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Does selective logging change ground-dwelling beetle assemblages in a subtropical broad-leafed forest of China?

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Abstract Selective logging with natural regeneration is advocated as a near-to-nature strategy and has been implemented in many forested systems during the last decades. However, the efficiency of such practices for the maintenance of forest species are poorly understood. We compared the species richness, abundance and composition of ground-dwelling beetles between selectively logged and unlogged forests to evaluate the possible effects of selective logging in a subtropical broad-leafed forest in southeastern China. Using pitfall traps, beetles were sampled in two naturally regenerating stands after clearcuts (ca. 50 years old, stem-exclusion stage: selectively logged 20 years ago) and two mature stands (> 80 years old, understory re-initiation stage: selectively logged 50 years ago) during 2009 and 2010. Overall, selective logging had no significant effects on total beetle richness and abundance, but saproxylic species group and some abundant forest species significantly decreased in abundance in selectively logged plots compared with unlogged plots in mature stands. Beetle assemblages showed significant differences between selectively logged and unlogged plots in mature stands. Some environmental characteristics associated with selective logging (e.g., logging strategy, stand age, and cover of shrub and moss layers) were the most important variables explaining beetle assemblage structure. Our results conclude that selective logging has no significant impacts on overall richness and abundance of ground-dwelling beetles. However, the negative effects of selective logging on saproxylic species group and some unlogged forest specialists highlight the need for large intact forested areas for sustaining the existence of forest specialist beetles.

Key words habitat affinity; management; microhabitat; species diversity; successional stage

Introduction

Forest loss, fragmentation and degradation resulting from human activities are responsible for biodiversity loss and increased rates of species extinction, especially in the two recent centuries (Didham *et al.*, 1996), and have become

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a central issue in conservation biology (Meffe & Carroll, 1997; Vitousek *et al.*, 1997). Therefore, attempts at minimizing the impacts on biodiversity are becoming recent concerns of forest managers (Franklin *et al.*, 1997; Spence, 2001; Mitchell & Beese, 2002; Paillet *et al.*, 2010). Instead of traditional clearcutting, alternative harvesting methods can mimic natural processes and preserve non-timber features such as biodiversity, and thus are developed as near-to-nature strategies in many forested ecosystems (e.g., Runkle, 1982; Fries *et al.*, 1997; Östlund *et al.*, 1997; Spence, 2001; Siiskonen, 2007; Lindenmayer *et al.*, 2012; Gossner *et al.*, 2013; Lange *et al.*, 2014).

Among alternative timber harvesting methods, selective logging that involves the removal of a single or small group of mature trees has the potential to mimic natural disturbances. Through creating an uneven-aged forest with a structurally diverse, within-stand habitat mosaic, selectively logged forests are different from the standardized structure of homogeneous, more intensively managed forests (Haila *et al.*, 1994; Dettki & Esseen, 1998; Kuuluvainen *et al.*, 2012). However, microenvironments such as decaying wood, leaf litter, shrub or herbaceous composition and diversity in selectively logged forests might be different from naturally developing forests (Kuuluvainen *et al.*, 2012). Therefore, it is necessary to compare the assemblages between selectively logged and naturally disturbed forests for evaluating the effectiveness of selective logging to preserve biodiversity. Some studies found that alternative harvesting methods did not bring about negative effects on biodiversity (e.g., Lewis, 2001; Edwards *et al.*, 2012). However, more and more studies have indicated that near-to-nature logging techniques are not able to mimic natural ecological processes and can potentially degrade the long-term economic returns and ecological diversity of forests (e.g., Simard & Fryxell, 2003; Müller *et al.*, 2007; Politi *et al.*, 2012; Bässler *et al.*, 2014).

Insects have rapid population responses to disturbance and are sensitive to changes in the biotic and abiotic environments. These characteristics make insects play an important role in assessing environmental changes, ecosystem function and whether current forest management strategies are successful (Wilson, 1987; Kremen *et al.*, 1993). Among the insects, ground-dwelling beetles (Coleoptera) are considered to be suitable bioindicators of monitoring habitat changes (e.g., Eyre *et al.*, 1996; Bohac, 1999; Pohl *et al.*, 2007). A number of investigators have examined the effects of human activities on beetle assemblages (e.g., Niemelä, 2001; Yu *et al.*, 2010, 2014; Luo *et al.*, 2013); however, few studies have looked specifically at selective logging (Koivula, 2002).

Subtropical forests which represent a formerly widespread ecosystem in south and east China (Wu, 1980) have high plant diversity, and they are similarly rich in woody species as tropical forests (Condit, 1995; Wills *et al.*, 2006; Legendre *et al.*, 2009). Extensive deforestation occurred in most parts of southeast China in the 1950s, leaving very few hectares of native forests standing. Only forests that occurred on very steep slopes or remote areas were preserved, many of which became the National Forest Reserves in the 1970s. Before the 1970s, a handful of commercially valuable trees were selectively logged many times for agricultural activities at the margin of these areas. However, whether this kind of selective logging in subtropical forests is effective in preserving biodiversity remains relatively obscure.

In this study, we compared the ground-dwelling beetle assemblages between selectively logged and unlogged forests of two successional stages (regenerating stands: ca. 50 years, stem-exclusion stage; mature stands: > 80 years, understory re-initiation stages; Oliver & Larson, 1996), to examine if and how the ground-dwelling beetles respond to selective logging. We considered the responses of beetles at three levels of community organization, from the total beetle community, to the abundance of component feeding guilds (e.g., saproxylic species, fungivorous species, predaceous and phytophagous species), and to the abundance of individual species. In addition, the effects of selective logging on beetle assemblages and the possible environmental variables determining the community structure were also examined by comparing the distribution of beetles between selectively logged and unlogged forests of the two successional stages. Specifically, we used these data to address the following questions. (i) Do differences in recent forest harvesting and current stand age affect species richness, abundance and composition of ground-dwelling beetle assemblages? (ii) Do different feeding guilds of beetles similarly reflect recent forest harvesting history and are the responses of individual species to recent forest harvesting similar to those of habitat affinity groups at higher assemblage levels? (iii) Are effects of recent forest harvesting on beetle communities mediated by environmental characteristics, and what is the relative important of each variable in explaining differences in assemblage structure between selectively logged and unlogged forests?

Materials and methods

Study area

We conducted this study in the Gutianshan National Nature Reserve (approximately 81 km² in area) located in Kaihua County, Zhejiang Province, East China (29°10′19″–29°17′41″ N, 118°03′50″–118°11′12″ E). Climatic conditions are characteristic of the subtropics with an annual average temperature of 15.3°C (minimum temperatures in January: -6.8°C, maximum temperatures in July: 38.1°C) and annual mean precipitation calculated from data from 1958 to 1986, is 1964 mm (Yu *et al.*, 2001). The vegetation is representative of the typical subtropical evergreen broad-leafed forest, dominated by *Castanopsis eyrei* (Champ. ex Benth.) Tutch. (Fagaceae) and *Schima superba* Gardn. et Champ. (Theaceae). They are the dominant species in evergreen broadleafed forests and are

broadly distributed in subtropical China (Yu *et al.*, 2001). Most stands in the reserve are secondary forests, evidenced by maximum tree age of only 180 years. These forests were heavily disturbed by many human activities in the recent 100 years, for example wildfire in the 1920s, clearcutting for timber and charcoal production in the 1950s, and selective logging of large high-quality trees for timber and charcoal production in the 1950s and 1980s (Zhu, 1995). As Bruelheide *et al.* (2011) suggested, the secondary forests in the reserve can be distinguished into five successional stages according to the age of the largest tree individuals in a given plot (1, < 20 years; 2, < 40 years; 3, < 60 years; 4, < 80 years; 5, > 80 years). At the present time, most of the forest in the reserve is in the middle (stem-exclusion) and late (understory re-initiation) successional stages (Oliver & Larson, 1996). For more detailed descriptions of climate, topography, flora and succession, see Legendre *et al.* (2009) and Bruelheide *et al.* (2011).

In the reserve, two massive selective loggings occurred in the 1950s and 1980s (Zhu, 1995), resulting in four main forest types: (i) naturally regenerating stands 50 years after clearcutting and 20 years after heavy selective logging of large high-quality trees (hereafter referred to as 'selectively logged in regenerating stands'); (ii) naturally regenerating stands 50 years after clearcutting without logging since the 1950s ('unlogged in regenerating stands'); (iii) mature stands (> 80 years) in which the largest trees of the best quality were selectively logged 50 years ago ('selectively logged in mature stands'); and (iv) mature stands (> 80 years) without logging since the 1920s ('unlogged in mature stands').

Plots were selected randomly to represent harvesting history, stratified by successional stage in the reserve. However, due to inaccessibility and extremely steep slopes, parts of the reserve had to be excluded from sampling, thus resulting in an uneven spatial distribution of some of the plots. In total, 19 plots were established in four sites: four selectively logged plots in regenerating stands (site 1), seven unlogged plots in regenerating stands (four plots in site 1, and three plots in site 2), four selectively logged plots in mature stands (site 3), and four unlogged plots in mature stands (site 4). The areas of study plots were about 4–6 ha, and the distance between the plots was at least 500 m.

Sampling

We collected beetles using pitfall traps (mouth diameter 75 mm, depth 90 mm), filled with ca.100 mL of a mixed trapping fluid (vinegar : sugar : alcohol : water,

10 mL : 5 g : 5 mL : 20 mL; Yu *et al.*, 2006). A small rainwater overflow hole (diameter ca. 2 mm) was drilled in each trap ca. 2.5 cm below the upper rim. At each plot, we set four trapping locations. Each location was composed of five traps that were placed into a cross at a distance of ca. 1 m between traps. Thus, a total of 380 traps were operated during this study. Due to the often low trap- and sampling-period-specific catches, and the short distance between adjacent traps potentially causing sample dependence (Digweed *et al.*, 1995), we pooled 20 traps of each plot for data analysis and thus we had 19 beetle samples. Sampling was conducted from June to October 2009 and May to June 2010. Traps were open for 3 days, once every 3 weeks. All arthropods were collected and beetles were sorted from these samples for this study and preserved in 70% alcohol.

All specimens were deposited in the Insect Museum, Institute of Zoology, Chinese Academy of Sciences. Only adult beetles were used in the analysis and were identified by taxonomists listed in the acknowledgments section. A full list of species is provided in Appendix 1.

As our previous studies suggested, fine-scale land cover type associated with canopy, shrub, grass litter and coarse woody debris (CWD) was one of most important determinants affecting the ground-dwelling beetle assemblages (Yu *et al.*, 2006, 2008, 2009, 2010, 2014). Thus, we included seven environmental variables to evaluate potential correlates of beetle species occurrence: litter depth (cm), the number of CWD (including fallen dead trees and broken branches on the ground) and percentage cover of overstory vegetation, shrubs, herbaceous understory, litter and moss. All variables were measured within a radius of 2 m around the center of each plot in July. For details of the sampling of environmental variables, see Appendix 2.

Data analysis

Pitfall trap captures were pooled at the plot level for the purposes of data analysis (i.e., pooling all 20 pitfall traps, across all time intervals, within each plot). We used generalized linear mixed models (GLMMs) to test the effect of logging strategy (selective logging or unlogged) and stand age (regenerating or mature stands), plus their interaction, on beetle abundance and species richness (Bolker *et al.*, 2009). We included site identity (four sites) as a random factor to account for the non-independence plots within sites (Digweed *et al.*, 1995). Model selection utilized a multi-model inference approach, with models within 2 AIC (Akiake Information Criterion) units of the best-fit model considered to have strong support (Burnham & Anderson, 2002). All analyses were conducted in R 3.1.2

software with the 'lme4' package (R development Core Team, 2014). To investigate whether species composition differed as a function of the logging strategy and stand age, we categorized beetle species according to their feeding strategies into saproxylic, fungivorous, predaceous, phytophagous, decomposer and scavenger guilds. In addition, the responses of the most abundant beetle species (> 1% of the total capture, 25 individuals) per habitat affinity group were analyzed in detail to explore species-specific response patterns.

We used non-metric multidimensional scaling (NMDS) to evaluate the importance of logging strategy (selective logging *vs*. unlogged) and stand age (regenerating *vs*. mature stands) in determining ground-dwelling beetle assemblages, applying Bray-Curtis dissimilarity measures with 200 iterations as the best representation of the dissimilarities (Clarke, 1993). We also conducted permutational multivariate analysis of variance (PERMANOVA) with the measure of Bray-Curtis dissimilarities to examine variation in sample heterogeneity among logging strategies of two stand ages, using site identity as a random factor (e.g., Anderson *et al.*, 2006). We ran the NMDS and PERMANOVA using the 'vegan' package in R 3.1.2 software (R Development Core Team, 2014).

A distance-based redundancy analysis (dbRDA) with Bray-Curtis as the distance metric was used to examine the relationship between beetle assemblage structure and the possible environmental variables. We included two treatments (logging strategy and stand age) and seven other environmental variables (i.e., percentage of overstory cover, shrubs, herbaceous understory, litter and moss, the number of CWD and litter depth) into the analysis. To take into account the variation due to site, we included site identity as a covariate to partial out the effect of site before analyzing the effects of possible environmental variables. The importance of these variables in explaining the abundance and distribution patterns of carabids was studied by a pseudo-F value, which is a measure of the significance of the overall analysis. Variables were thus added one by one into the model, starting from the most important one until the subsequent variable was statistically non-significant. dbRDA was performed using the 'vegan' package in R 3.1.2 software (R Development Core Team, 2014).

Results

We captured 2547 ground-dwelling beetles during the two study years, corresponding to 134 species (Appendix 1). A total of 30 species (1120 individuals) were saproxylic species with an affinity for CWD, 23 species (510 individuals) were fungivorous, 36 species (445 individu-

als) were predaceous beetles, 31 species (300 individuals) were phytophagous and 14 other species (172 individuals) were decomposers and omnivores (Appendix 1).

Abundance and species richness

No significant effects of selective logging and stand age were found in species richness and abundance (Table 1). After species were pooled according to their habitat affinity groups, the abundance of predaceous and phytophagous species did not show obvious responses to selective logging, but saproxylic and fungivorous species exhibited significant differences between selectively logged and unlogged plots in mature stands (Table 1). For example, the abundance of saproxylic species was significantly higher in the unlogged than in the selectively logged plots, whereas fungivorous species were significantly more numerous in selectively logged than in unlogged plots (Table 1). In addition, the abundances of fungivorous and phytophagous species showed significantly positive and negative responses to stand age, respectively (Table 1).

Of the eight saproxylic species, *Cryphalus exignus* Blandford, *Xylosandrus compactus* (Eichhoff) and *Xylosandrus crassiusculus* (Motschulsky) showed significantly negative abundance responses to selective logging, but *Cryphalus massonianus* (Tsai et Li) positively responded to selective logging (Table 1). In addition, *C. massonianus* and *X. crassiusculus* were more abundant in mature than in regenerating stands.

As for the two abundant fungivorous species, *Anotylus nitidifrons* (Wollaston) was more abundant in unlogged than in selectively logged plots of the two stand ages, but its abundance was much higher in selectively logged plots in mature stands (Table 1). *Catops* sp. was more abundant in unlogged than in selectively logged plots in mature stands, (Table 1). In addition, *Anotylus nitidifrons* was more abundant in mature stands, whereas *Catops* sp. was more numerous in regenerating stands (Table 1).

Of the three phytophagous species, *Coelosternulum* sp. and *Sipalinus gigas* (Fabricius) were more abundant in unlogged than in selectively logged plots, but more individuals of *Sipalinus gigas* were found in selectively logged plots in mature stands (Table 1). In addition, *Anthicus confucii* Marseul was more abundant in regenerating than in mature stands (Table 1).

Of the five predaceous species, *Pterostichus pratii* (Bates) and *Myas* sp. were more abundant in selectively logged than in unlogged plots, at least in mature stands (Table 1). *Orphnebius draco* Assing and *Synuchus* sp.1 were more numerous in regenerating than in mature stands (Table 1).

Table 1 The effects of logging strategy and stand age on species richness, abundance, habitat affinity groups and individual species as analyzed by means (with SD) of GLMM. Logging strategy: selecting logging ('S') and unlogged ('U'). Stand age: 50 years (regenerating stand, 'R') and > 80 years (mature stand, 'M').

	Intercept	Stand age	Logging	Stand age × logging
Species	3.57 (0.05)***	-0.14 (0.08) NS		
Abundance	4.88 (0.03) NS	0.05 (0.04) NS		
Saproxylic species	3.95 (0.07)***	-0.20 (0.10) NS	0.06 (0.09) NS	0.68 (0.13)***
				M: S < U
Cryphalus exignus	0.63 (0.26)*		0.73 (0.30)*	
			S < U	
Cryphalus massonianus	1.40 (0.21)***	0.60 (0.23)**	-0.54 (0.23)*	
		R < M	S > U	
Xyleborinus saxeseni	2.10 (1.23) NS	-1.89 (1.92) NS		
Xyleborus rubricollis	0.82 (0.83) NS	1.13 (1.15) NS		
Xyleborus truncatus	0.68 (0.33)*		-0.84 (0.47) NS	
Xylosandrus compactus	1.96 (0.18)***		0.67 (0.21)**	
			S < U	
Xylosandrus crassiusculus	-1.86 (0.60)**	1.95 (0.45)***	1.60 (0.49)**	
		R < M	S < U	
Xylosandrus germanus	2.85 (0.07)***	0.20 (0.10) NS		
Fungivorous species	2.93 (0.12)***	0.95 (0.14)***	0.09 (0.14) NS	-0.75 (0.19)***
		R < M		M: S > U
Anotylus nitidifrons	-1.39 (1.00) NS	4.88 (1.00)***	2.94 (1.02)**	-3.70 (1.03)***
		R < M	S < U	M: S > U
Catops sp.	2.28 (0.16)***	-1.36 (0.35)***	-0.02 (0.20) NS	0.85 (0.43)*
		R > M		M: S < U
Phytophagous species	2.95 (0.08)***	-0.54 (0.14)***		
		R > M		
Anthicus confucii	0.78 (0.20)***	-1.76 (0.61)**		
		R > M		
Coelosternulum sp.	2.04 (0.23)***	-0.46 (0.26) NS	0.43 (0.21)*	
			S < U	
Sipalinos gigas	-1.39 (1.00) NS	0.69 (1.22) NS	2.88 (1.02)**	-2.87 (1.43)*
			S < U	M: S > U
Predaceous species	2.95 (0.24)**	0.06 (0.13) NS		
Acrotona inornata	0.61 (0.46) NS		0.85 (0.59) NS	
Myas sp.	1.79 (0.34)**	0.24 (0.50) NS	0.20 (0.23) NS	-2.60 (0.80)**
				M: S > U
Orphnebius draco	0.69 (0.21)**	-1.16 (0.50)*		
		R > M		
Pterostichus pratlii	1.63 (0.16)***		-0.90 (0.26)***	
			S > U	
Synuchus sp.1	0.86 (0.20)***	-2.25 (0.73)**		
		R > M		

The given values are the coefficients (with their standard errors), followed by the significance level: ***$P \leq 0.001$; **$P \leq 0.01$; *$P \leq 0.05$; NS, not significant.

Table 2 Results of PERMANOVA analysis for testing the effects of logging strategy and stand age and their interactions on ground-dwelling beetle assemblage composition.

	Degrees of freedom	Mean squares	Pseudo-F value	R^2	Permutational P-value
Logging strategy	1	0.293	3.219	0.120	0.354
Stand age	1	0.519	5.694	0.213	0.017*
Logging strategy: stand age	1	0.260	2.859	0.107	0.291
Residuals	15	0.091		0.560	

*$P < 0.05$.
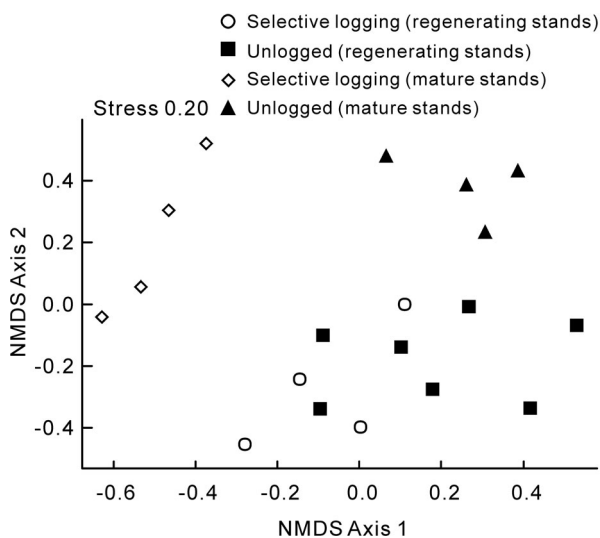
Fig. 1 Nonmetric multidimensional scaling (NMDS) ordination showing the ground beetle assemblages in selectively logged and unlogged forests of two successional stages. The stress value indicates the analysis performance; the axis values only aids in demonstrating the relative distances between samples.

Assemblage-level responses to selective logging and stand age

The NMDS indicated a divergence of beetle samples between the selectively logged and unlogged plots of the two stand ages (Fig. 1). The ordination separated beetle assemblages among the four forest types based on logging strategy by axis 1 (especially in the upper part of the ordination) and on stand age by axis 2. In mature stands, beetle samples of selectively logged samples were clustered in the left of axis 1, and samples of unlogged ones in the other end of axis 1, whereas in regenerating stands, the samples of selectively logged and unlogged plots clustered together. However, PERMANOVA indicated that only stand age significantly affected species composition and explained 21.3% of the variation ($P = 0.017$, 4999 permutations), and logging strategy and their interaction

(logging strategy × stand age) did not show statistically significant effects on species composition (logging strategy: $P = 0.354$; interaction: $P = 0.291$) (Table 2).

The distance-based redundancy analysis (dbRDA) showed a highly significant relationship between the environmental variables and beetle species distribution ($F = 1.88$; $P = 0.001$; 999 permutations). Of the nine environmental variables, logging strategy ($F = 3.57$, $P = 0.001$), stand age ($F = 2.31$, $P = 0.012$), cover of shrubs ($F = 2.08$, $P = 0.027$) and moss layer ($F = 1.86$, $P = 0.037$) were the only significant factors determining the shape of the ordination (Fig. 2). Unlogged plots were greatest on the lower right side of the ordination, and *Catops* sp., *Coelosternulum* sp. and *Xylosandrus compactus* fell in this direction. Stand age was greatest at the left right of the ordination space, and *Acrotona inornata* and *Anotylus nitidifrons* were located in this direction, indicating a preference to plots in mature stands. Cover of shrub layer was greatest at the lower left to the origin of ordination, and *Cryphalus massonianus*, *Myas* sp. and *Pterostichus pratii* fell in this direction. Cover of moss layer was at the upper part to the origin of ordination, and *Xyleborinus saxeseni*, *Xyleborus rubricollis* and *Xylosandrus germanus* were located at this direction.

Discussion

Richness and abundance

Consistent with many previous studies (Atlegrim *et al.*, 1997; Wermelinger *et al.*, 2002; Bouget, 2005), we identified significant effects of selective logging at the habitat affinity group level in mature stands. For example, a reduction in abundance of saproxylic beetles was found in selectively logged stands compared with unlogged ones, reflecting a pattern common to many other studies on saproxylic beetles (e.g., Gutowski, 1986; Chandler & Peck, 1992; Martikainen *et al.*, 1999; Siitonen & Saaristo, 2000; Grove, 2002a). However, an overall increase was observed in the abundance of fungivorous beetles which

usually prefer shaded microenvironments (especially in selectively logged mature stands).

Abundances of saproxylic beetles are usually determined by the volume of coarse woody debris, shaded environment, successional stage and management history (Speight, 1989; Grove, 2002b; Wermelinger *et al.*, 2002; Bouget, 2005). An ice storm caused severe damage to the forests and brought about many fallen trees in the study region in the spring of 2008 (Man *et al.*, 2011), thus resulting in an outbreak of saproxylic insects (44% of the total catch in this study; Appendix 1) (Speight, 1989). According to the general rule, more CWD and shadiness should attract more saproxylic beetles to colonize (Wermelinger *et al.*, 2002; Bouget, 2005). However, when we compared the number of fallen logs and standing dead snags (a crude estimation of the volume of coarse woody debris) and the coverage of canopy and shrub layer (a simple measure of shadiness), we found no significant difference between selectively logged and unlogged plots (Appendix 2). Therefore, rather than CWD and shadiness, other environmental factors such as successional stage and management history might be responsible for more individuals of bark beetles in the unlogged forests.

Fungivorous beetles depend on the availability of fungi which usually prefer a shaded microenvironment. Although no accurate data for the above environmental factors were obtained, we were still able to estimate some variables through several indirect ways, for example, estimating relative humidity by comparing the coverage of canopy, shrub and moss layers among different treatments. In this study, we found that selectively logged forests have higher moisture than unlogged forests in mature stands, and thus might explain the high number of fungivorous beetles in selectively logged forests. Higher moisture in selectively logged stands might result from the canopy closure of higher tree density. Selective logging 50 years ago can give an opportunity for more young trees to grow up to stem exclusion stage in mature stands, which leads to higher tree density in selectively logged stands, compared with unlogged stands.

Assemblage composition

As indicated by the results of the multivariate analysis (NMDS and dbRDA), species composition and distribution of ground-dwelling beetle assemblages in selectively logged plots differed greatly from those in unlogged plots (especially in mature stands), and were significantly affected by logging strategy, stand age, and cover of shrub and moss layer (Figs. 1, 2). Although most abundant species were captured in nearly all habitats, there were still some beetle species that showed strong responses to
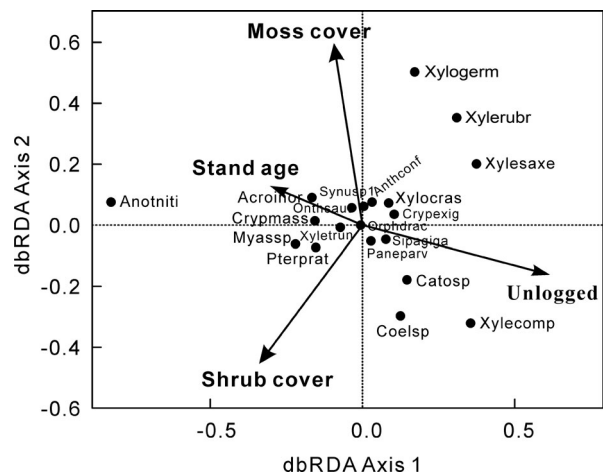

Fig. 2 Distance-based redundancy analysis (dbRDA) showing species-environment relationships for ground-dwelling beetle species in relation to dominant gradients of variation in logging strategy, stand age and cover of shrub and moss layers. Only species with more than 1% of the total catch (25 individuals) are presented. The beetle species are annotated with genus and species abbreviations (e.g., *Anotylus nitidifrons* = Anotniti); see Appendix 1 for details.

selective logging (Fig. 2; Table 1). For example, *Catops* sp., *Coelosternulum* sp. and *Xylosandrus compactus* preferred unlogged plots, *Cryphalus massonianus*, *Myas* sp. and *Pterostichus pratii* preferred selectively logged plots in mature stands (higher shrub cover), and *Acrotona inornata* and *Anotylus nitidifrons* preferred mature stands (Fig. 2; Table 1), which is corroborated by some previous studies (e.g., carabids: Koivula, 2002; Ulyshen *et al.*, 2006; saproxylic beetles: Grove, 2002a).

Differentiation of these beetles' habitat preferences might be related to microhabitat changes caused by management history and stand age. According to the definition of forest stand dynamic stages by Oliver & Larson (1996), 40–50-year-old forests are approaching the stem exclusion stage, closing the canopy with minimal die-off of neighboring trees. In our study, stands after logging usually had higher canopy closure (coverage of canopy and shrub layers) and moisture (coverage of moss layer), compared with the unlogged plots in the understory re-initiation stage (mature stands). In contrast, there were no significant differences between selectively logged and unlogged plots in the stem exclusion stage (regenerating stands) (Appendix 2), and thus these microhabitat variations among the forest types might result in forest specialists responding differently to selective logging and stand age (Fig. 2).

In addition, because the older stands are further from human settlements, the stand types (especially mature stands and regenerating stands) are spatially discrete within the reserve. This could easily confound apparent logging or stand age effects with pre-existing artefacts of site location, and leads to spatial autocorrelation of forest type effects. Normally this type of problem can influence the interpretation of results. In this study we at least minimized the effects of spatial autocorrelation by including site identity as a random factor in the models to account for the non-independence among plots within sites. Ultimately, the logging effects are the most likely explanation for the observed effects.

Management implications

As an alternative harvesting method to traditional clearcutting, selective logging is advocated as a new forest management practice to mimic natural processes and preserve non-timber features such as biodiversity (Franklin *et al.*, 1997; Mitchell & Beese, 2002). Our findings of no overall changes in total species richness and abundance of ground-dwelling beetles between selectively logged and unlogged stands and high proportion of habitat generalists partly supported this hypothesis. But consistent with many studies (e.g., Altegrim *et al.*, 1997; Lewis, 2001; Koivula, 2002; Ulyshen *et al.*, 2006; Gunawardene *et al.*, 2010), we also identified negative responses of saproxylic beetles to selective logging, and some specialists preferred unlogged forests, especially in the understory re-initiation stage. Therefore, selective logging advocated as an efficient way to preserve biodiversity should be treated with caution in subtropical forest ecosystems. Our results suggest the need to preserve large intact forested areas for sustaining the existence of forest specialists.

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Disclosure

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix 1: Ground-dwelling beetle species captured in a subtropical broad-leaved forest of China. Logging strategy: selective logging (S), unlogged (U); Stand age: regenerating stands (ca. 50 yr) and mature stands (> 80 yr).

Appendix 2: Mean of the environmental variables per trap location (with SE) in selectively-logged and unlogged stands of two stand ages (regenerating stands: ca. 50 yr; mature stands: > 80 yr) in a subtropical broad-leaved forest of China.