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Degradation of longicorn beetle (Coleoptera, Cerambycidae, Disteniidae) fauna caused by conversion from broad-leaved to man-made conifer stands of *Cryptomeria japonica* (Taxodiaceae) in central Japan

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Abstract We studied the species richness and assemblages of longicorn beetles (Coleoptera, Cerambycidae, Disteniidae) in ten secondary broad-leaved stands and eight plantation stands of Japanese cedar (*Cryptomeria japonica*) of various ages after clear-cutting or plantation in Ibaraki, central Japan. The species richness of longicorns, which were collected with Malaise traps, was the highest in young stands, decreasing with the age of the stand for both broad-leaved and conifer stands. A canonical correspondence analysis divided the 18 plots into three groups based on longicorn assemblages and environmental variables. These three groups consisted of (1) very young (1–4 years old) stands after clear-cutting or plantation; (2) 12- to over 100 year-old broad-leaved stands; (3) 7- to 76-year-old conifer stands. The species richness of the longicorns was the highest in the young stands followed, in order of decreasing species richness, by broad-leaved stands and conifer stands. Possible causes of the high species richness in young stands include large amounts of coarse wood debris and flowers, which are resources for oviposition and nutrition for adults, respectively. The lower longicorn diversity in conifer stands than in broad-leaved stands may be due to the lower diversity of trees available as host plants in the former. Almost all species that occurred in conifer stands were also collected in young and/or broad-leaved stands, but the reverse was not true, suggesting that conifer plantations cannot replace broad-leaved stands in terms of longicorn biodiversity. We argue that an extensive conversion of broad-leaved forests into conifer plantations will lead to an impoverishment of the longicorn fauna, which may result in the degradation of ecosystem functions possibly carried out by them.

Keywords Biodiversity · Chronosequence · Forest · Insect · Plantation

Introduction

Forestry, a human activity, has affected the natural habitats of plants and animals in various ways. In particular, plantation forestry often has negative effects on the biodiversity of various organisms in many parts of the world because of structural and functional dissimilarities between the native and replacement forest (Palik and Engstrom 1999; Moore and Allen 1999). Warnings have been given on the need to be careful about the possible degradation of ecological functions as well as of biodiversity caused by intensive silviculture associated with plantation practices (Hartley 2002).

In Japan, one of the largest impacts on habitats by forestry has been the conversion from natural or secondary broad-leaved forests to plantations of conifers, mainly of Japanese cedar (*Cryptomeria japonica*) and hinoki cypress (*Chamaecyparis obtusa*). The area occupied by plantations of these two conifers was greatly increased after the Second World War to fulfill a high demand for timber and currently represents about 19% of the total forest area in Japan (Japan Agriculture Statistics Association 2001).

Japanese conifer plantations are principally monocultures composed of one of the above two conifer species. The establishment of monocultures at the expense of natural mixed-species stands are expected to reduce the biodiversity of forest-dependent organisms (e.g. Palik and Engstrom 1999). In fact, the overstorey vegetation of Japanese cedar stands is poorer in biodiversity than natural or secondary forests of a similar age (Tanaka et al., unpublished data). This may lead to the impoverishment of biodiversity or, at the very least, to changes in the assemblage of forest animals that directly or indirectly depend on plants. To test this hypothesis and to determine to what extent insect assemblages of

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conifer plantations diverge from those of broad-leaved forests, we need to monitor insects along chronosequences of both types of forests because arthropod species richness and assemblages generally change as forests grow (e.g. Buddle et al. 2000; Inoue 2003; Trofymow et al. 2003; Sueyoshi et al. 2003; Makino et al. 2006).

Although a number of studies have been published which compare species richness and assemblage of insects between Japanese cedar or hinoki cypress plantations and broad-leaved forests (e.g. Ohashi et al. 1992; Shibata et al. 1996; Mizota and Imasaka 1997; Maeto and Makihara 1999; Maeto et al. 2002; Maeto and Sato 2004; Sayama et al. 2005), the study plots of these studies consisted of only a few age classes of conifer stands. There is a scarcity of studies that have been conducted with the aim of comparing insect biodiversity between the two types of forests through their chronosequences. To this end, we conducted the present investigation in which we monitored longicorn beetles in both conifer plantations of Japanese cedar and secondary deciduous broad-leaved forests of a wide range of ages.

Longicorn beetles are typical forest-dependent insects because they almost exclusively feed on living, dying or dead trees in the larval stage (Linsley 1959, 1961; Hanks 1999). Saproxylous insects, including most longicorns, thus depend on dead wood and old trees, and they mediate or promote decomposition processes of microorganisms (Grove 2002). Additionally, many longicorn adults visit flowers to feed on nectar and/or pollen (e.g. Linsley 1959, 1961; Kuboki 1987); as such, they act as pollinators for some plant species (Kuboki 1998). These facts suggest that the functions possibly performed by longicorn beetles in forest ecosystems should not be overlooked. If their abundance and/or assemblages are greatly affected by the conversion of a broad-leaved forest to a conifer plantation, a loss or degradation of their functions may follow.

The aim of this study was, therefore, to determine the extent to which the conversion of broad-leaved forests into conifer plantations affects the species richness and assemblages of longicorns in central Japan, and how they respond to chronosequential changes in forest characteristics.

Materials and methods

Study areas

This study was conducted in two areas, Ogawa and Satomi, Ibaraki Prefecture, central Japan. Both areas have plantations of *Cryptomeria japonica* and *Chamaecypress obtusa*, although the percentage of plantation areas is much larger in Satomi than in Ogawa (94 vs. 47% of total forested area; Tanaka et al., unpublished data). Ogawa is located at the southern edge of the Abukuma Mountains in Kitaibaraki (approximately

36°56'N, 140°35'E; 580–800 m a.s.l.). The dominant large trees in deciduous broad-leaved forests in the area are *Quercus serrata*, *Q. mongolica* and *Fagus crenata*. Some areas of the broad-leaved forests in Ogawa have been subjected to human activities, such as burning, cattle grazing and clear-cutting for fuel wood (Suzuki 2002), and the small-scale clear-cutting of broad-leaved stands has been repeatedly carried out up to the present time to collect bed logs for mushroom culture. In addition, following the Second World War, the area converted from broad-leaved stands to conifer plantations greatly increased. These human practices have resulted in a mosaic-like landscape composed of secondary broad-leaved stands and conifer plantations of various ages. We selected ten plots in broad-leaved stands to obtain stands that formed a chronosequence from 1 to over 100 years old after clear-cutting (Table 1). All plots were located within an approximately 30-km² area. Satomi (approximately 36°50'N, 140°34'E; 700–800 m a.s.l.) is about 10 km southwest of the Ogawa area. We set eight plots of Japanese cedar plantations in an approximately 10-km² area in Satomi. The conifer plots also formed a chronosequence from 1 to 76 years old in age after plantation. In Ogawa, the annual mean temperature is 10.7°C and mean annual precipitation is 1910 mm (Mizoguchi et al. 2002).

Forest characteristics

In order to determine how forest characteristics affect longicorn assemblages, we carried out plant censuses in the above plots. We established a line transect at each plot from September 2000 to October 2003. Each transect line was 100 m long and was set to cover the entire variation of the forest. All trees and vines of at least 2 m in height and at least 5 cm in diameter at breast height (DBH) were counted, and their girth at breast height (GBH) was measured in a total of forty 5 × 5-m quadrats along both sides of the 100-m transect line mentioned above; the frequency of trees smaller than 5 cm in DBH in the 40 quadrats was also censused. Forest floor vegetation with a height of less than 2 m (forest floor plants) was censused following the Braun–Blanquet method for a 1 × 1-m subquadrat which was set in each 5 × 5-m quadrat.

Insect collection

We collected longicorn beetles with standard Towns-type Malaise traps (Golden Owl Publishers; 180 cm long, 120 cm wide, 200 cm high) in 2002 in Ogawa and 2003 in Satomi. The traps were placed inside the stand to avoid the edge effect, except in very young, grassland-like plots which had no tall trees. Trapped insects were collected every 2 weeks from late April to early November in both areas. A mixture of ethanol and propylene glycol was used as preservative in the insect

Table 1 Study plots and collection summary of longicorn beetles (Coleoptera, Cerambycidae, Disteniidae)

Site	Plot code	Age (year)	Area (ha)	Number of longicorn species	Number of longicorn individuals	1-D ^a
Ogawa	O1	1	3	52	329	0.946
	O4	4	5	43	339	0.852
	O12	12	4	38	145	0.923
	O24	24	24	39	150	0.941
	O51	51	10	30	144	0.870
	O54	54	14	27	109	0.928
	O71	71	19	33	153	0.935
	O128	> 100	98	34	119	0.939
	O174	> 100	11	27	106	0.933
	O178	> 100	10	35	149	0.930
Satomi	S3	3	4	40	357	0.677
	S7	7	6	24	142	0.840
	S9	9	5	27	55	0.968
	S20	20	5	16	29	0.951
	S29	29	14	18	61	0.922
	S31	31	12	27	93	0.916
	S75	75	3	19	57	0.933
	S76	76	3	12	24	0.935

^a Simpson's index of diversity (see section analyses of insect assemblages)

containers of the traps. The collected insects were morphologically identified to the species level. Longicorn samples from two traps, 10 m distant from each other, were used for each plot in the following analysis. All voucher specimens are deposited at the Forestry and Forest Products Research Institute.

Analyses of insect assemblages

Data of longicorn beetles were pooled for each plot throughout the season and analyzed for a comparison of species richness or assemblage among the plots. As an index of diversity, we calculated Simpson's index of diversity, which is the complement of D defined as follows (Magurran 2004):

$$D = \sum \frac{n_i(n_i - 1)}{N(N - 1)}$$

where N is the total number of individuals and n_i is the number of individuals of the i th species. In order to test differences in the number of longicorn species or individuals or in the diversity indices among stands or forest types, the analysis of variance (ANOVA) was carried out with SYSTAT ver. 9.01 for Windows (SPSS 1998) and STATISTICA for Windows (StatSoft Inc. 2000). If data were not normally distributed, they were log-transformed. Canonical correspondence analysis (CCA) was performed with CANOCO for Windows, ver. 4.5 (ter Braak and Smilauer 2002) to make an ordination analysis of longicorn assemblages among the plots and to relate environmental variables (see below) with the assemblages. Only those longicorn species with a total count of at least three individuals were used. As environmental variables for CCA, we used the following plant community indices: species richness of plants for three size classes (trees with DBH \geq 5 cm; trees with DBH < 5 cm; forest floor plants), the density of trees

with DBH \geq 5 cm and the maximum and average diameter of trees at breast height. In this analysis, the scores of the first and second axis in a detrended correspondence analysis (DCA) for the plant community group ordination for the three size classes were also used in order to investigate the effects of the composition of the plants species on communities of longicorn beetles. In the DCA of plant communities, species with at least three individuals in total were used, and population data were transformed using logarithmic transformation, $\log_{10}(x + 1)$. In the DCA of trees with DBH \geq 5 cm, the 1-year-old site (O1) and the 4-year-old site (O4) were excluded because there were no trees of these size classes. Likewise, in the DCA of forest floor plants, the 1-year-old site was excluded. Population data were transformed using logarithmic transformation, $\log_{10}(x + 1)$. Environmental variables were tested by forward selection of variables with the Monte Carlo test using 499 unrestricted permutations ($P < 0.05$).

The indicator species analysis (Dufrêne and Legendre 1997) was performed with PC-ORD ver. 4 (McCune and Mefford 1999) in order to identify the representative species of longicorn beetles for the groups of sites identified during the ordination processes. This analysis produced indicator values (IndVals) for each species in each group of sites, which were subsequently tested for statistical significance using a Monte Carlo technique.

Results

Longicorn species richness

We collected a total of 2561 individuals of 106 longicorn species in two sites (see Appendix): 99 species in ten plots in broad-leaved stands in Ogawa and 66 species in eight conifer plots in Satomi (Table 1). The average number of longicorn species (species richness) was larger in the

broad-leaved plots (35.8; SD: 7.7) than in coniferous ones (22.9; SD: 8.7) (ANOVA: $df = 1, 16; F = 11.18; P = 0.004$). The average number of longicorn individuals was also larger in broad-leaved than in conifer stands (ANOVA, log-transformed data: $df = 1, 16; F = 7.40; P = 0.017$). Simpson's index of diversity (1- D), however, was not different between them (ANOVA: $df = 1, 16; F = 0.02; P = 0.891$). In order to compare species richness in forests of different ages, plots of each area were divided into the following three age classes based on years after clear-cutting (for broad-leaved stands) or after plantation establishment (for conifer stands): 1–19 years old, 20–100 years old and over 100 years old (only in Ogawa). In both sites, longicorn species richness differed among the age classes (ANOVA: Ogawa, $df = 2, 7; F = 5.03; P = 0.044$; Satomi, $df = 1, 6; F = 6.03; P = 0.05$), with the youngest plots having more species than older ones (Fig. 1). In Ogawa, although pairwise comparisons with Bonferroni adjustment showed that differences were insignificant between any pair of the three age classes ($P > 0.05$), species richness was significantly higher in the youngest class (1–19 years old) than the seven older stands combined (ANOVA: $df = 1, 8; F = 11.48; P = 0.01$). Simpson's index was not different among the three age classes in Ogawa (ANOVA, $df = 2, 7; F = 0.27; P = 0.774$) or between the two classes in Satomi (ANOVA: $df = 1, 6; F = 2.42; P = 0.171$).

Longicorn assemblages

The result of CCA ordination is shown in Fig. 2. Eigenvalues of the first two axes and their cumulative percentage variance of species data were 0.271, 0.218 and 27.5%, respectively. The ordination divided the 18 plots into three groups, which correspond to three dif-

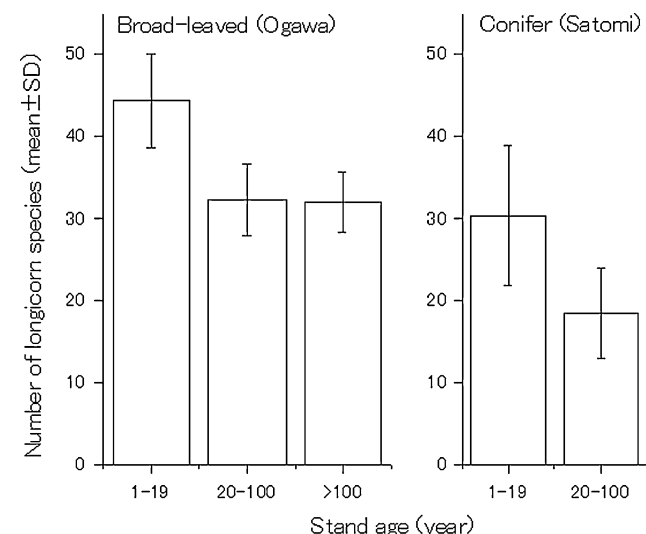


Fig. 1 Species richness of longicorn beetles in different age classes in broad-leaved and conifer plantation stands

ferent forest types as follows. The first type (initial stage stands; abbreviated as INI) was composed of the two youngest plots in Ogawa (O1, O4), which were open fields of herbs and shrubs after clear-cutting, and of one plot in Satomi (S3), which was a young plantation of seedlings of Japanese cedar. This forest type is thus characterized as plots of “stand initiation stage” (Oliver 1981) after disturbances. The second type (broad-leaved stands; BLD) consisted of eight broad-leaved plots in Ogawa (O12–O178), and the third type (coniferous plantations; CPL) comprised seven conifer plots in Satomi (S7–S76). The number of longicorn species was largest in INI, followed by BLD and CPL (smallest) (Fig. 3). The difference was highly significant among the three forest types (ANOVA: $df = 2, 15; F = 24.534; P < 0.001$) and between any pair after correction for multiple comparison with the Bonferroni adjustment (Fig. 3). Simpson's index, however, was not significantly different among the three types (ANOVA: $df = 2, 15; F = 1.263; P = 0.311$), showing that the evenness of longicorn assemblages did not change among them.

In CCA, forward selection for factors related to the species composition of longicorns revealed the following five significant ($P < 0.05$) variables of forest characteristics which are indicated with arrows in Fig. 2: scores of the second axis in DCA of forest floor plants (arrow A); the maximum DBH of trees (B); the number of tree species with DBH ≥ 5 cm (C); the number of floor plant species (D); the scores of the first axis in DCA of trees with DBH ≥ 5 cm (E). The directions of arrows B and C, both representing the maturation process of forest growth, are similar to that of the first axis of the CCA diagram (Fig. 2) and explain the discrimination in the composition of longicorn species between the two older forest types (BLD and CPL) and the young one (INI). In contrast, arrows A and E, which represent the scores of DCA of forest floor plants and trees, respectively, are more vertical in the CCA diagram; they explain the discrimination in the composition between BLD and CPL. Arrow D, which represents the species richness of the forest floor plants, was short, showing that its effect on the longicorn species composition may be marginal.

Longicorn species which had statistically significant index values (IndVals) with the indicator species analysis were found in the INI and BLD group (Table 2). In contrast, no species had significant IndVals in the CPL group.

Discussion

Species richness and stand age

In various insects, species richness changes with forest age (e.g. Buddle et al. 2000; Inoue 2003; Trofymow et al. 2003; Sueyoshi et al. 2003; Makino et al. 2006). In the present investigation, the species richness and the number of individuals of longicorns were found to show a similar response to the stand age in both the broad-

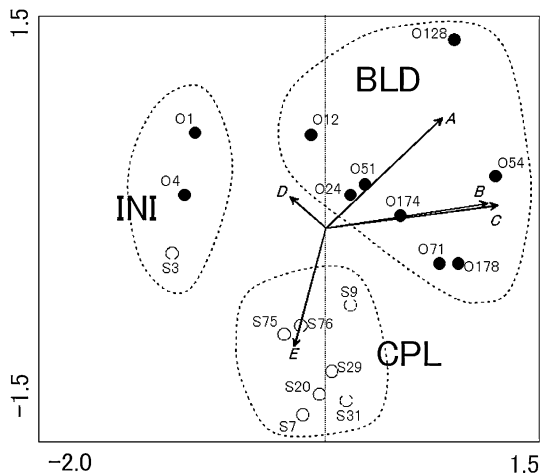


Fig. 2 Ordination of longicorn assemblages by canonical correspondence analysis (CCA) analysis. Three forest types are identified: *INI* initiation stage, *BLD* broad-leaved stands, *CPL* conifer plantations. The arrows denoted with *A–E* are vectors of environmental (vegetational) variables which were selected ($P < 0.05$) with forward selection. *A* Scores of the second axis in the detrended correspondence analysis (DCA) of forest floor plants, *B* maximum DBH of trees, *C* the number of tree species with DBH ≥ 5 cm, *D* the number of floor plant species, *E* scores of the first axis in DCA of trees with DBH ≥ 5 cm

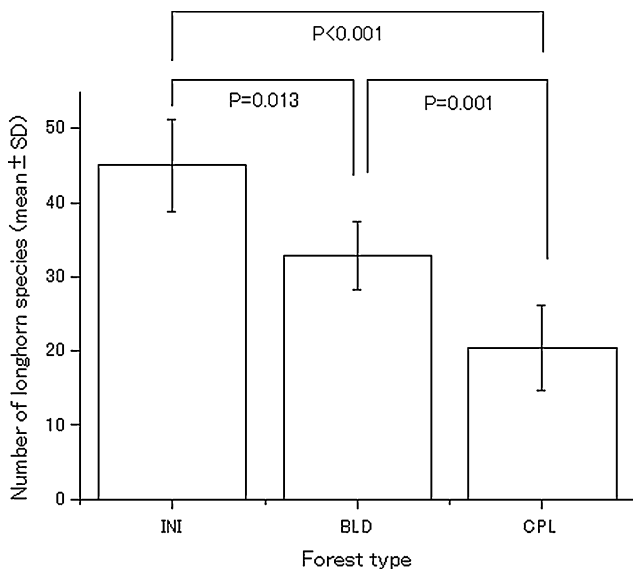


Fig. 3 Longicorn species richness of three forest types which were discriminated with CCA (Fig. 2). Results of ANOVA between the three types are given (corrected with Bonferroni adjustment)

leaved stands in Ogawa and the conifer (Japanese cedar) plantation stands in Satomi: the numbers of individuals and species were the largest in the youngest plots in both sites (O1, O4 and S3 in Table 1). One possible factor that may explain this is that the young plots abound with coarse wood debris (CWD), which is a suitable material for oviposition for some longicorn species (Linsley 1959, 1961). A preliminary CWD census in Ogawa showed that the youngest plots (O1 and O4) had

the largest amount of fallen logs or twigs (≥ 100 mm in length and ≥ 10 mm in diameter) among the ten plots studied (Makino et al., unpublished data). These dead wood materials were produced by the clear-cutting process, and they may have attracted longicorn adults seeking substrates for oviposition or adults may have emerged from them.

Another possibility is that the number of flowers that attract anthophilous longicorn adults is larger in young stands than in older ones. Because many longicorns visit flowers to feed on nectar and/or pollen (e.g. Linsley 1959, 1961; Kuboki 1987, 1998; Hanks 1999), their abundance may be positively correlated with the numbers of flowers present there. In addition, the composition of flowering species probably differs between young and old stands, and flowering species that are abundant in young plots may attract more longicorn species than the dominant flowering species of old plots, based on the observation that some anthophilous longicorns show preferences for the flowers that they visit (e.g. Kuboki 1987). A monitoring study of the densities and compositions of both the flowering species and the longicorns visiting them throughout their active period would test these hypotheses.

Maeto and Makihara (1999) and Sayama et al. (2005) monitored cerambycids in broad-leaved stands of different ages in Ogawa by means of Malaise traps and odor attractant traps, respectively. These researchers found that the species richness was smallest in the youngest plots, which is contrary to what we found. The reason for this difference in results is unclear. Following the line of reasoning mentioned above, however, the amount of CWD or density and compositions of flowers may have been different between their plots and the ones established by us in the present investigation, particularly in terms of the young plots. Our youngest plots were 1–4 years old, while those of Maeto and Makihara (1999) and Sayama et al. (2005) were 5 years old after clear-cutting; although the difference in age is as little as 1 year and a maximum of 4 years, early changes in the resources for oviposition (CWD) or for nutrition (flowers) may be much greater than expected. A continuous monitoring of longicorns as well as CWD and flowers throughout the initial forest succession process, from 0 to 10 years after clear-cutting, for example, would be helpful in explaining the difference in the results between the studies.

Effects of conifer plantation on longicorn diversity

The CCA divided the plots into three forest types, INI, BLD, and CPL, respectively, corresponding to very young plots at an initial stand stage, secondary broad-leaved plots 12 to over 100 years old and conifer plantation plots over 8 years old (Fig. 2). The forest type INI comprised the youngest three plots of all (O1, O4 in Ogawa and S3 in Satomi), suggesting that very young conifer plantations are similar to grassland-like, open fields just after clear-cutting in terms of insect diversity.

Table 2 Longicorn species with significant index values (IndVals) for two of three forest types discriminated by canonical correspondence analysis (CCA) (Fig. 2), with the number of individuals collected in each forest type

Forest type ^a	Species ^b	IndVal	Number of individuals		
			INI	BLD	CPL
INI	<i>Dinoptera minuta</i>	80.0*	156	8	8
INI	<i>Leptura ochraceofasciata</i>	67.2**	73	29	29
INI	<i>Pidonia amentata</i>	94.1**	57	4	4
INI	<i>Chlorophus japonicus</i>	100.0**	63	0	0
INI	<i>Pareutetrappa simulans</i>	72.4*	25	3	3
INI	<i>Demonax transilis</i>	59.5*	11	7	7
INI	<i>Glenea relictata relictata</i>	67.9*	12	8	8
INI	<i>Xylotrechus grayii</i>	92.6**	16	3	3
INI	<i>Cyrtoclytus caproides</i>	97.8**	17	1	0
INI	<i>Prionus insularis</i>	85.2**	12	4	4
INI	<i>Leptura latipennis</i>	66.7*	18	0	0
INI	<i>Eumecoceara trivittata</i>	60.5*	11	3	0
INI	<i>Pterolophia angusta</i>	94.1**	12	2	0
INI	<i>Pterolophia zonata</i>	72.3**	6	5	1
INI	<i>Leptura modicenotata</i>	60.9*	9	0	2
INI	<i>Pogonocherus seminiveus</i>	60.2*	8	0	2
INI	<i>Phytoecia rufiventris</i>	66.7**	7	0	0
INI	<i>Megasemum quadricostulatum</i>	58.3*	3	0	0
INI	<i>Mesosa japonica</i>	56.1*	2	1	0
BLD	<i>Pidonia signifera</i>	67.5**	6	90	24
BLD	<i>Pterolophia tsurugiana</i>	70.5**	0	41	15
BLD	<i>Pidonia discoidalis</i>	90.4**	0	43	4
BLD	<i>Pidonia simillima</i>	67.6**	0	35	9
BLD	<i>Acalolepta sejuncta</i>	60.6*	1	24	7
BLD	<i>Judolia japonica</i>	75.0*	0	21	0
BLD	<i>Parastrangalis shikokensis</i>	61.0*	0	15	3

Values significant at:

** $P < 0.01$; * $P < 0.05$

^a INI, Initiation stage stands;

BLD, broad-leaved stands

^b No species had significant

IndVal for the forest type CPL (coniferous plantations)

In this initial stage, only little divergence seems to occur between secondary broad-leaved stands and conifer plantations. The difference in longicorn assemblages and species richness between the broad-leaved and conifer plots increased thereafter.

The forest types INI and BLD both had longicorn species with significant IndVals; these species therefore preferentially occurred in younger or older broad-leaved plots, respectively. In INI, which is characterized as a stand at a very initial stage after clear-cutting or as a new plantation, there are many species with statistically significant IndVals. As mentioned earlier, those open and light plots immediately after clear-cutting may attract various longicorns which are searching for oviposition sites or for flowers as a food source. For example, the genera such as *Leptura* or *Judolia*, which have relatively large bodies, can fly long distances to visit flowers (Starzyk and Starzyk 1975); they may even have a tolerance for the higher temperatures and light intensities found in open fields (Kuboki 1987). The significant IndVals of three *Leptura* species (Table 2) are consistent with this reasoning: these anthophilous species appear to have been attracted to flower-rich resources in INI.

In contrast, no species had a significant IndVal for CPL, showing that no species preferentially or selectively occurred in conifer stands that were over 8 years old after plantation. This is well illustrated by Fig. 4, which shows that most of the species collected in the conifer plots were common to INI and/or BLD. Although four species were collected in the conifer stands only (Fig. 4), the catches were very small (one to four individuals per species: see Appendix). In addition, the

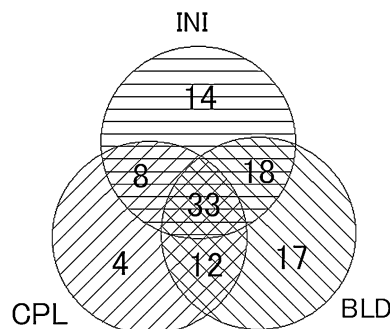


Fig. 4 The number of longicorn species collected in a single or multiple forest type. Three circles represent the number of species in the three forest types denoted as INI (initiation stage), BLD (broad-leaved stands) and CPL (conifer plantations). Overlapped areas show the number of species that are common to two or three forest types

recorded host plants of these species are mainly broad-leaved trees and do not include Japanese cedar (Kojima and Nakamura 1986). Therefore, these species most likely arrived quite by accident from outside of the conifer plots or emerged from understory trees in the plots. Makihara et al. (2004), who examined longicorn faunas of various parts of eastern Honshu, the mainland of Japan, also found that those species that occurred in Japanese cedar plantations were also collected in broad-leaved forests in the same area. This result also suggests that conifer plantations are incomplete substitutes of broad-leaved stands in terms of longicorn assemblages.

Japanese cedars are not attractive host plants for longicorns. Kojima and Nakamura (1986) published the

host records of 468 Japanese longicorn species, of which 30 (6%) feed on (or emerge from) Japanese cedar. However, only two species, *Semanotus japonicus* and *Anaglyptus subfasciatus*, are recorded as specialists of Japanese cedar or related conifers; the other species usually have wider host ranges, including broad-leaved trees (Kojima and Nakamura 1986). These results suggest that a great majority of Japanese longicorn species can live without Japanese cedar, which dominate forested areas in many parts of Japan. Conversely, a significant decrease in the area occupied by broad-leaved forests and an increase in the area established by cedar plantations may lead to the impoverishment of longicorn faunas because most species simply have hosts other than Japanese cedar. Although conifer plantations often have rich understories of various herbs and trees (Ito et al. 2004; Nagaike et al. 2005; Tanaka et al., unpublished), our present results suggest that they are not large or diverse enough to carry a whole range of longicorns that would inhabit broad-leaved stands of comparable ages. Based on our results, it appears that those species with high IndVals for broad-leaved stands (BLD in Table 2) decrease in diversity and in population size with the conversion to a conifer plantation.

A number of other studies have also shown negative effects on the species richness of insects following the conversion of broad-leaved stands to monoculture plantations of conifers; these include carabid beetles in *Picea sitchensis* plantations (Fahy and Gormally 1998) and weevil beetles in *Larix kaempferi* (Ohsawa 2005). Additionally, the species compositions of various insects have been reported to differ between conifer plantations and broad-leaved forests, such as longicorn beetles (Shibata et al. 1996; Ohsawa 2004b; Maeto et al. 2002), clickbeetles (Ohsawa 2004a), cerambycid beetles (Day et al. 1993) and ants (Maeto and Sato 2004). It is apparent from these studies, including the present one, that conifer plantations cannot totally replace natural or semi-natural broad-leaved forests in terms of insect biodiversity. In order to conserve biodiversity at the landscape level, we should avoid an extensive monoculture plantation of conifers and attempt to retain natural broad-leaved stands within and among the plantations (Lindenmayer and Franklin 2002).

Appendix

Table 3 Number of individuals of longicorn beetles collected in the study plots^a

Number	Species	Study plot																Total number		
		O1	O4	O12	O24	O51	O54	O71	O128	O174	O178	S3	S7	S9	S20	S29	S31		S75	S76
1	<i>Corymbia succedanea</i>	27	0	0	1	0	0	0	1	0	0	199	43	4	2	4	3	0	0	284
2	<i>Parastrangalis nymphula</i>	5	9	35	12	13	9	26	8	17	27	11	25	4	4	12	23	7	4	251
3	<i>Dinoptera minuta</i>	29	117	11	21	46	2	10	0	2	3	10	2	3	0	0	0	3	0	259
4	<i>Leptura ochraceofasciata</i>	19	24	4	9	13	10	7	0	10	9	30	11	2	0	6	0	6	4	164
5	<i>Pidonia signifera</i>	1	4	8	10	12	12	16	1	9	22	1	3	1	2	4	3	9	2	120
6	<i>Stenygrium quadrinotatum</i>	5	20	3	18	0	0	0	12	10	0	1	0	1	0	0	0	0	0	70

Implications of conifer plantation for ecosystem functioning

Decomposition is one of the major aspects of ecosystem functions. Although decomposition is principally brought about by microorganisms, it is often mediated by saproxylic insects (Grove 2002; Hartely and Jones 2004). Longicorn beetles may play an important role in promoting or accelerating decomposition processes through, for example, larval feeding on dead or moribund trees. In fact, one experiment revealed that the time required for wood to decay increased from 12 to 20 years in oak and from 7 to 12 years in pine when the macrofauna, including longicorns, was excluded from wood (Mamaev 1961, cited in Dajoz 2000).

From the viewpoint of ecosystem functions, longicorn adults may have an important function as potential pollinators (Maeto et al. 2002). Kato et al. (1990) found that longicorn beetles were the most frequent flower visitors among the beetles in a beech forest. Further, adults of the genus *Pidonia* often visit species-specific flowers (Kuboki 1987). Although their status as pollinator is not clear yet in almost all species, Kuboki (1998) recorded a case of pollination by *Pidonia* adults in *Magnolia sieboldii*.

An extensive conifer plantation may lead to the degradation of these functions through the impoverishment of local or regional longicorn faunas. Detailed studies focusing on quantitative analyses of ecosystem functions by insects are needed.

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Table 3 (Contd.)

Number	Species	Study plot																Total number		
		O1	O4	O12	O24	O51	O54	O71	O128	O174	O178	S3	S7	S9	S20	S29	S31		S75	S76
72	<i>Rondibilis saperdina</i>	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
73	<i>Arhopaloscels bifasciatus</i>	0	0	0	0	0	0	0	3	0	1	0	0	0	0	0	0	0	0	4
74	<i>Anoplocleromorpha excavata</i>	1	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	4
75	<i>Macroleptura regalis</i>	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	3	
76	<i>Paramenesia kasugensis</i>	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	3	
77	<i>Anoplophora malasiaca</i>	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	3	
78	<i>Mesosa japonica</i>	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	3	
79	<i>Paraclytus excultus</i>	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	3	
80	<i>Pseudalosterna misella</i>	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	3	
81	<i>Cleptomastopus bimaculata</i>	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	3	
82	<i>Eutetrappa chrysochloris</i>	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0	3	
83	<i>Pterolophia leiopoina</i>	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	3	
84	<i>Phymatodes maaki</i>	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	2	
85	<i>Brachyelytus singularis</i>	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	
86	<i>Eustrangalia distenioides</i>	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	
87	<i>Mesosa senilis</i>	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	
88	<i>Xenicotela pardalina</i>	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	
89	<i>Mesosa longipennis</i>	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	
90	<i>Epiclytus yokoyamai</i>	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2	
91	<i>Lemula nishimurai</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
92	<i>Exocentrus lineatus</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
93	<i>Mesosa hirsuta</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	
94	<i>Grammographus notabilis</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
95	<i>Asaperda rufipes</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	
96	<i>Nanohammus rufescens</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	
97	<i>Pterolophia castaneivora</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
98	<i>Atimura japonica</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
99	<i>Stehomalus takaosamus</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	
100	<i>Egesina bifasciana</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	
101	<i>Eumecocera argyrosticta</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	
102	<i>Rhopaloscels unifasciatus</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	
103	<i>Rhuphum diminuta</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	
104	<i>Nakanea vicaria</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
105	<i>Mesosa poecila</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	
106	<i>Dolichoprosopus yokoyamai</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	

^a See Section Study areas and Table 1 for explanation of the plots

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