this. The increased abundances of forest species and no increase or decrease in the open-land species along the trunk basal area resulted in significant increases in the total abundance of all species and the total biomass in this study. The significantly lower abundances of the total forest species and *N. quadripunctatus* at the site logged in both 2015 and 2016 than in 2014 is notable because this result suggests the rapid recovery of the forest species in the harvested area. Periods needed for recovering forest species depend on species or groups (Magura et al. 2015). The continued study at the same sites of this study will clarify whether the forest species increase in the harvested area year by year.

The 0.36 ha unharvested forest patch in the aggregated retention was thought not to act as a lifeboat for forest species in this study because the assemblages were almost identical to those outside the forest patch and those in the whole clear-cuts. On carabid beetles, the 0.36 ha unharvested forest patch clearly acted as a life-boat for forest species (Yamanaka et al. 2021). Similar results were found on carabid beetles in other studies (Baker et al. 2009; Work et al. 2010; Baker et al. 2016; Wu et al. 2019). These results largely differed from our results on necrophagous silphid and dung beetle assemblages. Three of the four forest species in this study belong to the genus *Nicrophorus,* which flies well and needs a large foraging area in which search for patchy distributed resources such as the dead bodies of small vertebrates (Creighton and Schnell 1988; Attisano and Kilner 2015). The unharvested patch was too small to maintain the population of forest *Nicrophorus,* and its surrounding clear-cut area limited the migration of the beetles lured by the bait odour of the trap to reach the unharvested patch. In contrast, many forest dowelling species or individuals of carabid beetles are brachypterous, which leads to their populations remaining in relatively small habitats (Boer 1970; Koivula et al. 2004). Another forest species in this study, *G. laevistriatus*, is known to be flightless in Hokkaido (Suzuki et al. 2001), but this species was originally present at low abundance in conifer plantations. Since the open-land species *O. ater* were abundant in the unharvested forest patches as well as outside the patches and the whole clear-cuts, the unharvested forest patch may have not influenced this species. The same abundances of open-land species between in- and outside the unharvested forest patches were also observed on carabid beetles (Yamanaka et al. 2021).

Mitigation of logging impacts by small-sized clear-cutting

No difference in each forest species between small-sized clear-cuttings (ca 1-ha) and whole clear-cuttings (> 6 ha) indicated that the small-sized clear-cuttings did not mitigate the logging impacts on each species level. However, the significant difference in the total abundance of forest species suggests that the small-sized clear-cuttings weakly mitigate the logging impacts for the forest species in total. Ueda and Sato (2020) utilized the same traps used in this study and collected necrophagous silphid and dung beetles at the centres of 30×30 m (0.09 ha) and 100×80 m (0.8 ha) clear-cuttings that were surrounded by 40-year-old conifer plantations in Sapporo. They showed that the beetle assemblage in the 0.09 ha area was the same as that of conifer plantations but that in the 0.8 ha area was the same as that of the nearby grassland. Ueda (2020) also showed that the beetle assemblage on the centre line of 20-m wide strip-cuts in a conifer plantation resembled those ca. 20-year-old natural forests and differed from those in the other open-lands used as the log yards. Since the beetle assemblages in the small clear-cuts in this study clearly differed from those in unharvested stands, the size of the small clear-cut in this study was too large for almost all beetles of the forest species to be lured to the centre of the unfavourable open-land. However, a few beetles of forest species reached the centre and this made the small clear-cut in this study weakly mitigate the logging impacts compared to the whole clear-cut. Since the open-land species *O. ater* did not differ in abundance between the small clear-cuts and the whole clear-cuts, the small-sized clear-cuttings may have not influenced this species. An open-land species in Kyushu, southern Japan, *Onthophagus nitidus*, was more abundant in the centre line of 20 m-wide strip-cuts than in the other open-lands used as log yards (Ueda 2020), suggesting that this open-land species prefers small open-lands to large ones. Further studies in a variety of sizes of clear-cuttings will clarify the area-dependent effects on the logging impacts for necrophagous silphid and dung beetle assemblages.

Habitat preferences of the beetles

N. quadripunctatus has been identified as a forest species in many studies (Katakura and Fukuda 1974; Katakura and Ueno 1985; Katakura et al. 1985; Ohkawara et al. 1998; Nagano and Suzuki 2003; Sugiura et al. 2012; Ueda 2016) as well as in this study. *N. tenuipes* was also identified as a forest species in a study (Katakura and Fukuda 1974) as well as in this study. These two species must be the forest species. Although *N. investigator* was identified as a forest species in this study, Katakura and Fukuda (1974) showed that *N. investigator* was abundant in both forests and open-lands in northern Hokkaido. Moreover, Wilhelm et al. (2001) showed that *N. investigator* preferred open-lands to forests on Great Island, Canada. *N. investigator* may prefer forests in warm regions such as the sites of this study, central Hokkaido, and change to open-land habitat in cold weather. Conversely, although *O. ater* was identified as an open-land species in this study, *O. ater* was abundant in both forests and open-lands in Sapporo, lowland of central Hokkaido (Ueda and Sato 2020). Moreover, *O. ater* was identified as a forest species in Kyushu, the southern island of Japan (Ueda 2016, 2020). *O. ater* may also prefer forests in warm regions and change to open-land habitat in cold weather, similar to the sites of this study. Further studies are needed to clarify the habitat preferences of these two species.

It is known that the seasonal segregation of *Nicrophorus* species that overlap in body size occurs (Wettlaufer et al. 2021). However, the typical forest species, *N. quadripunctatus*, decreases its activity in summer in warm regions, although there are no competitive *Nicrophorus* species that overlap body sizes with *N. quadripunctatus* (Nagano and Suzuki 2003; Ueda and Ohara 2018). This species may control its activity to endure the hot season in warm regions without habitat change. *G. laevistriatus* was remarkably abundant in the unharvested natural broad-leaved stands in this study, and this was also observed in Sapporo, Hokkaido (Ueda and Sato 2020). These results suggest that this species is an indicator species of natural broad-leaved forests in Hokkaido. However, the abundances of this species were not different between natural broad-leaved forests and conifer plantations in Kyushu (Ueda 2016, 2020). Further studies are needed to clarify the local differences in the habitat preference of this species.

Silpha perforate is known to prefer sites with high vegetation cover degrees irrespective of the light environment (Ueda and Sato 2020). Conversely, *Nicrophorus maculifrons* is known to prefer sites with low vegetation cover degrees irrespective of the light environment (Ueda and Sato 2020). Neither *S. perforate* nor *N. maculifrons* showed preferences for the light environments in this study nor in previous studies (Katakura and Fukuda 1974; Katakura and Ueno 1985; Katakura et al. 1985; Ueda and Sato 2020). However, these two species also did not show preferences for the vegetation cover degrees in this study. Some flightless forest carabid beetles are known not to decrease their abundances a few years after logging (Koivula 2002). Since *S. perforate* is flightless (Ikeda et al. 2007), the density of this species before logging may still strongly affect the abundances in this study irrespective of the vegetation ground cover. It is difficult to discuss the reason why *N. macurifrons* did not show a clear preference for low vegetation ground cover levels in this study.

Conclusion

In Japan, conifer plantations mature and become ready for harvesting in the large areas. To conserve forest ecosystems, harvesting methods that mitigate logging impacts need to be developed. Among harvesting methods, retention forestry and small-sized clear-cuttings are thought to partially mitigate logging impacts, and they were evaluated in mature Sakhalin fir plantation forests in Hokkaido, northern Japan, where a variety of logging operations have been conducted. We collected necrophagous silphid and dung beetles in logged stands, unharvested natural broad-leaved forests, and unharvested plantation forests using carrion-baited pitfall traps. All logging operations strongly affected the beetle assemblages. The beetle assemblages in the 0.36 ha unharvested forest patch under the aggregated retention stands were almost identical to those outside the unharvested forest patch and those in the whole clear-cuts. This result suggested that the unharvested forest patch did not act as refugia (lifeboat) for the forest species. However, the total biomass (dry weight) of beetles, the total abundance of forest species, and the abundances of two dominant forest species were significantly and positively related to the trunk basal area of retained trees in the dispersed retention stands. This result indicated that dispersed retention mitigated the logging impacts for forest species and the estimated ecological function of the beetles. The total abundance of forest species was significantly higher in the small clear-cuts than in the whole clear-cuts. This result showed that the small-sized clear-cuttings weakly mitigated the logging impacts. An open-land species, *O. ater*, was abundant in the harvested area irrespective of the amount of retained trees, the retained forest patch, and the size of the clear-cutting area. These results indicated that the retention forestry and the small clear-cuttings did not prevent this open-land species from entering the harvested area. Finally, we concluded that the dispersed retentions and the small-sized clear-cuttings are more useful harvesting methods for conserving forest species of necrophagous silphid and dung beetles than whole clear-cuttings and for preserving the habitats of open-land species as well as whole clear-cuttings.

O. ater and *N. investigator* were identified as open-land species and forest species, respectively, in this study, but these species may change their habitats along with longitudinal and/or altitudinal temperature changes.

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Authors contributions AU conceived the ideas and designed the methodology; AU and SS collected the data; AU and HI analysed the data; AU wrote the manuscript; all authors contributed critically to the drafts and gave final approval for publication.

Ethical standards

Conflict of interest The authors declare no conflicts of interest.

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Figure legends

Fig. 1 Photos of traps set at NC1 (photo A), PC1 (B), SL3 (C), SM3 (D), SS1 (E), GRR2 (F), GRC2 (G), SC3-1 (H), and CC2 (I). All photos were taken on 13-15 June, 2017. Refer to Table 1 for site names.

Fig. 2 Relationships among the abundances of dominant beetle species, the trunk basal area, and rank of vegetation ground cover in the whole harvested stands and the unharvested stands. Open circle: whole harvested stand, grey circle: unharvested natural broad-leaved forest, and closed circle: unharvested fir plantation forest. (O): species categorized as open-land species, (F): species categorized as forest species.

Fig. 3 Results of NMS analysis as applied to ordinate sites with similarities of necrophagous silphid and dung beetle assemblages

Final stress = 8.3%. Abbreviations of site categories are defined in Table 1. Parenthesized % on titles of axes indicate the proportion of variance represented by each axis, based on the r^2 between the distance in the ordination space and the distance in the original space.

Fig. 4 Relationships between trunk basal area and total abundance (a), total biomass (b), and total abundance of forest species (c) in the dispersed retention sites and the whole clear-cuts.

Fig. 5 Relationships between trunk basal area and total abundance (a), species richness (b), total biomass (c), total abundance of forest species (d), and an open-land species, *Onthophagus ater* (e), in the unharvested fir plantation forest (closed circle), inside the 0.36 ha unharvested forest patch in aggregated retention (open circle), outside the unharvested forest patch in aggregated retention (closed triangle), and in the whole clear-cut (open triangle).

Fig. 6 Total abundance of forest species in small clear-cuts and whole clear-cuts

Titles and footnotes of tables

Table 1 Characteristics of study sites, environmental variables used for analyses, number of traps set, and trapping period

BLT means broad-leaved tree

a Referred Akashi et al. (2017) except for GRR3, where windthrow had occurred before beginning.

b Mean of each trap site. The vegetation ground covers were observed on 28-31 Aug. 2017.

c Result from the trees in a 10×10 m plot in which the centre was a trapping site measured on 28 Aug. 2017.

d Two traps were set, but one trap was broken by animals.

Table 2 Results of analyses for the effects of dispersed retention

O: open-land species, F: forest species. nb means negative binomial distribution. t value was used for normal distribution.

Table 3 Results of analyses for the effects of small clear-cutting

O: open-land species, F: forest species. nb means negative binomial distribution. t value was used for normal distribution.

Appendix table 1 Number of beetles captured in each collection period

Appendix table 2 Number of beetles captured in each trap

Table 1 Characteristics of study sites, environmental variables used for analyses, number of traps set, and trapping period

Site	Site name	Site No.	Area (ha)	Year of harvest	Tree density[a] (n/ha)	BLT density[a] (n/ha)	Basal area[a] (m^2/ha)	BLT basal area[a] (m^2/ha)	Vegetation ground cover[b] (index 0-5)	No. traps set	Trapping period in 2017 (days)
Unharvested natural broad-leaved tree (BLT) forest	NC	1	4.96	-	994	994	51.68	51.68	3.0	2	15 Jun - 3 Oct (110)
		2	5.55	-	787	756	36.75	34.91	2.5	2	13 Jun - 2 Oct (111)
		3	6.61	-	825	744	28.47	19.42	1.5	2	14 Jun - 2 Oct (110)
Unharvested Sakhalin fir plantation forest (ca 50 years old)	PC	1	5.87	-	868	239	39.91	3.99	4.0	2	15 Jun - 3 Oct (110)
		2	7.63	-	964	175	41.68	3.92	2.5	2	14 Jun - 3 Oct (111)
		3	6.26	-	700	136	35.88	2.92	2.5	2	14 Jun - 2 Oct (110)
Dispersed retention-cutting with large-amount of BLT (ca 100 trees/ha)	SL	1	7.94	2014	103	103	5.79	5.79	4.5	2	15 Jun - 3 Oct (110)
		2	7.92	2015	109	109	7.50	7.50	3.0	2	14 Jun - 3 Oct (111)
		3	6.99	2016	107	107	7.37	7.37	2.0	2	15 Jun - 3 Oct (110)
Dispersed retention-cutting with middle-amount of BLT (ca 50 trees/ha)	SM	1	7.85	2014	51	51	3.76	3.76	4.0	2	15 Jun - 3 Oct (110)
		2	7.10	2015	60	60	2.17	2.17	4.5	2	13 Jun - 2 Oct (111)
		3	7.72	2016	57	57	4.26	4.26	4.0	1[d]	15 Jun - 3 Oct (110)
Dispersed retention-cutting with small-amount of BLT (ca 10 trees/ha)	SS	1	6.30	2014	11	11	0.59	0.59	3.0	2	15 Jun - 3 Oct (110)
		2	7.49	2015	13	13	0.75	0.75	5.0	2	13 Jun - 2 Oct (111)
		3	5.76	2016	10	10	0.46	0.46	3.5	2	13 Jun - 2 Oct (111)
60×60 m unharvested patch of aggregated retention-cutting	GRR	1	0.36	-	833	47	49.16	1.32	1.0	1	15 Jun - 3 Oct (110)
		2	0.36	-	661	36	48.92	1.60	3.0	1	13 Jun - 2 Oct (111)
		3	0.36	-	100[c]	0[c]	1.19[c]	0[c]	5.0	1	14 Jun - 2 Oct (110)
Clear-cutting area of aggregated retention-cutting	GRC	1	6.42	2014	0	0	0	0	4.0	2	15 Jun - 3 Oct (110)
		2	7.87	2015	0	0	0	0	3.0	1[d]	13 Jun - 2 Oct (111)
		3	6.03	2016	0	0	0	0	3.0	2	14 Jun - 2 Oct (110)
Quadrilateral small-sized (ca 1-ha) clear-cutting	SC	2-1, 2, 3	1.00×3	2015	0	0	0	0	4.0	1×3	14 Jun - 2 Oct (110)
		3-1, 2	1.00×2	2016	0	0	0	0	3.0	1×2	13 Jun - 2 Oct (111)
Whole clear-cutting	CC	1	6.89	2014	0	0	0	0	5.0	2	14 Jun - 3 Oct (111)
		2	7.87	2015	0	0	0	0	4.5	2	13 Jun - 2 Oct (111)
		3	6.17	2016	0	0	0	0	3.5	2	14 Jun - 2 Oct (110)

BLT means broad-leaved tree

[a] Referred Akashi et al. (2017) except for GRR3, where windthrow had occurred before beginning.

[b] Mean of each trap site. The vegetation ground covers were observed on 28-31 Aug. 2017.

[c] Result from the trees in a 10×10 m plot in which the centre was a trapping site measured on 28 Aug. 2017.

[d] Two traps were set but one trap was broken by animals.

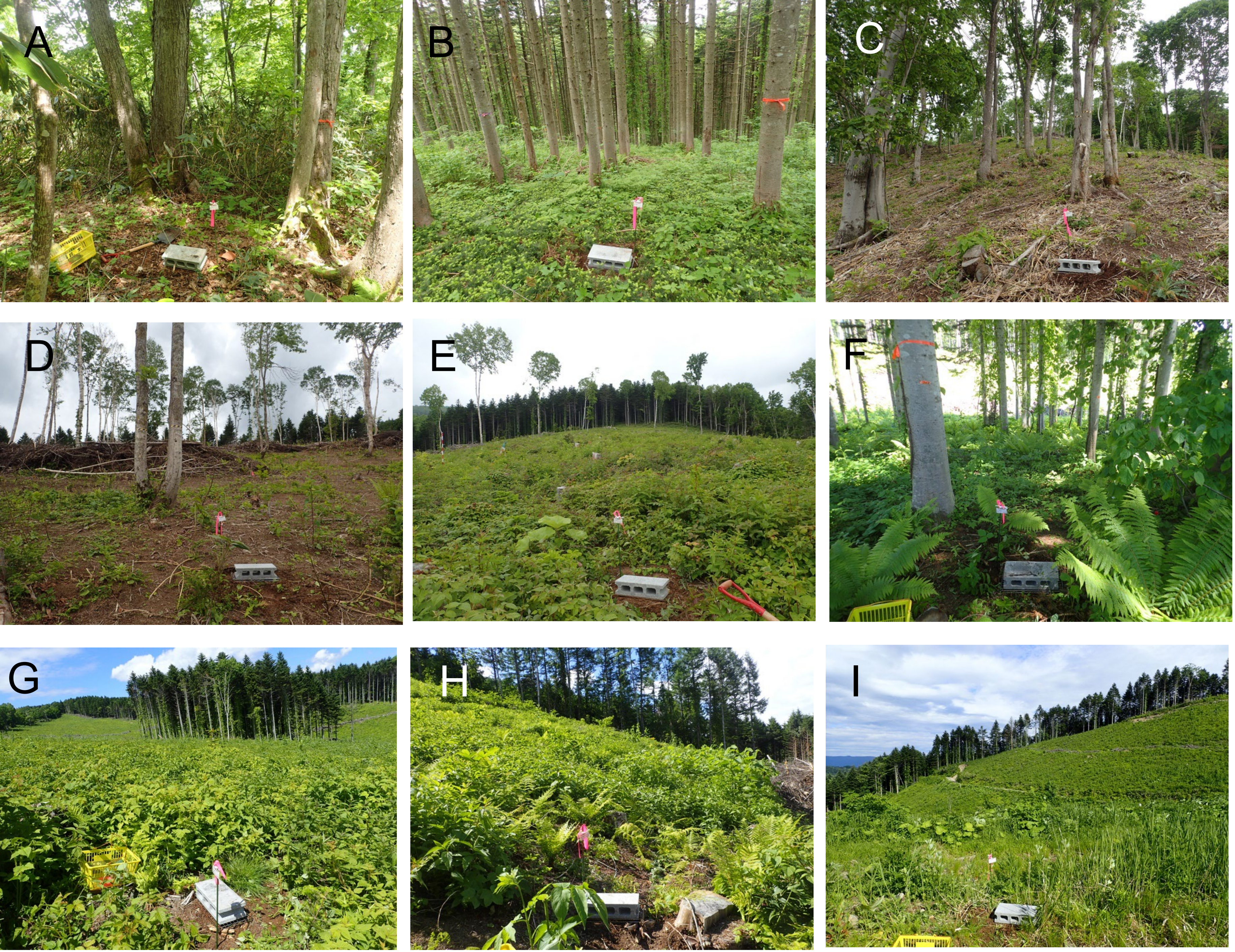
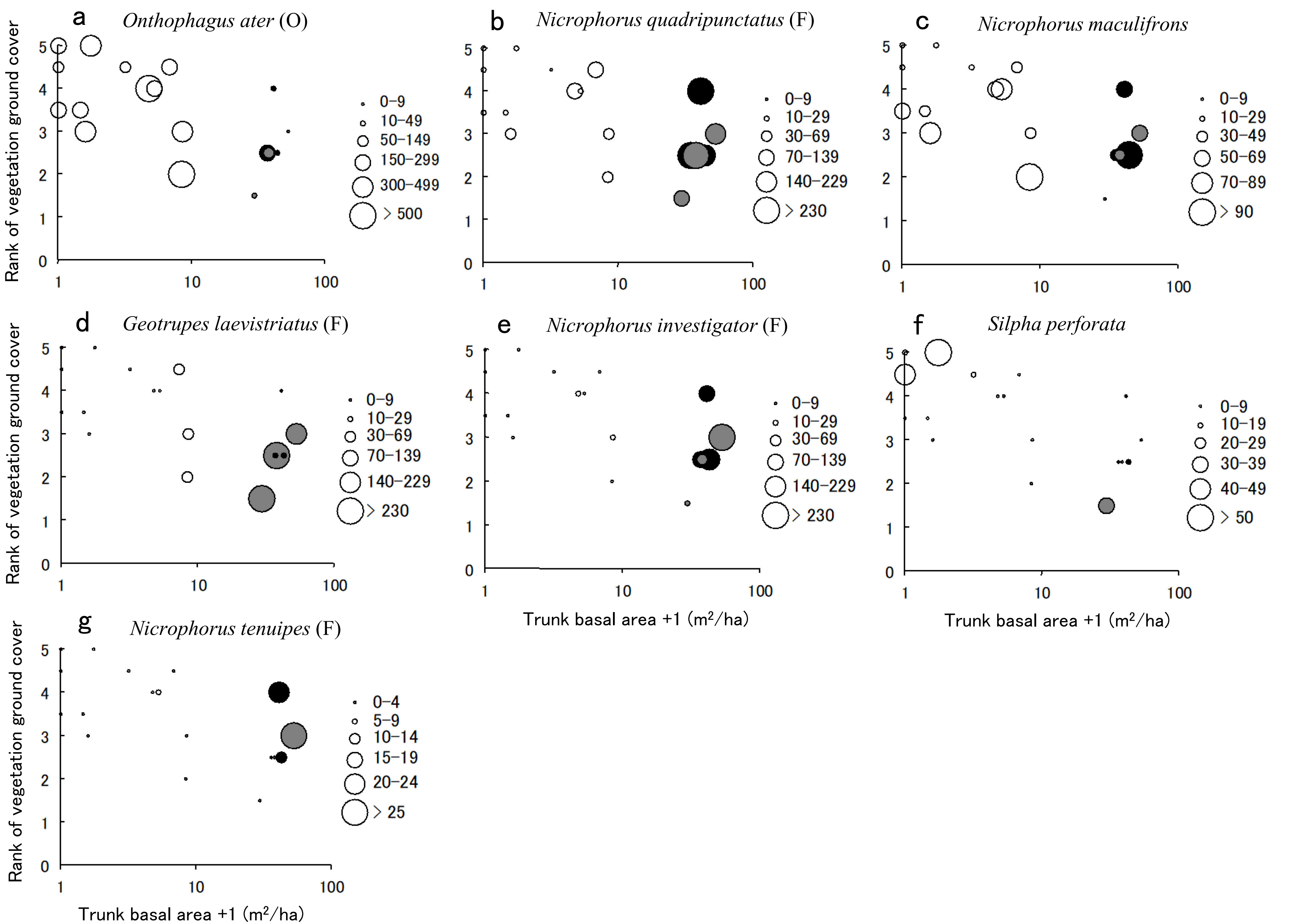


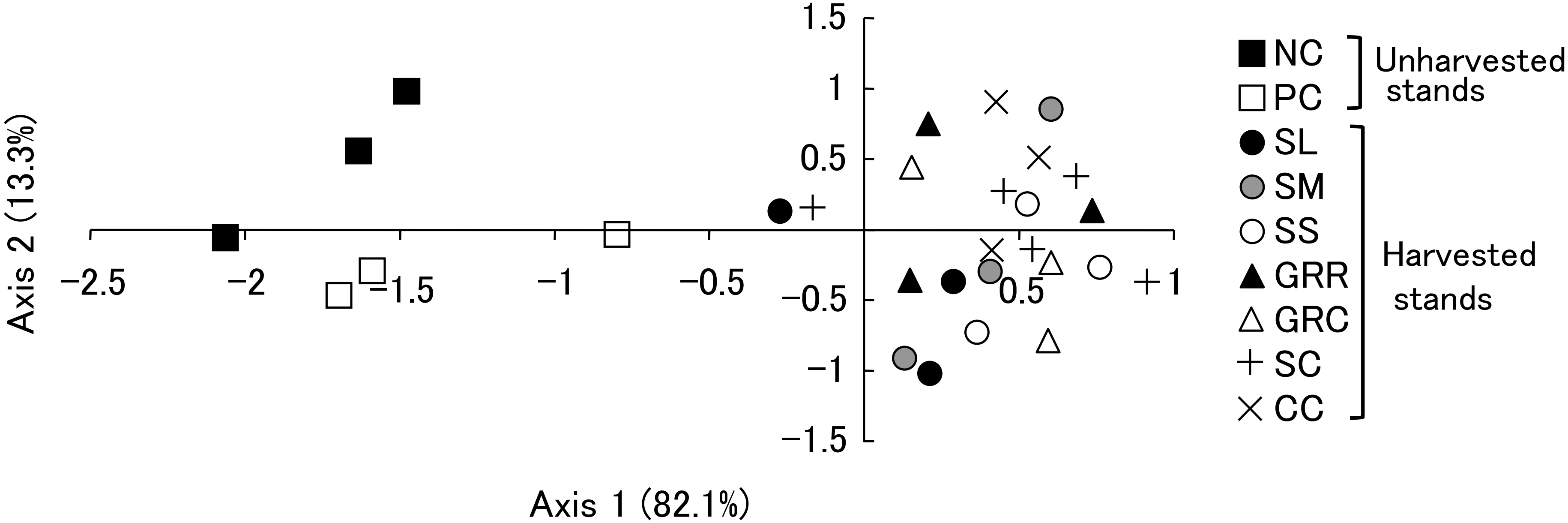
Figure 1

Figure 2



a
Onthophagus ater (O)
b
Nicrophorus quadripunctatus (F)
c
Nicrophorus maculifrons
d
Geotrupes laevistriatus (F)
e
Nicrophorus investigator (F)
f
Silpha perforata
g
Nicrophorus tenuipes (F)
Rank of vegetation ground cover
Trunk basal area +1 (m2/ha)
0-9
10-49
50-149
150-299
300-499
> 500
0-9
10-29
30-69
70-139
140-229
> 230
0-9
10-29
30-49
50-69
70-89
> 90
0-9
10-19
20-29
30-39
40-49
> 50
0-4
5-9
10-14
15-19
20-24
> 25

Figure 3



1.5
1
0.5
−0.5
−1
−1.5
−2.5
−2
−1.5
−1
−0.5
0.5
1
Axis 2 (13.3%)
Axis 1 (82.1%)
NC
PC
Unharvested stands
SL
SM
SS
GRR
GRC
SC
CC
Harvested stands

Figure 4

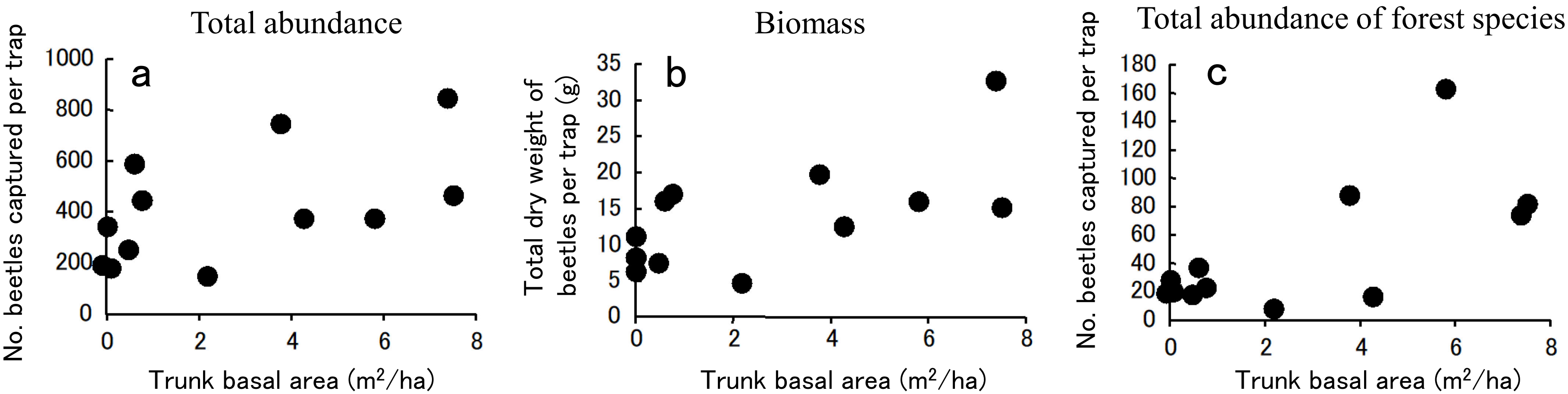
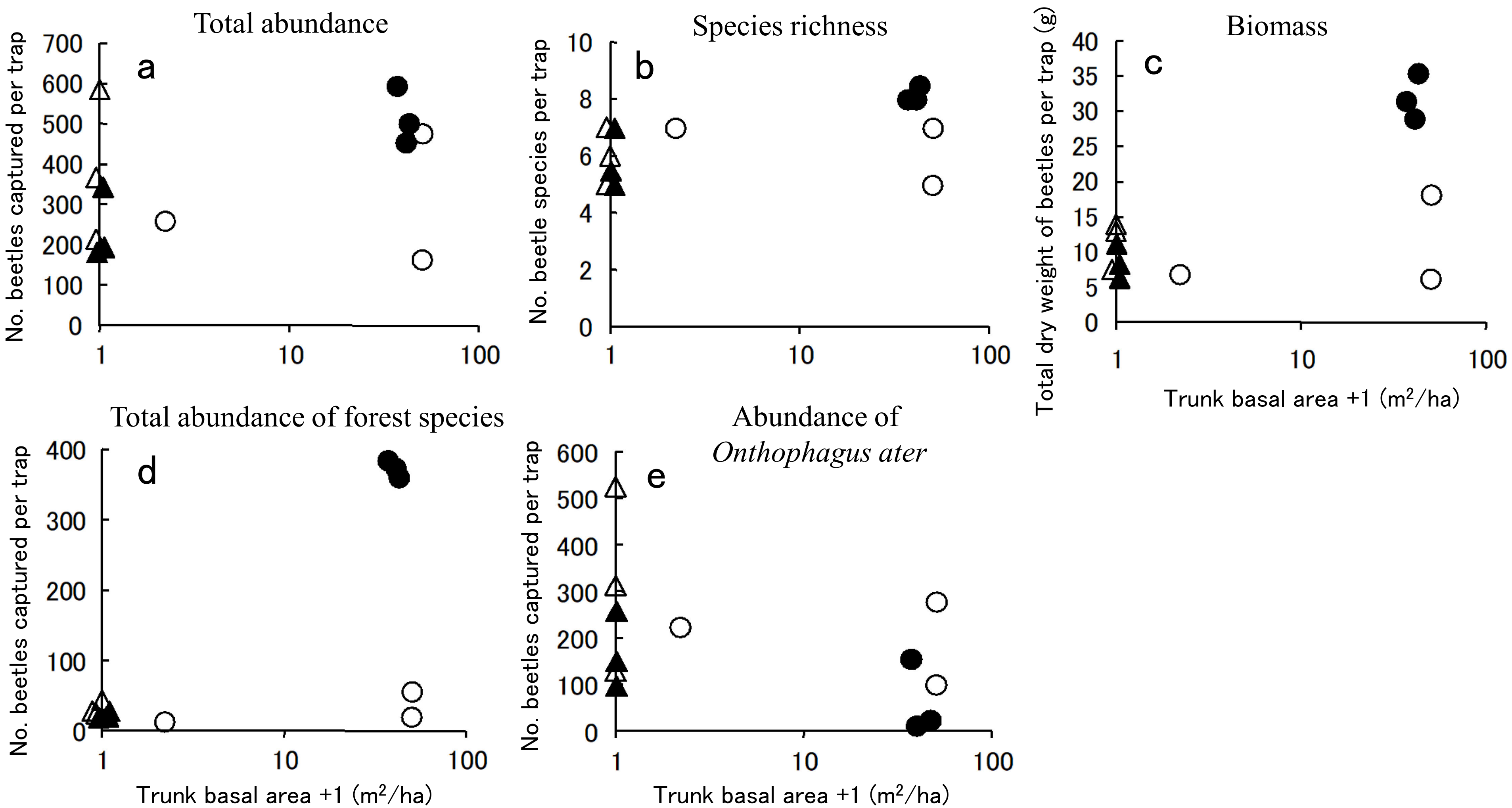
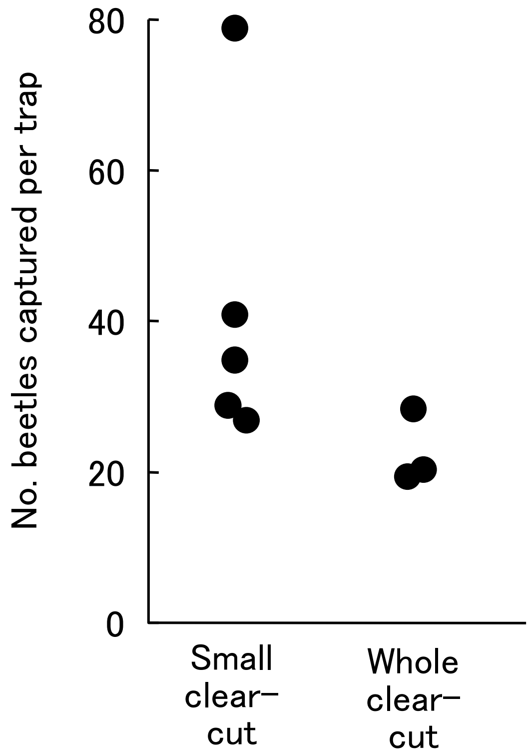

Total abundance
a
No. beetles captured per trap
1000
800
600
400
200
0
0
2
4
6
8
Trunk basal area (m2/ha)
Biomass
b
Total dry weight of beetles per trap (g)
35
30
25
20
15
10
5
0
0
2
4
6
8
Trunk basal area (m2/ha)
Total abundance of forest species
c
No. beetles captured per trap
180
160
140
120
100
80
60
40
20
0
0
2
4
6
8
Trunk basal area (m2/ha)

Figure 5



Total abundance
a
No. beetles captured per trap
700
600
500
400
300
200
100
0
1
10
100
Species richness
b
No. beetle species per trap
10
8
6
4
2
0
1
10
100
Biomass
c
Total dry weight of beetles per trap (g)
40
35
30
25
20
15
10
5
0
1
10
100
Trunk basal area +1 (m2/ha)
Total abundance of forest species
d
No. beetles captured per trap
400
300
200
100
0
1
10
100
Trunk basal area +1 (m2/ha)
Abundance of
Onthophagus ater
e
No. beetles captured per trap
600
500
400
300
200
100
0
1
10
100
Trunk basal area +1 (m2/ha)

Figure 6



No. beetles captured per trap
80
60
40
20
0
Small clear-cut
Whole clear-cut