



# ORIGINAL ARTICLE

# Composition and distribution of ground-dwelling beetles among oak fragments and surrounding pine plantations in a temperate forest of North China

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**Abstract** In this study, we compared ground-dwelling beetle assemblages (Coleoptera) from a range of different oak fragments and surrounding conifer plantations to evaluate effects of forest size and surrounding matrix habitat in a temperate forest of north China. During 2000, beetles were sampled via pitfall traps within two large oak fragments (ca. 2.0-4.0 ha), two small oak fragments (ca. 0.2-0.4 ha) and two surrounding matrices dominated by pine plantations (>4 ha) in two sites of different aspects. Overall, no significantly negative effects from forest patch size and the surrounding matrix habitat were detected in total species number and abundance of ground-dwelling beetles. However, compared with small oak patches or pine plantations, more species were associated with an affinity for at least one large oak patch of the two aspects. Multivariate regression trees showed that the habitat type better determined the beetle assemblage structure than patch size and aspect, indicating a strong impact of the surrounding matrix. Linear mixed models indicated that species richness and abundance of all ground-dwelling beetles or beetle families showed different responses to the selected environmental variables. Our results suggest that more disturbed sites are significantly poorer in oak forest specialists, which are usually more abundant in large oak fragments and decrease in abundance or disappear in small fragments and surrounding matrix habitats. Thus, it is necessary to preserve a minimum size of forest patch to create conditions characteristic for forest interior, rather than the more difficult task of increasing habitat connectivity.

**Key words** forest patch size, fragmentation, ground-dwelling beetles, North China, surrounding matrix habitat, temperate forest

## Introduction

Natural environments are heterogeneous, and individuals within populations differ from each other, resulting in spatial variations in diversity patterns of communities (Haila *et al.*, 1994; Neimelä *et al.*, 1996). The increase of the fragmentation of natural habitats by forest and agri-

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cultural managements during the twentieth century has changed the nature of land use through habitat loss and isolation of remnant habitat patches (Magura *et al.*, 2001; Fahrig, 2003; Ewers & Didham, 2006; Filgueiras *et al.*, 2011), resulting in high heterogeneity in spatial scales in natural environments. Habitat fragmentation has become an important process contributing to the present-day concern for the loss of biodiversity and increased rates of species extinction (Didham *et al.*, 1996), and has become a central issue in conservation biology (Meffe & Carroll, 1997).

Fragmentation *per se* is a landscape level phenomenon in which species that live in the habitat fragment (remnant) are suffering a drastic change due to a modified

environment of reduced habitat size and quality, increased isolation and new ecological boundaries (Fahrig, 2003; Ewers & Didham, 2006). In recent years, several reviews based on extensive literature on habitat fragmentation have focused on the effects of habitat fragmentation on biodiversity at the landscape scale (Fahrig, 2003), ecological responses to habitat edges created by fragmentation (Ries et al., 2004), plant-insect interactions in fragmented landscapes (Tscharntke & Brandl, 2004), or confounding factors in the detection of species responses to habitat fragmentation (Ewers & Didham, 2006). However, fragmentation effects in the empirical literature can be still commonly summarized into five fields: fragment area, edge effects, fragment shape, fragment isolation and matrix structure. All of them together describe the spatial attributes of individual patches in fragmented landscapes (Ewers & Didham, 2006). Therefore, if we want to understand how biodiversity is affected by fragmentation, and find a better way to manage fragmented landscapes, it is still necessary to focus on these aspects again and further take a mechanistic approach to the study of fragmentation for future research.

Liaodong oak woods (Quercus liaotungensis Koidz.) as the dominant forest type of natural woodlands once cover most of northern China. Because of extensive deforestation and difficulty in natural regeneration for low survival rate of seedlings, continuous oak forests now become fragmented, and most natural oak forests are preserved as forest patches surrounded by conifer plantations, which have been planted extensively after the logging of natural oak woods since the 1960s. Compared with natural oak forests, conifer plantations bring about drastic changes in vegetation and matrix, so much effort has been put into testing the negative effects of conifer reforestation on local arthropod assemblages surviving in natural oak forests (Yu et al., 2004, 2006a, 2010). However, few studies have been conducted to test if forest fragmentation could bring about negative effects on forest arthropod communities. Ground-dwelling beetles (Coleoptera) respond rapidly to habitat changes and are considered to be suitable bioindicators for environmental changes by human activities (Jennings et al., 1986; Eyre et al., 1996; Lövei & Sunderland, 1996; Davies & Margules, 1998; Bohac, 1999; Niemelä, 2001; Pohl et al., 2007; Yu et al., 2006b, 2010; Korasaki et al., 2013).

In this study, we examined the effects of fragmentation on the composition and distribution of ground-dwelling beetle assemblages in a north China forest, and focused on the two fields of fragmentation, fragment area and surrounding matrix (which makes oak forest patches more or less isolated). The following questions are addressed: (i) how do fragment area and surrounding matrix affect the species richness and abundance of ground-dwelling beetle assemblages in a north China forest; (ii) are there any differences in species responses between oak fragments of different areas; and (iii) does individual species associated with natural oak fragments convert to the surrounding matrix (conifer plantation)?

#### Materials and methods

Study area and sampling

This study was conducted at Beijing Forestry Ecosystem Research Station (BFERS, about 114 km west of Beijing) on Dongling Mountain (40°00'N, 115°26'E, 800-2300 m) which is a part of the Taihang Mountain Ranges, north China. The soil type in this region is a brown mountain soil (Chen & Huang, 1997). A cool-temperature monsoon climate with an average annual temperature of 4.8°C (January –10.1°C, July 18.3°C) dominates in this region (Chen & Huang, 1997). Annual mean precipitation is 611.9 mm, and 78% of annual rainfall occurs from June to August (Chen & Huang, 1997). In this region, Liaodong oak forest is the most extensive native forest type. In the 1960s, the oak forests were extensively logged, and then conifer plantations of pine (Pinus tabulaeformis) and larch (Larix principis-rupprechtii) were planted. Thus, most oak forests were fragmented and surrounded by conifer plantations, and the patch sizes of these fragments range from 0.1 ha to 6 ha. All these forests have a closed canopy with tree height of 8-15 m (max. 20 m). For more detailed description of these forest types, see Yu et al. (2006c).

To test the effects of fragment area and the surrounding matrix (conifer plantation) on diversity of grounddwelling beetles, three treatments (habitat types) in two sites near the BFERS were selected for this study: (1) large oak patch (more than 2 ha); (2) small oak patch (less than 0.4 ha); and (3) surrounding matrix habitat (pine plantation; more than 4 ha). One site facing the southwestern aspect (SW Aspect: slope, 22°; elevation, 1 160 m−1 250 m) was approximately 0.5 km north to the BFERS, and another site facing the southeastern aspect (SE Aspect: slope, 21°; elevation, 1 250 m-1 300 m) was approximately 1.5 km south to the BFERS. The sizes of the large oak forest patch, small oak forest patch and pine plantation were 2 ha, 0.24 ha and 4 ha in the SW Aspect, and 4 ha, 0.36 ha and 4 ha in the SE Aspect, respectively. The experimental design and some important environmental characteristics of each habitat are summarized in Table 1. A total of six important environmental variables, including the proportion of broad-leaved tree

**Table 1** Experimental design and some environmental characteristics of three habitats in two sites with southwestern (SW) and southeastern (SE) aspects.

	Habitat						
Aspect	Large oak patch	Small oak patch	Surrounding pine plantation				
SW							
Sample number	$2 \times 3$	$2 \times 3$	$2 \times 3$				
Patch size (ha)	2	0.24	4				
POBL (%)	75	80	20				
CC (%)	50	65	80				
SC (%)	25	30	20				
HC (%)	20	35	10				
LC (%)	45	85	90				
LD (cm)	2.5	3.5	4.0				
SE							
Sample number	$2 \times 3$	$2 \times 3$	$2 \times 3$				
Patch size (ha)	4	0.36	4				
POBL (%)	90	80	25				
CC (%)	50	60	75				
SC (%)	20	35	25				
HC (%)	15	30	15				
LC (%)	60	80	90				
LD (cm)	3.0	3.0	4.0				

Samples for each habitat in each site included six replications, which were set in a two-by-three grid. POBL, proportion of broad-leaved trees; CC, canopy cover; SC, shrub cover; HC, herb cover; LC, litter cover; LD, litter depth.

species, canopy cover, shrub cover, herb cover, litter cover and litter depth were also measured in this study (Table 1). The coverage of each layer was measured by visible estimation, the proportion of broad-leaved tree species by count of tree number, and depth by a ruler.

Beetles were captured using pitfall traps in all habitats. For more details on this method, see Yu *et al.* (2004, 2006b). Sampling was conducted from June to September in 2000. As our previous studies suggested, most beetle species could be found in this period in this region (Yu *et al.*, 2002, 2006c). Six beetle samples were established in each studied forest patch in a three-by-two grid (Table 1). To provide adequate statistical independence for pitfall traps, samples were set at least 15 m from each other (Digweed *et al.*, 1995). Five traps in each sample were placed in a cruciform pattern with a distance of 1 m between the traps. Thus, a total of 180 traps were used in this study. Traps were open for 3 days once a month. Five traps from each sample were pooled for data analysis.

## Data analysis

A nested analysis of variance (ANOVA) for the habitat type as the fixed variable and the aspect (site) as the random variable was used to test the differences in species richness and abundance (catches for total individuals and abundant species with more than 50 individuals) of beetles among large oak patches, small oak patches and surrounding pine plantations. Thus, we were primarily interested in differences between two oak patches and pine plantations (main effect), but also in the variation within the two aspects. Data were log-transformed to approximate normality to comply with the parametric test assumptions (Sokal & Rohlf, 1981). All analyses were made with SPSS 7.5 (SPSS Inc., 1997).

The variation in beetle assemblage structure among different forest patches was compared using multivariate regression trees (MRT) (De'ath, 2002), which creates dichotomies based on environmental variables. It is a hierarchical technique, where each split is chosen to minimize the dissimilarity in the sites within the clusters. The distance measure used was Bray-Curtis pairwise similarities between samples, including 55 species occurring in two or more samples only. The beetle community was compared with one categorical variable (aspect), and seven important environmental variables, including the proportion of broad-leaved tree species, canopy cover, shrub cover, herb cover, litter cover, litter depth and patch size in this study (Table 1). MRT were computed using R 2.15.1 (R Development Core Team, 2012) and the mypart library (Therneau & Atkinson, 2005).

The relationship between total species richness and abundance and environmental structure of the forest patches was studied by linear mixed models (LMM). In the models, the abundance and species richness were the response variable, and the environmental variables are the fix effects and the aspects (sites) and habitat types were considered as the random effects. The possible collinearity among explanatory variables might influence linear mixed models, for it can lead to the exclusion of one of two variables with a similar pattern and then mask the possible relative importance of the excluded variable. Thus, after log-transformation of these variables, we ran a Pearson correlation to detect such possible collinearity (Table 2). High positive correlations (r > 0.85) between canopy cover, litter cover and litter depth, and between herb cover and shrub cover, indicated that each variable group might have a similar pattern, thus only canopy cover and herb cover were considered into the models together with the proportion of broad-leaved tree species and patch size. The best-fit model was selected as the one with the

**Table 2** Pearson correlation coefficient among six selected environmental variables.

	CC	SC	НС	LC	LD
POBL	-0.862***	0.421*	0.714***	- 0.568***	-0.801***
CC		-0.054	-0.326	0.878***	0.935***
SC			0.885***	0.181	-0.214
HC				-0.036	-0.388
LC					0.894***

\*P < 0.05; \*\*\*P < 0.001. POBL, proportion of broad-leaved trees; CC, canopy cover; SC, shrub cover; HC, herb cover; LC, litter cover; LD, litter depth.

lowest Akaike's information criterion (AIC). However, models within 2 AIC units of the minimum are also considered to have strong support (Burnham & Anderson, 2002). Then, likelihood ratio tests were used to select the best one from several models within 2 AIC units of the minimum. All analyses were conducted in R 2.15.1 (R development Core Team, 2012). Linear mixed models (LMM) were fitted by the 'lmer ()' function in the 'lme4' package with the Laplace approximation method (Bates *et al.*, 2008).

### Results

A total of 1 025 specimens of beetles were captured, corresponding to 95 species in 10 families (Appendix 1). The most species-rich families were: Staphylinidae (31 spp), Curculionidae (26 spp) and Carabidae (17 spp).

Results of the ANOVA using habitat as the fixed variable and aspect (site) as the random variable and species richness or abundance as the response variable revealed that there were no significant changes in species richness or abundance of all beetles and staphylinids among large oak patches, small oak patches and surrounding pine plantations, but curculionid richness and abundance, and carabid richness showed significant differences between the two aspects, and species richness of curculionids significantly decreased from large oak patches, small oak patches to surrounding pine plantations (Table 3; Fig. 1). In addition, there was a significant interaction between habitat and aspect in carabids (Table 3). Moreover, when abundant species with individuals of >50 were tested, no species showed significant response to habitat or aspect, but Carabus manifestus and Rhynchaenus sp.1 showed significant interactions between habitat and aspect (Table 4). Both of these two species significantly decreased from large oak patch, small oak patch to pine plantation in the SE Aspect, and more Carabus

**Table 3** Results of the ANOVA to examine habitat as fixed variable and aspect (site) as random variable to predict the richness and abundance of beetles, carabids, staphylinids and curculionids.

Taxon	Source of variation		Mean square	F	P
Beetles					
Species	Habitats	2	0.122	5.744	0.148
	Aspects	1	0.098	4.608	0.165
	Habitats × Aspects	2	0.022	1.570	0.225
Abundance	Habitats	2	0.378	13.571	0.069
	Aspects	1	0.005	0.196	0.701
	Habitats × Aspects	2	0.028	0.792	0.462
Carabids					
Species	Habitats	2	0.136	1.318	0.431
	Aspects	1	2.098	20.319	0.046*
	Habitats × Aspects	2	0.103	4.381	0.021*
Abundance	Habitats	2	0.343	1.092	0.478
	Aspects	1	4.391	13.994	0.065
	Habitats × Aspects	2	0.314	4.993	0.013*
Staphylinids					
Species	Habitats	2	0.124	1.445	0.409
	Aspects	1	0.005	0.053	0.839
	Habitats × Aspects	2	0.086	1.135	0.335
Abundance	Habitats	2	0.519	3.138	0.242
	Aspects	1	0.071	0.427	0.581
	Habitats × Aspects	2	0.165	1.363	0.217
Curculionids					
Species	Habitats	2	0.071	24.173	0.040*
	Aspects	1	0.102	34.932	0.027*
	Habitats × Aspects	2	0.003	0.212	0.810
Abundance	Habitats	2	0.214	17.132	0.055
	Aspects	1	0.430	34.459	0.028*
	Habitats × Aspects	2	0.012	0.309	0.737

<sup>\*</sup>P < 0.05.

**Table 4** Results of the ANOVA to examine habitat as fixed variable and aspect (site) as random variable to predict the abundance of five selected most abundant species.

Taxon	Source of variation	df	Mean square	F	P
Carabus	Habitats	2	0.346	0.598	0.626
manifestus	Aspects	1	2.445	4.221	0.176
	Habitats × Aspects	2	0.579	11.774	0.000***
Rhynchaenus	Habitats	2	0.554	1.411	0.415
sp.1	Aspects	1	1.006	2.563	0.251
•	Habitats × Aspects	2	0.393	8.143	0.001**
Sympiezomias	Habitats	2	0.005	0.071	0.933
sp.1	Aspects	1	0.001	0.003	0.964
	Habitats × Aspects	2	0.070	0.823	0.449
Sympiezomias	Habitats	2	0.037	0.181	0.847
sp.2	Aspects	1	0.003	0.016	0.910
	Habitats × Aspects	2	0.203	2.227	0.125
Acrotrichis	Habitats	2	0.342	1.336	0.428
sp.	Aspects	1	0.182	0.713	0.487
-	Habitats × Aspects	2	0.256	3.263	0.052

<sup>\*\*</sup>P < 0.01; \*\*\*P < 0.001.

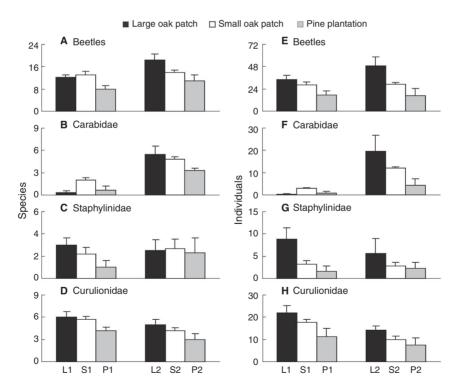
*manifestus* was found in the SE Aspect than in the SW Aspect (Fig. 2).

According to the Appendix 1 (beetle species captured more than five individuals), more species were significantly abundant in at least one large oak patch and could be considered as the endemic species associated with the large oak patch, i.e., *Carabus manifestus*, *C. sculptipennis*, *Pterostichus fortives* and *Blaps rugosa* were more numerous in the large oak patch in the SE Aspect; *Macrocorynus* sp.2, two curculionids (sp.1, sp.2) and two staphylinids (sp.2, sp.3) were more abundant in the two large oak patches. However, only one species was most abundant in small oak patches or surrounding pine plantations, which might be considered as a species with an affinity for this specific habitat, for example, *Notiophilus impressifrous* associated with the small oak patch and one staphylinid (sp.5) with the pine plantation.

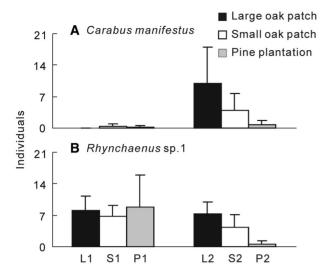
The MRT indicated that the habitat type was the most important factor explaining beetle assemblage structure (Fig. 3). The first split, based on the canopy cover (a threshold of 70%), explained approximately 77.8% of the variation and separated oak forests from pine plantations. The second split divided large oak patches and small oak patches and explained 15.7% of the variation. The third

and last splits were based on aspect, explaining 1.4% of variation respectively. The entire MRT explained 96.3% of the variation and had a low cross-validated relative error (0.0563), indicating a strong predictive power for a new dataset.

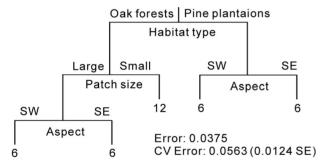
Based on linear mixed models (Table 5), species richness and abundance of all ground-dwelling beetles or beetle families showed different responses to the selected environmental variables: (i) patch size, proportion of broad-leaved trees and canopy cover were the three most important factors to determine the species richness of all beetles and carabids; (ii) canopy cover determined species richness of staphylinids and curculionids, and abundance of all beetles and curculionids; and (iii) the abundance of carabids were influenced by all four environmental variables, and the abundance of staphylinids by the three variables except the patch size. When abundant species with individuals of >50 were tested, the occurrence of Carabus manifestus and Rhynchaenus sp.1 were determined by all environmental variables: Sympiezomias sp.1 by herb cover only, Sympiezomias sp.2 by the three variables except the proportion of broad-leaved trees, and Acrotrichis sp. by the three variables except the patch size (Table 6).



**Fig. 1** Average number (with SD) of abundance and species richness per trap site of ground-dwelling beetles for three habitats. L1, S1, P1, L2, S2 and P2 represent large oak patches, small oak patches and surrounding pine plantations in two sites, southwestern (SW) and southeastern (SE) aspects, respectively.



**Fig. 2** Average number (with SD) of two abundant species per trap site of ground-dwelling beetles for three habitats. L1, S1, P1, L2, S2 and P2 represent large oak patches, small oak patches and surrounding pine plantations in two sites, southwestern (SW) and southeastern (SE) aspects, respectively.



**Fig. 3** Multivariate regression tree for ground-dwelling beetle assemblages of three habitats in two sites, southwestern (SW) and southeastern (SE) aspects. The numbers below each end branch show the number of samples falling into that branch.

# **Discussion**

Our results indicated that no significantly negative effects from fragment area and surrounding matrix habitat were found to contribute to the variation in species richness and abundance of beetle assemblages, except curculionids. Fragment area (patch size) did not show significant effects on composition and distribution of ground-dwelling beetle assemblages, but the matrix was found to significantly affect beetle structure, resulting in the assemblages in surrounding conifer plantation being distinct from those in the oak fragments.

The influence of forest patch size on ground-dwelling beetles

Reduced habitat area is thought to be one of the major causes of species extinctions and strongly and negatively affects biodiversity (Tilman et al., 1994; Fahrig, 2003). Following species-area (SA) curves constructed by classical island biogeography theory (IBT) (MacArthur & Wilson, 1967), it is easy to expect that species loss will increase with the decreasing fragment area. A lot of studies have supported this assumption and found a general negative effect of habitat fragmentation on species richness and abundance in invertebrate taxonomic or functional guilds (Klein, 1989; Burke & Goulket, 1998; Gibbs & Stanton, 2001; Barbosa & Marguet, 2002; Andresen, 2003; Feer & Hingrat, 2005; Nichols et al., 2007; Filgueiras et al., 2011). This phenomena was usually explained based on dispersal and colonization extinction dynamics by some authors (De Souza & Brown, 1994; Daily & Ehrlich, 1995; De Vries et al., 1996; Shahabuddin & Terborgh, 1999), who thought that most forest species would decrease in abundance or diminish in small fragments because of isolation and extinctions, and resulting in a decrease of species richness in fragmented forests.

However, our finding did not support SA prediction and suggested that fragment area did not bring about significantly negative effects on overall diversity (species richness and abundance) of ground-dwelling beetles. Two reasons might lead our data to the deviation from SA prediction. First, the possible exaggeration of the extinction rates by the raw SA prediction might not explain the relationship between fragment size and species loss very well for several reasons, i.e., habitat "island" analogous to real islands, mixture of endemic (specialist) and non-endemic (generalist) species, and the non-random nature of this habitat loss (Ewers & Didham, 2006). For instance, more endemic species (oak forest specialists) were abundant in large oak fragments than the small oak fragments in our study (Appendix 1), suggesting that the richness of endemic species supported the SA prediction. Moreover, a lower proportion of generalists in large fragments also indicated a significant negative relationship between forest fragment area and the proportion of generalist species (Appendix 1). This finding corroborates results from the studies in Europe that large forest fragments were favored by forest specialist species and forest generalists dominated the smaller forest fragments (Magura et al., 2001; Lövei et al., 2006; Gaublomme et al., 2008). Second, the area of large oak patches in our study was only less than 4 ha, and was considered as medium fragments only in the above studies. Thus, the difference in forest size between large and small oak patches might not be enough to

**Table 5** Akaike's information criterion (AIC) values and coefficients (and standard errors) estimated by the best-fit models (linear mixed models) of environmental variable effects on beetle assemblages.

	AIG					
	AIC	Intercept	Patch size	POBL	CC	НС
Beetles						
Species richness	-31.870	-2.711(2.365)	0.336 (0.178)	0.846 (0.348)	1.223 (0.947)	
Abundance	-6.379	4.688 (0.716)			-1.817(0.397)	
Carabidae						
Species richness	-11.200	-10.726(3.203)	0.514 (0.473)	1.688 (0.245)	4.466 (1.275)	
Abundance	20.090	-14.735(5.468)	0.177 (0.699)	2.973 (1.006)	6.622 (0.803)	-1.382(2.130)
Staphylinidae						
Species richness	18.790	2.417 (1.037)			-1.102(0.575)	
Abundance	36.531	12.008 (5.395)		-1.532(1.108)	-5.726 (0.800)	1.153 (2.537)
Curculionidae						
Species richness	-36.530	2.112 (0.452)			-0.765 (0.248)	
Abundance	0.232	3.561 (0.775)			-1.362 (0.425)	

POBL, proportion of broad-leaved trees; CC, canopy cover; HC, herb cover.

**Table 6** Akaike's information criterion (AIC) values and coefficients (and standard errors) estimated by the best-fit models (linear mixed models) of environmental variable effects on the occurrence of five selected abundant species.

	AIC	Fixed effects						
	AIC	Intercept	Patch size	POBL	CC	НС		
Carabus manifestus	12.290	-6.642 (4.920)	-0.931 (0.638)	2.729 (0.726)	4.072 (1.958)	-3.587 (0.895)		
Rhynchaenus sp.1	10.830	-2.103(5.075)	-1.211(0.675)	2.117 (0.757)	2.284 (2.115)	-3.363(0.895)		
Sympiezomias sp.1	22.640	0.083 (0.342)				0.174 (0.260)		
Sympiezomias sp.2	28.122	-3.349(3.459)	1.013 (0.739)		0.422 (1.340)	1.865 (1.069)		
Acrotrichis sp.	23.330	-5.965 (6.566)		2.709 (2.952)	2.165 (1.019)	-1.833(0.701)		

POBL, proportion of broad-leaved trees; CC, canopy cover; HC, herb cover.

bring about some significant or drastic variation in species richness and abundance of ground-dwelling beetles in this region.

The influence of the matrix on ground-dwelling beetles

The surrounding matrix is different from the forest patch itself and its quality is crucially important in determining the abundance and composition of species within fragments (Laurance, 1991; Gascon *et al.*, 1999; Kotze & Samways, 1999; Cook *et al.*, 2002; Perfecto & Vandermeer, 2002). Our results have demonstrated that the matrix dominated by conifer plantation has a detrimental effect on beetle richness and abundance, as well as on composition and distribution of the assemblages in forest fragments, consistent with previous studies in China (Yu *et al.*, 2004, 2006a, 2008, 2010).

However, the widespread species (habitat generalists) have substantial habitation overlap between fragments and matrix habitats (Cook et al., 2002), so the matrix may not be completely inhospitable to the fragment-dwelling fauna (Niemelä et al., 1988; Bauer, 1989; Usher et al., 1993; Halme & Niemelä, 1993; Davies & Margules, 1998; Estrada & Coates-Estrada, 2002; Magura et al., 2010), and even in some cases, through species invasion from the surrounding matrix habitats (especially in open habitats such as pasture and field) into the fragments, species richness and abundance increased in a short term (Web & Hopkins, 1984; Magura et al., 2001). In contrast to the above studies, conifer plantations in our study were established after the logging of natural oak forests ca. 40 years ago. Even if there would be increase of species richness through invasion from the surroundings at the early stage of succession, when pine plantations reached the stage of mature forests with closed canopies, the open-habitat species would diminish from closed-canopy pine plantations as our previous studies suggested (Yu *et al.*, 2006a, 2008, 2010).

Since habitat generalists (widespread species) might be favored by these disturbances, resulting in an increase in richness, simply counting the number of species and individuals provides little information on the assemblages and may even be misleading (Margules et al., 1994; Davies & Margules, 1998). Taking into account the habitat preferences of different species showed that the surrounding matrix habitat by conifer plantation has detrimental effects on the abundances of all forest specialists (habitat affinity groups). In this study, the abundance of the vast majority of studied species was negatively affected by the conifer plantation, i.e., most oak forest specialists (e.g., Carabus manifestus, Notiophilus impressifrous, Pterostichus acutidens, Pt. fortives, Macrocorynus sp.1, Macrocorynus sp.2, Rhynchaenus sp.2) were more abundant in the oak fragments (for some species at least in one aspect) and would diminish or decrease in abundance in the surrounding conifer plantations (Appendix 1). The degree of specialization of different species can hence be an important factor determining their susceptibility toward the surrounding matrix (Didham et al., 1996; Magura et al., 2004; Sadler et al., 2006; Gaublomme et al., 2008). Therefore, more specialist species in this study appeared to be more sensitive than generalist species, likely because they show little flexibility to cope with a changing environment.

In addition, we also found that there was a great difference in richness and abundance between the two aspects, although the same trapping regime was used for both of them. The variation in microenvironment between the two aspects, for example, humidity and temperature (or sun exposure), might result in this difference. Compared with the SE Aspect, the SW Aspect in this study is much closer to the mountaintop, perhaps resulting in a longer sun exposure and relatively drier microenvironment. All of these are usually not appropriate to the survival of ground-dwelling forest beetle species (Lövei & Sunderland, 1996; Thayer, 2005). However, since we do not have accurate data on these environmental variables, further study is still needed to test this assumption.

#### Conclusion

Two important fields of fragmentation impacts, remnant habitat areas and surrounding matrix habitats, contribute significantly to population decline in many species (Ewers & Didham, 2006). Our findings confirm that negative effects of small fragment size and surrounding conifer

plantations slightly influence species richness and abundance but have a major influence on species composition and distribution. Thus, when compared to overall diversity values of the assemblages, species turnover might be more important as a consideration.

Moreover, species responses to habitat fragmentation are governed by individual species' traits. Compared with widespread species, forest specialist species are highly susceptible to fragmentation and should be considered the most important target group for forest conservation management (Rainio & Niemelä, 2003; Ewers & Didham, 2006). Our findings also show that more disturbed sites are significantly poorer in oak forest specialists, which are only restricted within large oak fragments and decrease in abundance or disappear in small fragments and surrounding conifer plantations. Because these oak forest specialist species may not be able to disperse via corridors or stepping stones, it is necessary to preserve a minimum size of forest patch to create conditions characteristic of the forest interior, rather than the more difficult task of increasing habitat connectivity (Lövei et al., 2006).

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## **Disclosure**

This manuscript and its authors are not involved in any potential conflicts of interest, including financial interests and relationships and affiliations.

#### References

Andresen, E. (2003) Effect of forest fragmentation on dung beetle communities and functional consequences for plant regeneration. *Ecography*, 26, 87–97.

Barbosa, O. and Marquet, P.A. (2002) Effects of forest fragmentation on the beetle assemblage at the relict forest of Fray Jorge, Chile. *Oecologia*, 132, 296–306.

- Bates, D., Maechler, M. and Dai, B. (2008) lme4: Linear Mixed-Effects Models Using S4 Classes. R Package Version 0.999375–28. Available at: http://lme4.r-forge.r-project.org/.
- Bauer, L.J. (1989) Moorland beetle communities on limestone 'habitat islands'. I. Isolation, invasion and local species diversity in carabids and staphylinids. Journal of Animal Ecology, 58, 1077-1098.
- Bohac, J. (1999) Staphylinid beetles as bioindicators. Agriculture, Ecosystems & Environment, 74, 357-372.
- Burke, D. and Goulket, H. (1998) Landscape and area effects on beetle assemblages in Ontario. Ecography, 21, 472–479.
- Burnham, K.P. and Anderson, D.R. (2002) Model Selection and Multimodel Inference: A Practical Information-theoretic Approach. 2nd edn. Springer, New York.
- Chen, L.Z. and Huang, J.H. (1997) The Study on Structure and Function of Forest Ecosystem in Warm Temperate Zone. Beijing Science Press, Beijing (in Chinese with English abstract).
- Cook, W.M., Lane, K.T., Foster, B.L. and Holt, R.D. (2002) Island theory, matrix effects and species richness patterns in habitat fragments. Ecology Letters, 5, 619–623.
- Daily, G.C. and Ehrlich, P.R. (1995) Preservation of biodiversity in small rainforest patches: rapid evaluations using butterfly trapping. Biodiversity and Conservation, 4, 35-55.
- Davies, K. and Margules, C.R. (1998) Effects of habitat fragmentation on carabid beetles: experimental evidence. Journal of Animal Ecology, 67, 460-471.
- De'ath, G. (2002) Multivariate regression trees: a new technique for modeling species-environment relationships. *Ecology*, 83, 1105-1117.
- De Souza, O.F.F. and Brown, V.K. (1994) Effects of habitat fragmentation on Amazonian termite communities. Journal of Tropical Ecology, 10, 197-206.
- De Vries, H.H., Den Boer, P.J. and Van Dijk, T.S. (1996) Ground beetle species in heathland fragments in relation to survival, dispersal, and habitat preference. Oecologia, 107, 332–342.
- Didham, R.K., Ghazoul, J., Stork, N.E. and Davis, A.J. (1996) Insects in fragmented forests: a functional approach. Trends in Ecology and Evolution, 11, 255–260.
- Digweed, S.C., Currie, C.R., Cárcamo, H.A. and Spence, J.R. (1995) Digging out the digging-in effect of pitfall traps: influences of depletion and disturbance on catches of ground beetles (Coleoptera: Carabidae). Pedobiologia, 39, 561–576.
- Estrada, A. and Coates-Estrada, R. (2002) Dung beetles in continuous forest, forest fragments and in an agricultural mosaic habitat island at Los Tuxtlas, Mexico. Biodiversity and Conservation, 11, 1903-1918.
- Ewers, R.M. and Didham, R.K. (2006) Confounding factors in the detection of species responses to habitat fragmentation. Biological Reviews, 81, 117–142.
- Eyre, M.D., Lott, D.A. and Garside, A. (1996) Assessing the potential for environmental monitoring using ground beetles

- (Coleoptera: Carabidae) with riverside and Scottish data. Annales Zoologici Fennici, 33, 157-163.
- Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution and Systematics, 34, 487-515.
- Feer, F. and Hingrat, Y. (2005) Effects of forest fragmentation on a dung beetle community in French Guiana. Conservation Biology, 19, 1103-1112.
- Filgueiras, B.K.C., Iannuzzi, L. and Leal, I.R. (2011) Habitat fragmentation alters the structure of dung beetle communities in the Atlantic Forest. Biological Conservation, 144, 362-
- Gascon, C., Lovejoy, T.E., Bierregaard, R.O., Malcolm, J.R., Stouffer, P.C., Vasconcelos, H. L., Laurance, W.F., Zimmerman, B., Tocher, M. and Borges, S. (1999) Matrix habitat and species richness in tropical forest remnants. Biological Conservation, 91, 223-229.
- Gaublomme, E., Hendrickx, F., Dhuyvetter, H. and Desender, K. (2008) The effects of forest patch size and matrix type on changes in carabid beetle assemblages in an urbanized landscape. Biological Conservation, 141, 2585-2596.
- Gibbs, J.P. and Stanton, E.J. (2001) Habitat fragmentation and arthropod community change: carrion beetles, phoretic mites, and flies. Ecological Applications, 11, 79-85.
- Haila, Y., Hanski, I.K., Niemela, I.K., Punttila, P., Raivio, S. and Tukia, H. (1994) Forestry and the boreal fauna: matching management with natural forest dynamics. Annales Zoologici Fennici, 31, 187-202.
- Halme, E. and Niemelä, J. (1993) Carabid beetles in fragments of coniferous forest. Annales Zoologici Fennici, 30, 17-30.
- Jennings, D.T., Houseweart, M.W. and Dunn, G.A. (1986) Carabid beetles (Coleoptera: Carabidae) associated with strip clear-cut and dense spruce-fir forest of Maine. The Coleopterists Bulletin, 40, 251-263.
- Klein, B.C. (1989) Effects of forest fragmentation on dung and carrion beetle communities in Central Amazonia. Ecology, 70, 1715-1725.
- Korasaki, V., Lopes, J., Brown, G.G. and Louzada, J. (2013) Using dung beetles to evaluate the effects of urbanization on Atlantic Forest biodiversity. Insect Science, 20, 393-406.
- Kotze, D.J. and Sammays, M.J. (1999) Invertebrate conservation at the interface between the grassland matrix and natural Afromontane forest fragments. Biodiversity and Conservation, 8, 1339-1363.
- Laurance, W.F. (1991) Ecological correlates of extinction proneness in Australian tropical rain forest mammals. Conservation Biology, 5, 79-89.
- Lövei, G.L. and Sunderland, K.D. (1996) Ecology and behavior of ground beetles (Coleoptera: Carabidae). Annual Review of Entomology, 41, 231–256.

- Lövei, G.L., Magura, T., Tóthmérész, B. and Ködöböcz, V. (2006) The influence of matrix and edges on species richness patterns of ground beetles (Coleoptera: Carabidae) in habitat islands. *Global Ecology and Biogeography*, 15, 283–289.
- MacAthur, R.H. and Wilson, E.O. (1967) *The Theory of Island Biogeography*. Princeton University Press, Princeton. 203 pp.
- Magura, T., Ködöböcz, V. and Tóthmérész, B. (2001) Effects of habitat fragmentation on carabids in forest patches. *Journal of Biogeography*, 28, 129–138.
- Magura, T., Tóthmérész, B. and Molnar, T. (2004) Changes in carabid beetle assemblages along an urbanisation gradient in the city of Debrecen, Hungary. *Landscape Ecology*, 19, 747–759.
- Magura, T., Lövei, G.L. and Tóthmérész, B. (2010) Does urbanization decrease diversity in ground beetle (Carabidae) assemblages? *Global Ecology and Biogeography*, 19, 16–26.
- Margules, C.R., Davies, K.F., Meyers, J.A. and Milkovits, G.A. (1994) Contrasting effects of habitat fragmentation on the scorpion *Cercophonius squama* and amphipod *Arcitalitrus* sylvaticus. Ecology, 75, 2033–2042.
- Meffe, G.K. and Carroli, C.R. (1997) *Principles of Conservation Biology*, 2nd edn. Sinauer Associates, Sunderland. 729 pp.
- Nichols, E., Larsen, T., Spector, S., Davis, A.L., Escobar, F., Favila, M.E. and Vulinec, K. (2007) Global dung beetle response to tropical forest modification and fragmentation: A quantitative literature review and meta-analysis. *Biological Conservation*, 37, 1–19.
- Niemelä, J. (2001) Carabid beetles (Coleoptera: Carabidae) and habitat fragmentation: a review. European Journal of Entomology, 98, 127–132.
- Niemelä, J., Haila, Y., Halme, E., Lahti, T., Pajunen, T. and Punttila, P. (1988) The distribution of carabid beetles in fragments of old coniferous taiga and adjacent managed forest. *Annales Zoologici Fennici*, 25, 107–119.
- Niemelä, J., Haila, Y. and Punttila, P. (1996) The importance of small-scale heterogeneity in boreal forests: variation in diversity in forest-floor invertebrates across the succession gradient. *Ecography*, 19, 352–368.
- Perfecto, I. and Vandermeer, J. (2002) Quality of agroecological matrix in a tropical montane landscape: ants in coffee plantations in southern Mexico. *Conservation Biology*, 16, 174–182.
- Pohl, G.R., Langor, D.W. and Spence, J.R. (2007) Rove beetles and ground beetles (Coleoptera: Staphylinidae, Carabidae) as indicators of harvest and regeneration practices in western Canadian foothills forests. *Biological Conservation*, 137, 294–307.
- R Development Core Team (2012) *R: A Language and Envi*ronment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN3-900051-07-0, URL http://www.R-project.org.

- Rainio, J. and Niemelä, J. (2003) Ground beetles (Coleoptera: Carabidae) as bioindicators. *Biodiversity and Conservation*, 12, 487–506.
- Ries, L., Fletcher, R.J.J., Battin, J. and Sisk, T.D. (2004) Ecological responses to habitat edges: mechanisms, models and variability explained. *Annual Review of Ecology, Evolution and Systematics*, 35, 491–522.
- Sadler, J.P., Small, E.C., Fiszpan, H., Telfer, M.G. and Niemelä, J. (2006) Investigating environmental variation and landscape characteristics of an urban-rural gradient using woodland carabid assemblages. *Journal of Biogeography*, 33, 1126– 1138.
- Shahabuddin, G. and Terborgh, J.W. (1999) Frugivorous butterflies in Venezuela forest fragments: abundance, diversity and the effects of isolation. *Journal of Tropical Ecology*, 15, 703–722.
- Sokal, R.R. and Rohlf, F.J. (1981) *Biometry*. Freeman, New York.
- SPSS, Inc. (1997) SPSS Base 7.5 for Windows User's Guide. SPSS Inc, Chicago.
- Thayer, M.K. (2005) 11.7. Staphylinidae. Handbook of Zoology, Vol. IV, Part 38, Coleoptera, Vol. 1: Morphology and systematics (Archostemata, Adephaga, Myxophaga, Staphyliniformia, Scarabaeiformia, Elateriformia) (eds. R.G. Beutel & R.A.B. Leschen), pp. 296–344. Walter de Gruyter, Berlin.
- Therneau, T.M. and Atkinson, B. (2005) R port by Brian Ripley. Rpart: Recursive Partitioning. R package version 3.1–23. S-PLUS 6.x original at http://www.mayo.edu/hsr/Sfunc.html (a library for software).
- Tilman, D., May, R.M., Lehman, C.L. and Nowak, M.A. (1994) Habitat destruction and the extinction debt. *Nature*, 371, 65–66
- Tscharntke, T. and Brandl, R. (2004) Plant–insect interactions in fragmented landscapes. *Annual Review of Entomology*, 49, 405–430.
- Usher, M.B., Field, J.P. and Bedford, S.E. (1993) Biogeography and diversity of ground-dwelling arthropods in farm woodlands. *Biodiversity Letter*, 1, 54–62.
- Web, N.R. and Hopkins, P.J. (1984) Invertebrate diversity of fragmented *Calluna* heathland. *Journal of Applied Ecology*, 21, 921–933.
- Yu, X.D., Luo, T.H. and Zhou, H.Z. (2002) Composition and seasonal dynamics of litter-layer beetle community in the Dongling Mountain region, North China. *Acta Entomologica Sinica*, 45, 785–793.
- Yu, X.D., Luo, T.H. and Zhou, H.Z. (2004) Carabus (Coleoptera: Carabidae) assemblages of native forests and non-native plantations in Northern China. Entomologica Fennica, 15, 129– 137.
- Yu, X.D., Luo, T.H. and Zhou, H.Z. (2006a) Effects of carabid beetles among regenerating and natural forest types in

- Southwestern China. Forest Ecology and Management, 231, 169–177.
- Yu, X.D., Luo, T.H., Yang, J. and Zhou, H.Z. (2006b) Distribution of ground-dwelling beetles (Coleoptera) across a forest-clearcut ecotone in Wolong Natural Reserve, Southwestern China. *Insect Science*, 13, 127–135.
- Yu, X.D., Luo, T.H. and Zhou, H.Z. (2006c) Habitat associations and seasonal activity of carabid beetles (Coleoptera: Carabidae) in Dongling Mountain, North China. *Entomologica Fennica*, 17, 174–183.
- Yu, X.D., Luo, T.H. and Zhou, H.Z. (2008) Distribution of carabid beetles among 40-year-old regenerating plantations and 100-year-old naturally regenerated forests in Southwestern China. Forest Ecology and Management, 255, 2617–2625.
- Yu, X.D., Luo, T.H. and Zhou, H.Z. (2010) Distribution of ground-dwelling beetle assemblages (Coleoptera) across ecotones between natural oak forests and mature pine plantations in North China. *Journal of Insect Conservation*, 14, 617–626.

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## **Appendix**

Ground-dwelling beetle species captured  $\geq 5$  individuals of three habitats in Dongling Mountain, Beijing, north China. L1, S1, P1, L2, S2 and P2 represent large oak patches, small oak patches and surrounding pine plantations in two sites, southwestern (SW) and southeastern (SE) aspects, respectively.

Species	SW Aspect (Southwestern aspect)			SE Aspect (Southeastern aspect)			Total
	L1	S1	P1	L2	S2	P2	
Carabidae							
Carabus manifestus	0	1	2	60	24	4	91
Carabus sculptipennis	0	0	0	5	0	2	7
Carabus smaragdinus	0	0	0	0	3	2	5
Carabus sui	0	0	0	4	6	4	14
Carabus vladimirskyi	1	0	0	3	1	5	10
Notiophilus impressifrous	0	3	2	3	8	0	16
Pristosia nitidula	0	0	1	3	0	1	5
Psendotaphoxenus	0	0	0	7	5	3	15
mongolicus							
Pterostichus acutidens	0	0	0	8	12	0	20
Pterostichus fortives	0	0	0	7	1	0	8
Syunchus intermedius	0	3	0	2	0	0	5
Synuchus orbicollis	1	8	0	15	10	4	38
Curculionidae							
Curculionidae, sp.1	32	7	10	10	4	16	79
Curculionidae, sp.2	4	1	5	1	0	0	11
Macrocorynus sp.1	4	5	1	3	4	1	18
Macrocorynus sp.2	4	0	1	3	0	0	8
Rhynchaenus sp.1	48	53	40	44	26	3	214
Rhynchaenus sp.2	12	12	0	4	1	0	29
Sympiezomias sp.1	11	8	5	6	15	10	55
Sympiezomias sp.2	15	14	3	8	5	14	59
Elateridae							
Elateridae, sp.	0	1	2	1	2	0	6
Ptiliidae							
Acrotrichis sp.	3	8	9	21	16	0	57
Scarabaeidae							
Seria orientalis	3	5	1	0	0	3	12
Staphylinidae							
Staphylinidae, sp.1	0	0	4	1	1	0	6
Staphylinidae, sp.2	36	6	1	22	1	2	68
Staphylinidae, sp.3	7	2	0	3	0	2	14
Staphylinidae, sp.4	0	2	1	2	2	2	9
Staphylinidae, sp.5	0	1	3	0	0	2	6
Tenebrionidae							
Anatolica externecostata	0	0	1	3	0	2	6
Blaps rugosa	0	1	1	5	0	0	7
Scytosoma sp.1	0	6	0	4	1	2	13
Scytosoma sp.2	0	2	0	6	0	4	12