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ORIGINAL ARTICLE

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A comparison of diversity and species composition of ground beetles (Coleoptera: Carabidae) between conifer plantations and regenerating forests in Korea

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Abstract Ground beetles were collected by pitfall trapping to compare their species richness between conifer plantations (14 sites) and regenerating forests (14 sites) and among forest ages and to examine how different functional groups responded to forest type, forest age, patch size, elevation, and geographic location in terms of abundance and richness. Ground beetles were collected from middle August to late October, 2008. A total of 34 species were identified from 3,156 collected ground beetles. Individual-based rarefaction curves showed greater species richness in regenerating forests, especially in 40–50-year-old forests, than in conifer plantations. Stepwise multiple regression analysis showed that patch size and elevation were major predictors of species richness and/or abundance of forest specialists, brachypterous species, and large- and medium-bodied species. A multivariate regression tree indicated that patch size and elevation were major predictors of assemblage structure. Although our results suggest that maintaining forest areas adjacent to agricultural landscapes may be essential to preserve ground beetle assemblages irrespective of forest types, further study is necessary to clarify the effects of habitat quality and amount on ground beetles in forests.

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Introduction

Conserving biodiversity in forests has become a key issue in national and international forest policy and management because forests support numerous species in many taxonomic groups including birds, invertebrates, and microbes (Lindenmayer et al. 2006). In particular, rapid changes in landscapes due to urbanization, agriculture, and road construction have caused forest loss and fragmentation, threatening forest biodiversity worldwide (Brockerhoff et al. 2008). Because of this problem, many studies have focused on the relationship between biodiversity and forest remnants (e.g., Gibbs and Stanton 2001; Niemelä et al. 2002; Magura et al. 2010).

In Korea, forests are important for conserving and enhancing biodiversity because they cover approximately 64 % of the nation (Lee 2012). During the Korean War and earlier, most primary forests in Korea were devastated, and growing stocks declined precipitously to 5.6 m^3/ha in 1952 (Lee 2012). Since the 1970s, a forest policy in Korea was enacted to prevent destructive logging, over-harvesting, forest fires, and illegal entry into forests and to require reforestation by logging operators (Woo and Choi 2009). During reforestation periods, coniferous trees (e.g., *Pinus* spp. and *Larix* spp.) were planted in urbanized areas or agricultural landscapes, while deciduous trees (e.g., *Quercus* spp., *Robinia pseudoacacia* L.) were regenerating or planted in mountainous areas. Consequently, growing stocks of Korean forests have increased to 126 m^3/ha in 2010 (Lee 2012).

Although reforestation in Korea was successful, several coniferous tree species, such as *Pinus densiflora* Sieb. et Zucc., *Pinus koraiensis* Sieb. et Zucc., *Larix kaempferi*

(Lamb.), and exotic *Pinus rigida* Mill., are now dominant, covering approximately 40 % of the Korean Peninsula (Lee 2012). Although these plantations may negatively affect the biodiversity of vegetation, birds, and beetles, some findings indicate that biodiversity in plantations may be similar to that in semi-natural forests (Carnus et al. 2006; Brockerhoff et al. 2008). In general, plantations and regenerating forests are potentially important for biodiversity in Korea, because about 82 % of all forest area in Korea comprises 30–50-year-old trees (Korea Forest Service 2014). Because of this short history of forest regeneration, the impacts of forest management are poorly known in Korea. Hence, investigation of the current biodiversity and community structure in these forests is highly valuable.

Ground beetles (Coleoptera: Carabidae) respond sensitively to many anthropogenic disturbances and are therefore suitable for environmental monitoring (Rainio and Niemelä 2003). They are diverse, ecologically well known, and abundant in most ecosystems (Lövei and Sunderland 1996). In addition, many species show highly specific habitat affinities (Thiele 1977) and often poor dispersal ability (Schuldt and Assmann 2009). In particular, large-bodied and poorly-dispersing ground beetles may be more vulnerable to disturbances than small, generalist species that fly well (Rainio and Niemelä 2003). Therefore, analyses of habitat affinity, wing morph, and body size of ground beetles, in addition to their assemblage structure, would provide useful diagnostic information on forest health.

In this study, we compared the species richness of ground beetles between conifer plantations and regenerating forests and among forest ages and examined how different ground beetle functional groups responded to forest type, forest age, patch size, elevation, and geographic location in terms of abundance and richness.

Materials and methods

Study sites

Twenty-eight sites encompassing 14 conifer plantations and 14 regenerating forests were selected to investigate the community structures of ground beetles throughout the country (Fig. 1). The study sites are described in Table 1. Latitudes and longitudes of the study sites were 34°34′–37°58′ and were 126°39′–129°27′, respectively. Elevations were 3–320 m.

Conifer plantations in our study sites were generally monocultures of *P. densiflora*, *P. koraiensis*, *L. kaempferi*, or *P. rigida*. *Pinus densiflora*, *L. kaempfer*, and *P. koraiensis* are the most abundant trees on the Korean Peninsula. *Pinus rigida* is also common, but this tree is primarily planted in urban and agricultural landscapes. In contrast, regenerating forests were composed of oaks (*Quercus* spp.), *R. pseudoacacia*, and conifers (*P. densiflora*, *P. koraiensis*, *P. rigida*, and *L. kaempferi*). *Pinus rigida* and *R. pseudoacacia* are exotic species used to regreen denuded lands.

Twelve study sites comprising conifer plantations were located at a lower elevation (<100 m), while many regenerating forests were at higher elevations (Table 1). The 28 sites were grouped into three forest-age categories: 30-year-old (6 sites), 40-year-old (12 sites), and 50-year-old (10 sites) forests. Forest types and forest ages in each site were confirmed using a forest geographic information system database (FGIS 2012).

Ground beetle sampling and identification

Ground beetles were collected from middle August to late October in 2008. Pitfall traps were placed approximately 30 m inside the edge of the study sites, and three traps were buried 10 m apart along a line transect in each site. Pitfall trapping is a standard sampling method for comparing the abundance or community structure of ground beetles (Niemelä 1996; Koivula et al. 2003). The traps were plastic bottles (500 mL, 10.5 cm diameter, 8 cm deep) with lids having six holes (2 cm diameter each) to prevent the catch of small mammals and herpetofauna. A plastic rain-cover was placed 3 cm above each trap. Traps were filled with preservative (300 mL 1:1 95 % ethyl-alcohol: 95 % ethylene–glycol) and replaced every month.

The collected beetles were identified to species level using a dissecting microscope (63×), according to Habu (1967, 1973, 1978, 1987), Kwon and Lee (1984), and Park and Paik (2001). Nomenclature follows Park and Paik (2001) and Park (2004). Voucher specimens were deposited at the Insect Ecology Laboratory, Entomology Program, Seoul National University, Korea. Habitat affinity of each identified species was determined according to Jung et al. (2011a, b, 2012a, b). The wing morph of each individual was determined by dissecting specimens. Body sizes were measured using digital calipers (Sanling Group, Ltd., Zhejiang, China; 0.01 mm accuracy) and, for analysis, the species were grouped into three classes based on mean size: small (5–14.99 mm), medium (15–24.99 mm), and large (25–40 mm). To measure of body size, 1–200 individuals (depending on availability) were randomly selected from all of the samples of that species.

Data analysis

We conducted ANOVA to explore the similarity of environmental variables between conifer plantations and regenerating forests. Species richness was measured based on the total number of species collected during the sampling period, and abundance was measured based on the total number of individuals collected in the three traps for each study site. To compare species richness by forest type and forest age, we estimated a species richness using rarefaction curves. This technique is based on

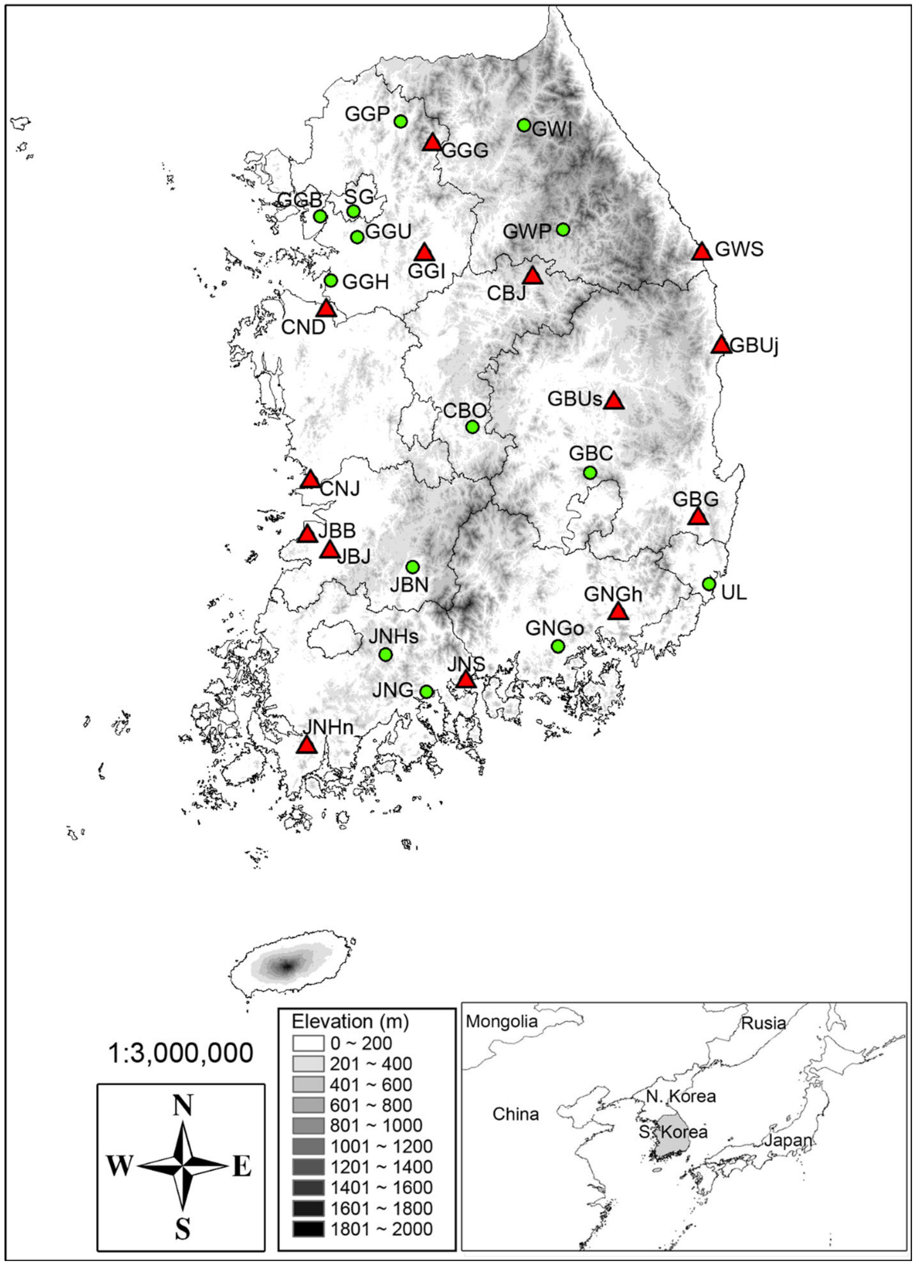

Fig. 1 Locations of 28 collection sites in South Korea. Abbreviations of sampling sites are given in Table 1 (*triangles* conifer plantations, *circles* regenerating forests)

random re-sampling of the pool of collected individuals and is used to estimate expected species richness at lower sample sizes (Gotelli and Colwell 2001). Rarefaction curves allow for meaningful standardization and comparison of datasets (Gotelli and Colwell 2001).

Stepwise multiple linear regression was used to test the relative importance of independent environmental variables (patch size, elevation, latitude, and longitude) in explaining the abundance and richness of different ground beetle functional groups. In addition, we further conducted stepwise multiple linear regression analyses for species that were selected based on their abundance (>30 individuals) and occupancy (present in ≥ 8 sites). Data on ground beetle assemblages were transformed by log $(N + 1)$ for normalization.

We further analyzed the assemblage-level responses to the four environmental variables by subjecting log-transformed data to multivariate regression tree analysis (MRT) based on Bray–Curtis pair-wise similarities between sample sites and included all species. We ran the MRT at least 50 times until we got the lowest cross-validated relative error (CV error). MRT analyzes community data but makes no assumptions about the form of relationships between species and their environment (De'ath 2002). MRT identifies groups of sites defined by environmental variables and can potentially account for non-linearities (De'ath 2002). Results are usually presented as a tree of dichotomies. Each dichotomy is chosen to minimize the dissimilarity of sample sites within each branch. We did the final tree

Table 1 Site descriptions of the 28 study sites

Forest type	Location[a]		Code	Dominant tree species in sampling site[b]	Location		Elevation (m)	Patch size (ha)	Forest age
					Latitude	Longitude			
Conifer plantation	GG	Gapyeong-gun	GGG	Korean pine	37°51′	127°30′	91	88.3	30
		Icheon-si	GGI	Pitch pine	37°15′	127°26′	82	80.1	40
		Samcheok-si	GWS	Pine	37°14′	129°20′	24	16.2	30
	CB	Jecheon-si	CBJ	Japanese larch	37°07′	128°10′	239	91.0	50
	CN	Dangjin-gun	CND	Pitch pine	36°57′	126°46′	4	2.4	40
		Janghang-eup	CNJ	Pine	36°00′	126°40′	10	27.2	40
	JB	Buan-gun	JBB	Pine	35°43′	126°39′	10	24.0	50
		Jeongeup-si	JBJ	Pine	35°36′	126°48′	46	11.2	50
	JN	Haenam-gun	JNHn	Pine	34°34′	126°39′	51	5.5	30
		Suncheon-si	JNS	Pine	34°51′	127°26′	5	45.0	40
	GB	Gyeongju-si	GBG	Pine	35°47′	129°16′	70	1.8	40
		Uiseong-gun	GBUs	Pine	36°26′	128°43′	152	16.5	30
		Uljin-gun	GBUj	Pine	36°43′	129°27′	9	669.4	50
	GN	Gimhae-si	GNGh	Pine	35°17′	128°43′	29	140.4	50
Regenerating native forest	S	Gwanak-gu	SG	Oak, pitch pine	37°27′	126°57′	193	> 1000.0	50
	U	Ulju-gun	UL	Oak, pine, pitch pine	35°25′	129°19′	43	281.6	40
	GG	Bupyeong-si	GGB	Oak, pine, pitch pine	37°27′	126°43′	74	39.1	30
		Hwaseong-si	GGH	Oak, pine, pitch pine	37°06′	126°48′	12	4.3	40
		Pocheon-si	GGP	Oak, Korean pine, pitch pine	37°58′	127°17′	257	> 1000.0	50
		Uiwang-si	GGU	Oak, pitch pine	37°20′	126°59′	93	13.6	40
	GW	Inje-gun	GWI	Oak, Korean pine, Japanese larch	37°57′	128°07′	320	> 1000.0	50
		Pyeongchang-gun	GWP	Oak, Japanese larch, pine	37°22′	128°23′	307	158.3	40
	CB	Okcheon-gun	CBO	Oak, pine, pitch pine	36°18′	127°45′	108	153.7	40
	JB	Namwon-si	JBN	Oak, pine	35°32′	127°21′	131	13.7	50
	JN	Gwangyang-si	JNG	Oak, pine	34°55′	127°42′	3	2.2	30
		Hwasun-gun	JNHs	Oak, pine, pitch pine	35°04′	127°10′	192	> 1000.0	50
	GB	Chilgok-gun	GBC	Oak, Korean pine, pine	36°03′	128°32′	196	338.3	40
	GN	Goseong-gun	GNGo	Oak, pine, pitch pine	35°06′	128°19′	194	237.7	40

[a] Location: *CB* Chungcheongbuk-do, *CN* Chungcheongnam-do, *GG* Gyeonggi-do, *GB* Gyeongsangbuk-do, *GN* Gyeongsangnam-do, *GW* Gangwon-do, *JB* Jeollabuk-do, *JN* Jeollanam-do, *S* Seoul, *U* Ulsan

[b] Dominant tree: pine, *Pinus densiflora*; Korean pine, *Pinus koraiensis*; pitch pine, *Pinus rigida*; Japanese larch, *Larix leptolepsis*; oak, *Quercus* spp.

selection by detecting the tree size (number of 'end' branches) with the lowest CV error followed by the 1-SE rule of Breiman et al. (1998). The CV error better estimates the predictive accuracy of the resulting model and it varies from 0 for a perfect predictor of community structure to close to 1 for a poor predictor (De'ath 2002).

The species richness estimate calculated by Species Diversity and Richness v3.0 software (Henderson and Seaby 2002) was used to evaluate sample size adequacy and to compare species richness between forest types. Stepwise multiple regression, ANOVA, and MRT were conducted using the statistical software package R (R Development Core Team 2010).

Results

Environmental variables

Patch size (conifer plantations, 87.07 ± 46.19 ha (mean ± SE); regenerating forests, 374.46 ± 87.07 ha, $F_{1,26}$ = 5.51, P = 0.027) and elevation (conifer plantations, 58.71 ± 17.90 m; regenerating forests, 151.64 ± 27.32 m, $F_{1,26}$ = 8.09, P = 0.009) were significantly different between conifer plantations and regenerating forests. In contrast, latitude and longitude did not differ significantly between the two forest types.

Patches of 40–50-year-old conifer plantations were generally larger and at higher elevation than those of 30-year-old conifer plantations but not significantly so. For regenerating forests, only patch size differed significantly among age classes (30-year-old forests, 20.65 ± 18.45 ha; 40-year-old forests, 169.64 ± 48.23 ha; 50-year-old forests, 802.74 ± 197.26 ha, $F_{2,11}$ = 9.17, P = 0.005).

Community structure of ground beetles

A total of 34 species belonging to 19 genera in nine subfamilies were identified among 3,156 collected ground beetles (Appendix Tables 3, 4). In conifer plantations, 18 species were identified from 712 ground beetles; in regenerating forests, 31 species were identified from 2,444 beetles. Three species, *Synuchus nitidus* (Motschulsky), *Synuchus cycloderus* (Bates), and *Synuchus* sp.1, were commonly abundant, and *Coptolabrus*

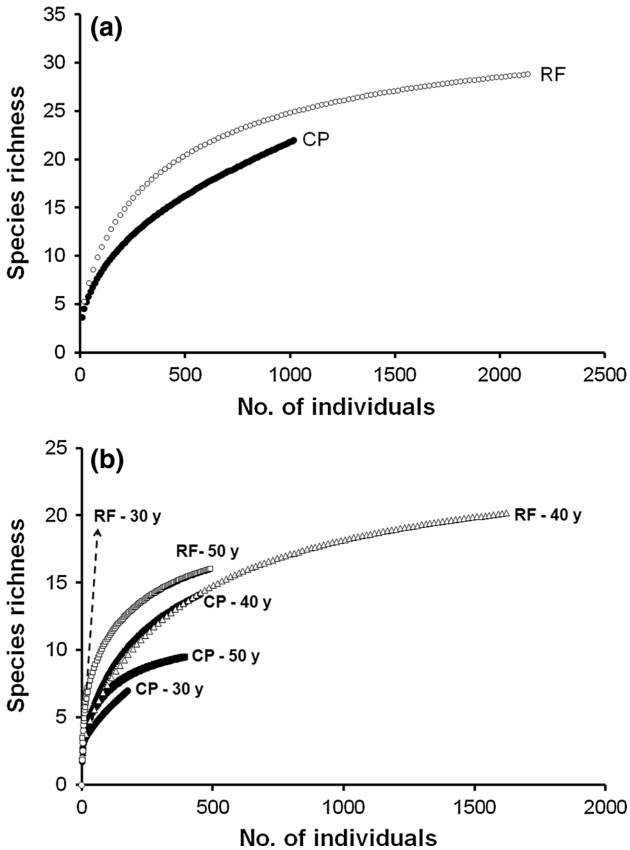

Fig. 2 Individual-based rarefaction curves for ground-beetle catches in conifer plantations (CP) and regenerating forests (RF) (**a**) and in forest age classes (*30 y* 30 years old, *40 y* 40 years old, *50 y* 50 years old) (**b**). Data points indicate average species numbers computed for the given number of individuals

jankowskii Oberthur and *Harpalus tridens* Morawitz were abundant only in some study sites. The dominant species at most sites were *S. nitidus* (1,122 individuals, 35.6 % of all beetles) and *S. cycloderus* (998, 31.6 %), which had the broadest distributions, irrespective of forest type.

Individual-based rarefaction curves indicated that higher species richness was found in regenerating forests than in conifer plantations (28.81 ± 1.50 and 21.99 ± 0.10, respectively) (Fig. 2a). In particular, species richness was generally higher in regenerating forests than conifer plantations except in 30-year-old regenerating forests (Fig. 2b).

Stepwise multiple regression also showed that patch size and elevation were significant predictor variables of the abundance and species richness of some functional groups, such as brachypterous and large-bodied species (Table 2). For forest specialists, species richness was affected by patch size and elevation. In contrast, open-habitat, macropterous, and small-bodied species were not influenced by patch size and elevation, although latitude was a significant predictor for the abundance and species richness of open-habitat species. Because three *Synuchus* species (*S. nitidus*, *S. cycloderus*, and *Synuchus* sp.1) were predominant in the most study sites, additional analyses were conducted by excluding them to check whether or not the results were solely caused by these abundant species. The general trend was similar, although patch size and elevation were the predictors for forest specialist abundance (y ~ patch size + elevation, adjusted $r^2 = 0.49$, $F_{4,23} = 7.57$, $P < 0.001$). At the species level, *C. jankowskii* was positively associated with increasing patch size and elevation, while *Chlaenius naeviger* Morawitz was negatively associated with increasing latitude. Other abundant species did not show significant relationships with these environmental variables.

The MRT analysis consistently produced a three-node tree with patch size, elevation, and latitude being the best predictors of ground beetle assemblages, together explaining 29.3 % of the variation in the data (Fig. 3). However, the CV error of 1.25 (SE = 0.163) was relatively high, indicating poor predictive value of the model.

Discussion

Our results indicated that ground beetle assemblages, including species richness, abundance, and species composition, were primarily influenced by patch size and elevation, although the rarefaction standardized richness estimates were generally higher in regenerating forests than in conifer plantations. Many studies have reported reduced abundance and species richness of ground beetles in coniferous forests compared to mixed and deciduous forests (Butterfield and Benitez-Malvido 1992; Butterfield et al. 1995; Fahy and Gormally 1998; Jukes et al. 2001; Kubota et al. 2001; Yu et al. 2006), although some of these studies (Jukes et al. 2001; Kubota et al. 2001; Yu et al. 2006) compared forest types of different successional phases. On the other hand, other studies (Niemelä 1993; Lee and Lee 1995; Koivula et al. 2002; Oxbrough et al. 2012) have found greater or equal beetle abundance and species richness in coniferous forests than in natural or mixed forests. These differences among studies may be in part due to different tree species at each study site (Yu et al. 2006). In addition, several environmental variables, such as elevation, geographic location, and habitat complexity (e.g., amount of dead wood, number of tree species, canopy cover, and leaf-litter depth), may also be more important factors affecting the distribution of ground beetles (Koivula et al. 2002; Fuller et al. 2008; Oxbrough et al. 2012).

Differences in ground beetle assemblages between forest types or management regimes have been widely examined but only rarely at national or larger spatial scales (but see Kotze and O'Hara 2003). Oxbrough et al. (2012) showed that species richness and assemblage composition of ground beetles in Ireland were similar in mixed plantations and monocultures of coniferous trees and suggested that several environmental variables,

Table 2 Relationship between ground beetle assemblages (log-transformed abundance and species richness) and selected independent variables as determined by stepwise multiple regression

Dependent variables	Parameter (β) of independent variables				Statistics			
	Patch size	Elevation	Latitude	Longitude	Adjusted r^2	$F_{4,23}$	P	Final model
Abundance								
Total	0.0005				−0.04	0.73	0.579	y ~ patch size
Forest specialists	0.0006				−0.02	0.85	0.509	y ~ patch size
Open-habitat species			−0.1800*		0.16	2.30	0.090	y ~ latitude
Brachypterous species	0.0008**	0.0025*			0.53	8.47	< 0.001	y ~ patch size + elevation
Macropterous species					−0.10	0.38	0.822	–
Large-bodied species	0.0007*	0.0021*			0.42	5.81	0.002	y ~ patch size + elevation
Medium-bodied species	0.0003		−0.0934		0.21	2.76	0.052	y ~ patch size + latitude
Small-bodied species			0.1701		0.09	1.63	0.201	y ~ latitude
Species richness								
Total		0.0010**	−0.0487		0.28	6.30	0.006	y ~ elevation + latitude
Forest specialists	0.0002	0.0008**			0.46	6.82	< 0.001	y ~ patch size + elevation
Open-habitat species			−0.1011*		0.12	1.96	0.135	y ~ latitude
Brachypterous species	0.0003*	0.0015**			0.51	8.10	< 0.001	y ~ patch size + elevation
Macropterous species					−0.01	0.95	0.453	–
Large-bodied species	0.0002	0.0011*			0.40	5.45	0.003	y ~ patch size + elevation
Medium-bodied species		0.0004	−0.0596		0.03	1.20	0.336	y ~ elevation + latitude
Small-bodied species		0.0004			0.02	0.89	0.488	y ~ elevation
Abundant species								
Chlaenius naeviger			−0.1212*		0.08	1.61	0.206	y ~ latitude
Coptolabrus jankowskii	0.0004***	0.0013*			0.64	12.8	< 0.001	y ~ patch size + elevation
Coptolabrus smaragdinus					−0.06	0.63	0.644	–
Harpalus tridens			−0.1120	0.0917	0.04	1.30	0.300	y ~ latitude + longitude
Synuchus cycloderus		0.0025			−0.07	0.53	0.714	y ~ elevation
Synuchus nitidus			0.2547	0.2296	0.07	1.52	0.230	y ~ latitude + longitude
Synuchus sp.1	−0.0002			−0.1997	0.07	1.48	0.241	y ~ patch size + longitude

Superscript asterisks indicate the significance of a P value (* < 0.05, ** < 0.01, *** < 0.001). Table includes the parameter (β, relative importance of the predictor) for each variable in the models as well as the significance level and adjusted r^2 for the overall models. Hyphen in final model indicates that any variables were not entered in regression models

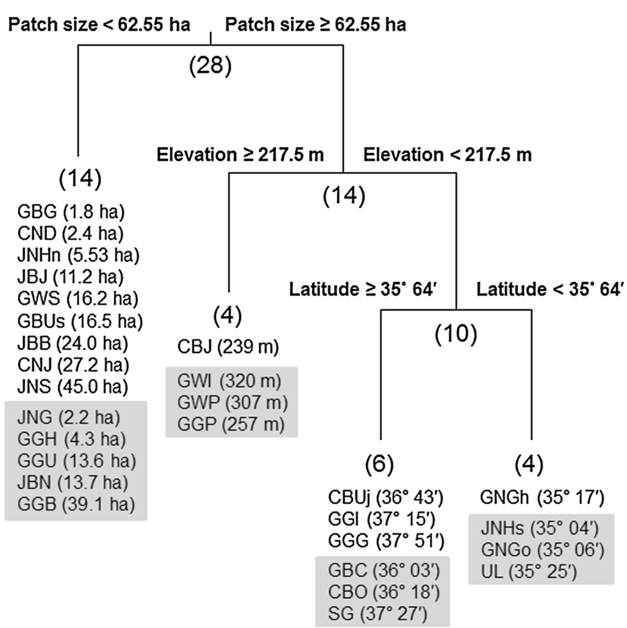

Fig. 3 Multivariate regression tree for ground beetle catches in our study of conifer plantations and regenerating forests. Bray–Curtis similarity was used for splitting based on log-transformed data. Numbers of site are shown in parentheses. Site codes (see Fig. 1) are shown under each column plot: *shaded site codes* indicate regenerating forests, and *unshaded codes* represent conifer plantations

including location, stand structure, vegetation, litter, and soil, may be more important factors than forest type. Although we did not conduct a pairwise comparison, our results also indicate that the species composition of ground beetle assemblages may not necessarily differ between forest types. Unfortunately, our study periods concentrated on late summer and autumn, so we probably missed many spring breeders, such as *Calosoma* spp., while autumn breeders, such as *Synuchus* spp. were abundantly collected in most sampling sites. In particular, *Calosoma* spp., a specialist on lepidopteran larvae, generally inhabit broad-leaved forests and may be underestimated in regenerating forests in our study. Nonetheless, based on our data, we hypothesize that the ground beetle assemblages appear to be similar between regenerating forests and conifer plantations.

In contrast, estimated species richness was higher in regenerating forests than in conifer plantations and was higher in 40–50-year-old forests than in 30-year-old forests. There are some potential factors affecting ground beetle species richness in forests, such as patch size, elevation, and forest age and type. The study sites were different in size and elevation. Regenerating forests were generally larger and located at the higher elevation than conifer plantations. Our results indicate that forest patch size and elevation are most important variables in determining species richness and abundance of forest specialists, brachypterous, and large-bodied species, and some abundant species such as *C. jankowskii* (Table 2). Forest specialists, brachypterous and/or large-bodied species were generally more frequently collected in 40–50-year-old forests (Appendix Tables 3, 4), supporting Riley and Browne (2011). For these reasons, higher species richness might be observed in regenerating forests, particularly 40–50-year-old forests. Thus, these differences in environmental characteristics among study sites may mask the relationships between ground beetle assemblage structure, forest type, and forest age. Hence further studies are needed to clarify the effects of patch size, elevation, and forest age and type on ground beetles. These studies should sample throughout the growing season.

In Korea, planted or regenerating forests are generally found throughout the nation, while primary forests are restricted to protected and higher mountainous areas, particularly national parks. Many studies in Korea have reported greater diversity of brachypterous and/or large-bodied ground beetles in deciduous forests in protected mountain forests (Lee and Lee 1995; Kubota et al. 2001; Jung et al. 2011a, b, 2012a). In our study, large- and medium-bodied species, such as *Aulonocarabus* spp., *C. jankowskii*, and *Eucarabus* spp., were frequently collected at sites within larger patches of mountainous area. In contrast, low abundance and species richness of forest specialists were found in small fragments of both coniferous and mixed forests, although some forest specialists, such as *S. cycloderus*, *S. nitidus*, and *Synuchus* sp.1 were still abundant at those sites.

In general, large-bodied species suffer greater declines during environmental change than smaller ones, possibly because of their lower reproductive and dispersal powers (Kotze and O'Hara 2003). In Korea, urbanization and habitat fragmentation have occurred at a high rate, especially in lowlands, and some ground beetles, such as brachypterous and/or large-bodied species, may not have been able to re-establish viable populations in small forest patches after habitat fragmentation. Koivula and Vermeulen (2005) explored the effect of roads on ground beetles, and they suggested that the tendency of forest specialists to avoid open habitat makes crossings of paved highway lanes unlikely. Unlike large-bodied species, some small-bodied forest specialists, such as *S. cycloderus*, *S. nitidus*, and *Synuchus* sp.1, were generally dominant and abundant at many sites in our study. That these forest specialists were less influenced by patch size is not surprising (see also Fujita et al. 2008).

Overall, ground beetles in forests can be influenced by patch size and elevation, in addition to forest type and forest age. Therefore, although retaining broadleaved stands in conifer plantations is essential to conserve populations of forest specialists (Fuller et al. 2008), preserving a large extent of forest is more important for biodiversity conservation within a fragmented landscape (Niemelä et al. 2002; Koivula and Vermeulen 2005; Magura et al. 2010). In addition, there is evidence on the importance of natural old-growth deciduous forest for ground beetles (Yu et al. 2006, 2010; Koivula 2012).

In conclusion, our results suggest that maintaining forest areas adjacent to agricultural landscapes may be essential to preserve ground beetle assemblages. However, qualitative improvements of habitat are critical, for example, minimizing adverse edge effects (Niemelä et al. 2007), increasing habitat complexity (e.g., amount of dead wood as shelter), and protecting large tracts of old-growth forest (Koivula 2012). Therefore, we still need to clarify the effects of habitat quality and amount on ground beetles in forests.

Acknowledgments This study was supported by the Brain Korea 21 project.

Appendix

See Tables 3, 4

Table 3 List of ground beetles with number of individuals caught per site per species in 14 coniferous forests

Subfamily	Species	Mean body size (mm)	Body size class[a]	Habitat types[b]	Wing morph[c]	Locations in three forest age													
						30 years				40 years					50 years				
						GGG	GWS	JNHn	GBUs	GGI	CND	CNJ	JNS	GBG	CBJ	JBB	JBJ	GBUj	GNGh
Carabinae	*Aulonocarabus koreanus*	28.6	L	F	Br					4									
	Coptolabrus jankowskii	35.1	L	F	Br										3				1
	Coptolabrus smaragdinus	36.6	L	F	Br					1			3	1		3		1	17
Nebriinae	*Nebria chinensis*	14.5	S	O	Ma					1					4		1		
Pterostichinae	*Pterostichus microcephalus*	9.9	S	O	Ma									1					
	Synuchus cycloderus	13.1	S	F	Ma	39	14	4		18		24	3	1	7		56	3	1
	Synuchus nitidus	14.8	S	F	Ma	10	30		25	123	7	14		3	7		8	104	16
	Synuchus sp.1	9.6	S	F	Ma	34		6	8	186	4	18	4	6		130	16	6	
	Trigonognatha coreana	19.4	M	F	Ma					1									
Harpalinae	*Harpalus roninus*	15.9	M	O	Ma						1								
	Harpalus tridens	11.6	S	O	Ma				1		3	3		1			1		4
Zabrinae	*Amara simplicidens*	8.1	S	O	Ma	1													
	Curtonotus giganteus	18.8	M	O	Ma														1
	Curtonotus macronotus	11.8	M	O	Ma									1					
Callistinae	*Chlaenius costiger*	23.6	M	O	Ma					1								1	
	Chlaenius naeviger	14.0	S	O	Ma			3		3	1	7							
	Chlaenius pictus	14.1	S	O	Ma					1					1				
Licininae	*Diplocheila zeelandica*	20.5	M	O	Ma							1							
Lebiinae	*Planets puncticeps*	12.1	S	F	Ma				1				2						1
	Cymindis daimio	8.7	S	F	Ma					1									
Brachininae	*Pheropsophus jessoensis*	15.5	M	O	Ma								1						

GGG Gapyeong-gun, *GGI* Icheon-si, *GWS* Samcheok-si; *CBJ* Jecheon-si, *CND* Dangjin-gun, *CNJ* Janghang-eup, *JBB* Buan-gun, *JBJ* Jeongeup-si, *JNHn* Haenam-gun, *JNS* Suncheon-si, *GBG* Gyeongju-si, *GBUs* Uiseong-gun, *GBUj* Uljin-gun, *GNGh* Gimhae-si

[a] Body size class: S $<$ 15 mm; 15 mm $\leq$ M $<$ 25 mm, 25 mm $\leq$ L

[b] Habitat types: *F* forest specialists, *O* open-habitat species

[c] Wing morph: *Br* brachypterous species, *Ma* macropterous species

Table 4 List of ground beetles with number of individuals caught per site per species in 14 regenerating forests

Subfamily	Species	Mean body size (mm)	Body size class[a]	Habitat types[b]	Wing morph[c]	Locations in three forest age													
						30 years		40 years							50 years				
						GGB	JNG	UL	GGH	GGU	GWP	CBO	GBC	GNGo	SG	GGP	JBN	JNHs	GWI
Carabinae	*Aulonocarabus koreanus*	28.6	L	F	Br						2		3					1	1
	Aulonocarabus semiopacus	26.3	L	F	Br						4								15
	Coptolabrus jankowskii	35.1	L	F	Br					3		1		2		18		45	6
	Coptolabrus smaragdinus	36.6	L	F	Br						1			1	1	1			
	Eucarabus cartereti	24.4	M	F	Br														9
	Eucarabus sternbergi	24.5	M	F	Br								2		3				
	Leptinocarabus wulffiusi	19.9	M	F	Br														12
Nebriinae	*Leistus niger*	11.6	S	F	Ma						1								
	Nebria chinensis	14.5	S	O	Ma		1	2			4		2			1	1	1	
Pterostichinae	*Dolichus halensis*	16.9	M	O	Ma			5						3					
	Pristosia vigil	14.3	S	F	Br								9						
	Pterostichus ishikawai	24.3	M	F	Br						1								
	Pterostichus microcephalus	9.9	S	O	Ma									2					
	Pterostichus sp.1	18.7	M	F	Br													1	
	Pterostichus sp.2	20.9	M	F	Br								2						
	Synuchus cycloderus	13.1	S	F	Ma		1	48		6		99	436	89	21	16	53		59
	Synuchus nitidus	14.8	S	F	Ma	1	5	29	126	8	1	239	283		4	8	10	41	20
	Synuchus sp.1	9.6	S	F	Ma	1		10	82	14	2	2	24	17	110	1	7	1	19
	Synuchus sp.2	10.2	S	F	Br														37
	Trigonognatha coreana	19.4	M	F	Ma									1					
Harpalinae	*Harpalus tridens*	11.6	S	O	Ma		1	23		2	1			12				1	
Zabrinae	*Amara simplicidens*	8.1	S	O	Ma				1										
Callistinae	*Chlaenius costiger*	23.6	M	O	Ma		2												
	Chlaenius naeviger	14.0	S	O	Ma	1	4	2						6			2	1	
	Chlaenius pictus	14.1	S	O	Ma														
Licininae	*Diplocheila zeelandica*	20.5	M	O	Ma						1						1		
Lebiinae	*Cymindis collaris*	8.4	S	F	Ma								3						
	Cymindis daimio	8.7	S	F	Ma											1			
	Planets puncticeps	12.1	S	F	Ma	2						1							
Brachininae	*Brachinus scotomedes*	15.2	M	O	Ma		2												
	Pheropsophus jessoensis	15.5	M	O	Ma							1		3				2	

SG Gwanak-gu, *UL* Ulju-gun, *GGB* Bupyeong-si, *GGH* Hwaseong-si, *GGP* Pocheon-si, *GGU* Uiwang-si, *GWI* Inje-gun, *GWP* Pyeongchang-gun, *CBO* Okcheon-gun, *JBN* Namwon-si, *JNG* Gwangyang-si, *JNHs* Hwasun-gun, *GBC* Chilgok-gun, *GNGo* Goseong-gun

[a] Body size class: S < 15 mm; 15 mm ≤ M < 25 mm, 25 mm ≤ L

[b] Habitat types: *F* forest specialists, *O* open-habitat species

[c] Wing morph: *Br* brachypterous species, *Ma* macropterous species

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