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Short-Term Responses of Ground-Dwelling Beetles to Ice Storm-Induced Treefall Gaps in a Subtropical Broad-Leaved Forest in Southeastern China

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Abstract

Periodic natural disturbances shape the mosaic character of many landscapes and influence the distribution and abundance of organisms. In this study, we tested the effect of ice storm-induced treefall gaps on ground-dwelling beetle assemblages in different-aged successional stands of subtropical broad-leaved forest in southeastern China. We evaluated the relative importance of gap-phase microhabitat type (within gap, gap edge, and interior shaded) within different stand ages (regenerating stands and mature stands) as determinants of changes in beetle diversity and community structure. At 18 replicate sites sampled during 2009–2010, no significant differences were found in species richness and the abundances of the most common beetle species captured in pitfall traps among the three gap-phase microhabitat types, but the abundances of total beetles, as well as fungivorous and phytophagous species groups, were significantly lower in gap microhabitats than in interior shaded microhabitats in mature stands. Beetle assemblage composition showed no significant differences among the three microhabitat types, and only the fauna of gap plots slightly diverged from those of edge and shaded plots in mature stands. Cover of shrubs and stand age significantly affected beetle assemblage structure. Our results suggest that beetle responses to gap-phase dynamics in early successional forests are generally weak, and that effects are more discernible in the mature stands, perhaps due to the abundance responses of forest-specialist species.

Key words: beetle assemblage, disturbance, habitat affinity, opening, successional dynamics

Disturbances create spatio-temporal heterogeneity within natural ecosystems and have a major influence on stand-age distributions, plant species composition, and functional relationships with higher trophic-level consumers within forested systems (Connell 1978, Matson and Boone 1984, Brokaw 1987, Bengtsson et al. 2000). Periodic natural disturbances such as fire or windstorms are well known to shape the mosaic character of many landscapes and influence the abundance and distribution of particular species (Levin and Paine 1974, Paine and Levin 1981) as well as community diversity (Connell 1978, Bengtsson et al. 2000). Unlike other kinds of disturbances, ice storms can cause comparatively "selective' crown loss to cold-intolerant species, thus resulting in sudden and multifaceted damage to the forest canopy (Horsley et al. 2000), such as the effects of the 1951 ice storm on Carolina Chickadee *Parus carolinensis* in Tennessee (Goodpasture 1955) and the effects of the 1998 ice storm on the deciduous forests of northeastern North America (Irland 1998).

Natural disturbances can result in the death of canopy trees and create a patchwork of canopy openings (forest gaps) of various ages and sizes within the forest. These processes initiate a dynamic succession from a gap phase characterized by little or no canopy to a mature phase with closed canopy (Whitmore 1978, Ulanova 2000, Bouget and Duelli 2004). The forest gap phase is always associated with rapid plant growth and colonization (Burton and Mueller-Dombois 1984, Denslow 1987) as well as increased flower and fruit production (Levey 1988, Smith et al. 1992), which can affect plant growth strategies (Coley 1983, 1993; Gorham et al. 2002; Cavieres and Fajardo 2005; Norghauer et al. 2008), forest regeneration cycles (Denslow 1987, Oliver and Larson 1990), and the spatio-temporal distribution of plants and the animals that interact with them (Schemske and Brokaw 1981, Harrison 1987, Brokaw and Scheiner 1989, Greenberg 2001). Although forest gaps also have the potential to influence the dynamics of animal communities, the response of animal communities to forest gaps has not been as well studied as the responses of plant communities (but see: Schemske and Brokaw 1981; Koivula and Niemelä 2003; Bouget 2005a,b; Patrick et al. 2012).

Insects, in particular, are highly sensitive to changes in environmental characteristics such as vegetation structure, temperature and moisture levels, the presence of specific microhabitats, and the quality and quantity of resources (food and shelter; Blake and Hoppes 1986; Lövei and Sunderland 1996; Bouget and Duelli 2004). Compared to habitats shaded by forests, forest gaps change some abiotic conditions and provide a wide range of microhabitats (Scharenbroch and Bockheim 2007, Stokland et al. 2012). A gap differs from the shaded understory in food resources (e.g., amounts of coarse woody debris [CWD], stressed foliage, and supplies of litter, blossoms, seeds, and fruits) and living conditions (e.g., microclimate, high light environments on the forest floor, shelter in CWD, microsites, or structurally diverse vegetation), all of which may affect forest insect communities (Bouget and Duelli 2004; Bouget 2005a,b). Several studies have found that different feeding guilds showed different responses to forest gap formation. For example, phytophagous lepidopterans needing young leaves for food appear to favor seedlings in light-rich canopy gaps (Norghauer et al. 2008), saproxylic beetles associated with CWD are influenced by the presence of forest gaps (e.g., Jonsell et al. 1998, Gorham et al. 2002, Bouget and Duelli 2004), and predaceous ground beetle activity has been found to decline following ice storm damage in maple stands of southwestern Quebec (e.g., Saint-Germain and Mauffette 2001). Therefore, it is necessary to assess the effects of forest gaps on insect communities according to their feeding guilds.

In January 2008 an intense ice storm hit South China, covering large tracts of forests with ice for ~3 wk. This storm is considered to have been the most severe ice storm to occur in the region in the past 50 yr, and >18.6 million hectares of forested land were affected (Zhu 2008). In this study, we examine the effects of treefall gaps on ground-dwelling beetle assemblages one year following ice storm disturbance in a subtropical forest of East China. Because beetle abundance and richness naturally vary through time with stand age, and the underlying successional stage of forest dynamics following earlier disturbances (Yu et al. 2006a,b,c, 2008; Luo et al. 2013), we also contrasted beetle assemblage responses to gap-phase dynamics between two forest stands of differing successional stages (naturally regenerating stands after clearcuts that occurred ca. 50 yr earlier, versus mature stands >80 yr old). We considered the responses of beetles at three levels of community organization, from the total beetle community, to the abundances of component feeding guilds (e.g., saproxylic species, fungivorous species, entomophagous and phytophagous species), to the abundances of individual species. We addressed the following key questions: 1) Does species richness and composition of beetle assemblages differ between treefall gaps and adjacent intact forest stands, and are particular species and feeding guilds more sensitive to ice storm disturbance? 2) Are there interaction effects between gap phase and successional stand age in the differing responses of species and feeding guild to disturbance?

Materials and Methods

Study Area

We conducted this study in the Gutianshan National Nature Reserve (GTS, ~81 km^2 in area) located in Kaihua County, Zhejiang Province, East China (29° 10′19″–29° 17′41″ N, 118° 03′50″–118° 11′12″ E; Fig. 1a, b). The climate is strongly seasonal, typically with two distinct dry seasons (July–August and October–February; Lai et al. 2009). Annual mean temperature in the region averaged 15.3°C and annual mean precipitation averaged 1,964 mm between 1958 and 1986 (Yu et al. 2001). The forest is representative of Chinese mixed broad-leaved forests (Wu 1980, Hu and Yu 2008, Legendre et al. 2009), with typical subtropical evergreen species such as *Castanopsis eyrei* (Champ. ex Benth.) Tutch. (Fagaceae) and *Schima superba* Gardn. et Champ. (Theaceae) dominating the forest canopy (Yu et al. 2001). A total of 1,426 seed-plant species of 648 genera and 149 families have been recorded as occurring naturally in the Reserve, and about 258 of the species are woody (Lou and Jin 2000). The reserve consists mainly of secondary forest that has been disturbed by human activities over the past 100 yr, including wildfires in the 1920s, clearcutting for agriculture and charcoal production in the 1950s, and selective logging for charcoal production in the 1980s (Zhu 1995). As Bruelheide et al. (2011) suggest, 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 yr; 2, > 20 and < 40 yr; 3, > 40 and < 60 yr; 4, > 60 and <80 yr; 5, > 80 yr). Currently, most of the forest in the reserve is in the middle (ca. 40–50 yr) and late (>80 yr) forest successional stages. For more detailed descriptions of climate, topography, flora, and successional stages, see Legendre et al. (2009) and Bruelheide et al. (2011).

The ice storm in January 2008 lasted ~3 wk and caused severe damage to roughly one-third of the trees, leading to the formation of many treefall gaps throughout the Reserve (Man et al. 2011). Eighteen study sites in regenerating and mature forests were selected a priori to represent typical subtropical evergreen broad-leaved forests (Fig. 1b). Twelve sites were dominated by naturally regenerating stands after clearcut (ca. 50 yr), and six other sites were mature stands (>80 yr). Regenerating and mature stands correspond to the stage 3 (age: <60 yr; mean DBH: 22.80 cm; plant diversity: 96 species) and stage 5 (age: >80 yr; mean DBH: 33.93 cm; plant diversity: 104 species) during secondary forest succession in the study region, respectively (Bruelheide et al. 2011). Each site was centered on a canopy gap created by the ice storm and comprised 1) a “gap plot" (at the center of the treefall gap, without any standing dead trees), 2) an “edge plot" (at the edge of the treefall gap, with semiopen canopy), and 3) a “shaded plot" (in the adjacent shaded understory, with closed canopy; Fig. 1c). The distance between any two adjacent sites (i.e., between gap patches) was always >500 m. The area of gaps was 40–270 m^2 (mean ± SD: 120 ± 70 m^2) in regenerating stands, and 80–170 m^2 (mean ± SD: 125 ± 30 m^2) in mature stands.

Sampling

We collected beetles using pitfall traps (mouth diameter 75 mm, depth 90 mm), filled with ca.100 ml of preservative fluid (vinegar:sugar :alcohol:water, 10 ml:5 g:5 ml:20 ml; Yu et al. 2006a,b). A small rainwater overflow hole (diameter ca. 2 mm) was drilled in each trap ca. 2.5 cm below the upper rim. We placed a group of five traps in each of the gap, edge and shaded plots at each site (Fig. 1c). Thus, we had 54 samples and 270 traps used in this study, i.e., 18 sites, 3 plots per site, and 5 traps per plot.

The distances of the trap groups from the edge of a gap varied (negative values indicate gap plots and positive values indicate shaded plots) between −5 and −9 m (mean: −7 m) in the gap plots, between −1 and 1 m in edge plots (mean: 0 m), and between 15 m and 20 m in the shaded plots (mean: 18 m). Within each plot, the five traps were 1 m apart in a crossed pattern.

Sampling was conducted from June to October 2009 and May to June 2010. Traps were open for three consecutive days, once every three 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, CAS. Only adult beetles were used in the analysis and

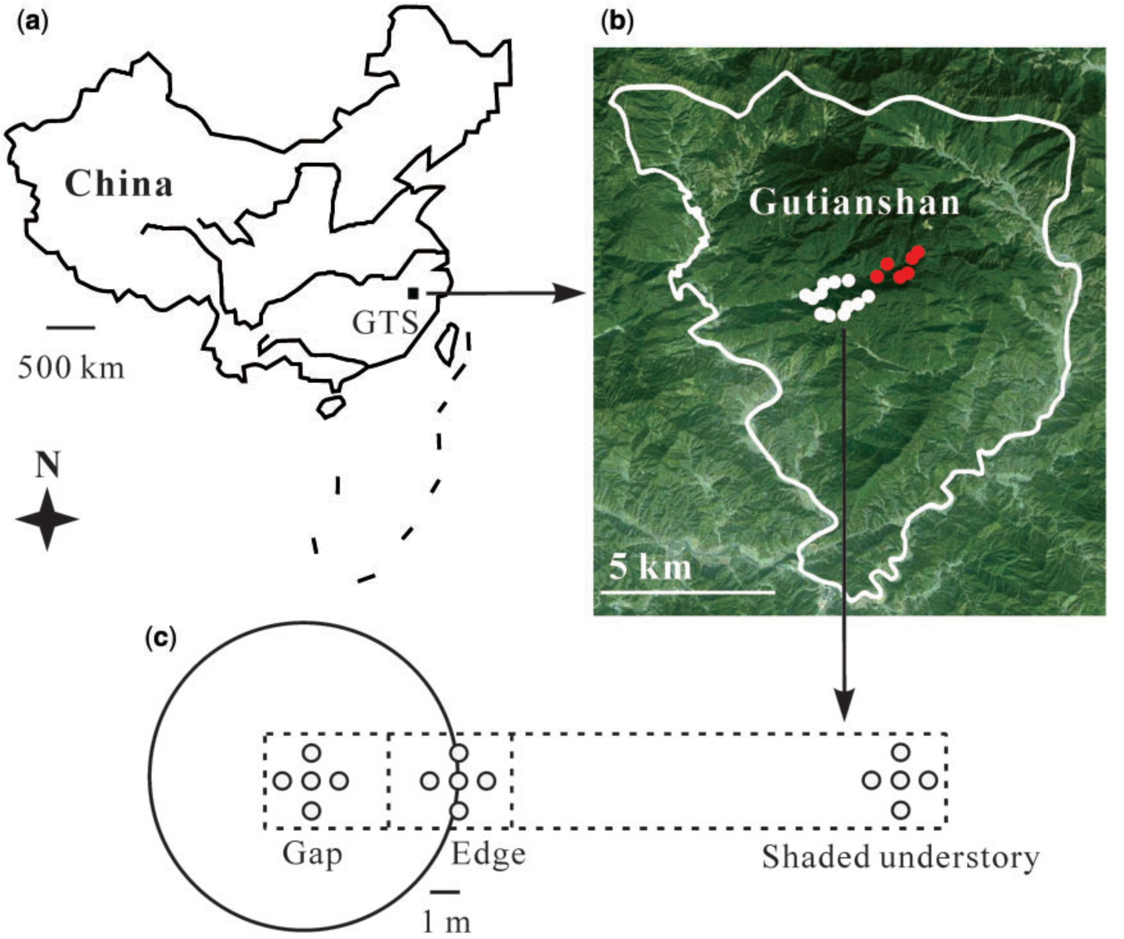

Fig. 1. Study areas and experimental design. The 18 sites, each consisting of a gap and its immediate surroundings, were situated in GTS. (a) The upper left-hand figure shows the location of the reserve. (b) The upper right-hand figure shows the locations (white dots: 50 yr old; red dots: > 80 yr old) of 18 sites in the reserve. (c) The bottom figure shows the experimental design in a hypothetical gap patch and pitfall traps are represented by circles. Traps in each plot type (gap, edge, and shaded understory) are outlined with dotted lines.

were identified by the taxonomists listed in the Acknowledgments section. A full species list is provided in Supp Appendix 1 (online only).

Seven environmental variables were selected 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 Supp Appendix 2 (online only).

Data Analysis

Pitfall trap captures were pooled at the plot level for the purposes of data analysis (i.e., pooling all five pitfall trap samples, across all time intervals, within each plot). We used generalized linear mixed models (GLMMs) to test the effect of stand age (regenerating or mature stands) and gap phase (gap, edge, or shaded), plus their interaction, on beetle abundance and species richness (Bolker et al. 2008). We specified site identity (18 sites) as a random factor to account for the nonindependence of plots within sites (Digweed et al. 1995, Matveinen-Huju et al. 2009). Model selection utilized a multimodel inference approach, with models within 2 AIC units of the best-fit model considered to have strong support (Burnham and Anderson 2002). All analyses were conducted in R 3.1.2 software with the "lme4" package (R development Core Team 2012). To investigate whether species composition differed as a function of the gap phase and stand age, we categorized beetle species according to their feeding strategies, into saproxylic, fungivorous, entomophagous, phytophagous, decomposer, and scavenger guilds. In addition, the responses of the most abundant beetle species (>1% of the total capture, 17 individuals) per habitat affinity group were analyzed in detail to explore species-specific response patterns.

We used nonmetric multidimensional scaling (NMDS) to evaluate the importance of gap phase (gap, edge, and shaded) and stand age (regenerating and 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 gap phases 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 2012).

Table 1. The effects of stand age and gap phase on total beetle species richness, total abundance, and the abundance of feeding guilds and their dominant component species (species with >1% of the total catch) by GLMMs

	Stand age	Gap phase	Stand age × gap phase
Species richness	NS		
Abundance	R < M***	NS	R: NS M: G = E < S***
Saproxylic species	NS		
Cryphalus exignus		G < E = S***	
Cryphalus massonianus	R < M***	NS	R: NS M: G < E = S**
Xyleborinus saxeseni	R > M***		
Xyleborus rubricollis		G > E > S**	
Xylosandrus compactus	R > M***		
Xylosandrus germanus	NS		
Fungivorous species	R < M***	NS	R: NS M: G < E = S**
Anotylus nitidifrons	R < M***	G < E < S***	
Catops sp.	R > M**		
Ptomaphaginus gutianshanicus	R < M**	E > G = S**	
Entomophagous species	R < M***		
Acrotona inornata	R < M***		
Myas sp.	R < M*		
Pterostichus pratii	R < M**		
Phytophagous species	NS	NS	R: NS M: G < E = S***
Coelosternulum sp.	R > M***	NS	R: NS M: G < E < S***
Sipalinus gigas	R > M**		

Stand age: R, regenerating stands (50 yr old); M, mature stands (>80 yr old); gap phase: G, gap; E, edge; S, shaded. Significance level for the coefficients in GLMMs: * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$, NS: not significant.

A distance-based redundancy analysis (dbRDA) with Bray-Curtis as the distance metric was used to compare the relationship between beetle assemblage structure and the possible environmental variables. We included two treatments (gap phase 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. We also used site identity as a covariate to partial out the effect of site before analyzing the effects of possible environmental variables. dbRDA was performed using the "vegan" package in R 3.1.2 software (R Development Core Team 2012).

Results

We captured 1,714 ground-dwelling beetles during the two study years, corresponding to 118 species (Supp Appendix 1 [online only]). A total of 31 species (700 individuals) were saproxylic species with an affinity for CWD, 19 species (354 individuals) were fungivorous, 31 species were entomophagous (288 individuals), 23 species were phytophagous (281 individuals), and 14 other species (91 individuals) were decomposers or scavengers.

Abundance and Species Richness

No significant effects of gap phase and stand age were found in species richness (Table 1). In contrast, total beetle abundance was significantly higher in mature stands than in regenerating stands, and total abundance was significantly higher in shaded plots than in gap and edge plots (Table 1). After species were pooled according to their feeding guilds, decomposers and scavengers had few species and individuals, so we did not include them in subsequent analyses. Saproxylic and entomophagous species did not show significant responses to the treefall gaps (Table 1). In contrast, fungivorous and phytophagous species showed negative responses to the treefall gaps, with significantly lower abundance in gap plots than in shaded plots and edge plots, at least in mature stands (Table 1). The abundance of entomophagous species and fungivorous species was significantly higher in mature stands than in regenerating stands (Table 1).

Of six saproxylic species, *Cryphalus exignus* Blandford and *Cryphalus massonianus* (Tsai et Li) showed negative responses to treefall gaps in mature stands, and their abundances were significantly lower within gap plots than in the shaded and edge plots, at least in mature stands. *Xyleborus rubricollis* (Eichhoff) responded positively to treefall gaps, and its abundance increased significantly from shaded plots and edge plots towards gap plots. Three other species did not show significant responses to treefall gaps (Table 1). In addition, *Xylosandrus compactus* (Eichhoff) and *Xyleborinus saxeseni* (Ratzeburg) were more abundant in regenerating stands than in mature stands, whereas *Cryphalus massonianus* was more numerous in mature stands (Table 1).

Of three abundant fungivorous species, *Anotylus nitidifrons* (Wollaston) showed a negative response to treefall gaps, and its abundance decreased significantly from shaded plots, gap edge plots toward within gap plots, but *Ptomaphaginus gutianshanicus* (Wang and Zhou) was significantly more abundant in gap edge plots than within gap and shaded interior plots (Table 1). In addition, more individuals of *Anotylus nitidifrons* and *Ptomaphaginus gutianshanicus* were found in mature stands than in regenerating stands, whereas *Catops* sp. was more abundant in regenerating stands (Table 1).

Three entomophagous species—*Acrotona inornata* (Kraatz), *Myas* sp., and *Pterostichus pratii* (Bates)—did not respond significantly to the treefall gaps, but all of them were more abundant in mature stands than in regenerating stands (Table 1).

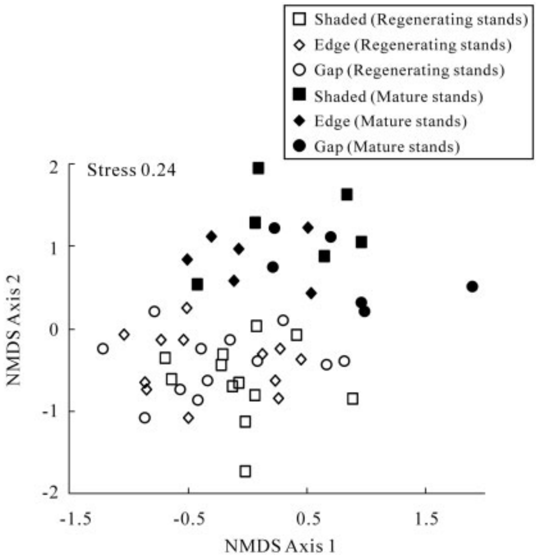

Fig. 2. NMDS solutions for ground-dwelling beetles. The stress value indicates the analysis performance; the axis values only aid in demonstrating the relative distances between samples.

Of two phytophagous species, only *Coelosternulum* sp. showed a significant response to the treefall gaps in mature stands, and its abundance decreased significantly from shaded interior plots, gap edge plots toward within gap plots (Table 1). Both *Coelosternulum* sp. and *Sipalinus gigas* (Fabricius) were also more abundant in regenerating stands than in mature stands (Table 1).

Species Composition

NMDS indicated a divergence between regenerating and mature stands (Fig. 2). In addition, there was also a difference among the plot types in mature stands, especially between the shaded and within gap plots, but the regenerating stands showed a considerable overlap among the plot types. PERMANOVA also indicated that only stand age significantly affected species composition ($F = 12.74$, df = 1, $P = 0.0001$); gap phase and their interaction (gap phase × stand age) did not show statistically significant effects on species composition (gap phase: $F = 0.90$, df = 2, $P = 0.588$; interaction: $F = 1.03$, df = 2, $P = 0.395$).

The dbRDA showed a highly significant relationship between the environmental variables and beetle species distribution ($F = 1.26$; $P = 0.001$; 999 permutations). Of the nine environmental variables, only cover of shrubs ($F = 1.76$, $P = 0.005$) and stand age ($F = 2.47$, $P = 0.001$) were significant determinants of beetle species composition in the ordination analysis (Fig. 3). Cover of shrubs associated with shaded understory habitats in mature stands was greatest at the upper left of the ordination, and only *Xylosandrus germanus* (Blandford) was associated with this gradient in shrub cover (Fig. 3). Stand age was greatest at the left of the ordination space, and most species clustered in this direction, indicating a preference for plots in mature stands, i.e., *Acrotona inornata*, *Anotylus nitidifrons*, *Cryphalus massonianus*, *Myas* sp., *Onthophagus hayashii* (Masumoto), *Pterostichus pratii*, *Ptomaphaginus gutianshanicus*, and *Xyleborus rubricollis* (Fig. 3). In addition, *Catops* sp., *Coelosternulum* sp., *Sipalinus gigas*, *Xyleborinus saxeseni*, and *Xylosandrus compactus* were located on the opposite direction of the axes of stand age and cover of shrubs, suggesting a preference for open habitats in regenerating stands (Fig. 3).

Discussion

Gap Phase Effects

Compared to the shaded intact forests, forest gaps change some abiotic and biotic conditions such as CWD, foliage, litter, microclimate, sun exposure, plant diversity, and vegetation structure (Bouget and Duelli 2004; Bouget 2005a,b; Scharenbroch and Bockheim 2007; Stokland et al. 2012). Many studies have found significant negative or positive effects of forest gaps on species richness, abundance, and composition of insect communities, especially for some specific species groups associated with CWD (saproxylic species: e.g., Jonsell et al. 1998, Gorham et al. 2002, Bouget and Duelli 2004), young foliage (phytophagous species: e.g., Norghauer et al. 2008), and sun exposure or shadiness (fungivorous species or entomophagous species: e.g., Saint-Germain and Mauffette 2001). Corroborated with these above studies, our study also found significant differences in beetle abundances and composition between gap and shaded plots at three levels of community organization (total beetle community, component feeding guilds, and individual species) at least in mature stands. Moreover, some particular feeding guilds (fungivorous and phytophagous species groups) and abundant species were tested to be more sensitive to ice storm disturbance, indicating the roles of microhabitat variables associated with gap phases (e.g., CWD, sun exposure, and young foliage) on beetle abundance and assemblage composition.

Fresh deadwood (CWD) which are usually more abundant in forest gaps always attract many saproxylic beetles to colonize, especially for bark beetles (pioneer xylophagous species; Wermelinger et al. 2002, Bouget 2005a). However, we counted the number of available CWD and found that there was no significant difference in CWD in the shaded and gap plots (Supp Appendix 2 [online only]); thus, CWD might not be a limiting factor for saproxylic beetles in our study. Some studies found that many kinds of fungal species occupied sun-exposed sites and were easy to be developed on fresh dead wood, so the increasing sun-exposed CWD might attract some specific fungivorous beetles to colonize in the forest gaps (Rukke and Midtgaard 1998, Sippola et al. 2002, Bouget 2005a). In this study, we did not observe any fungivorous species preferring forest gaps. Extensive rainfall throughout the study region during our sampling periods could have affected the development of sunlight-demanding fungi in CWD, thus resulting in the lack of fungivorous specialists preferring sunlight-demanding fungi in the forest gaps (Table 1).

Sun exposure or shadiness (associated with humidity, temperature) is one of the most important determinants in habitat preferences of most ground-dwelling beetles (e.g., Blake and Hoppes 1986; Lövei and Sunderland 1996; Yu et al. 2006a,b, 2010, 2014). For example, some saproxylic species preferred dense and shady microenvironments in intact forests (Wermelinger et al. 2002, Bouget 2005a), and fungivorous beetles depended on the availability of fungi which usually live in shaded microenvironments (except those sunlight-demanding fungi). Therefore, a high proportion of shadiness in intact forests in our study (Supp Appendix 2 [online only]) might attract more saproxylic and fungivorous beetles to colonize in shaded intact forests at least in mature stands, e.g., *Cryphalus exignus*, *Cryphalus massonianus*, and *Anotylus nitidifrons* (Table 1). Similarly, most forest entomophagous beetles (e.g., carabids and staphylinids) usually preferred the closed-canopy (shaded) microhabitats to open habitats (Yu et al. 2006a, 2007). However, we did not find obvious preferences of entomophagous species to any microhabitat type. Small size of forest gaps might be possible explanations for these findings. The forest openings in our study

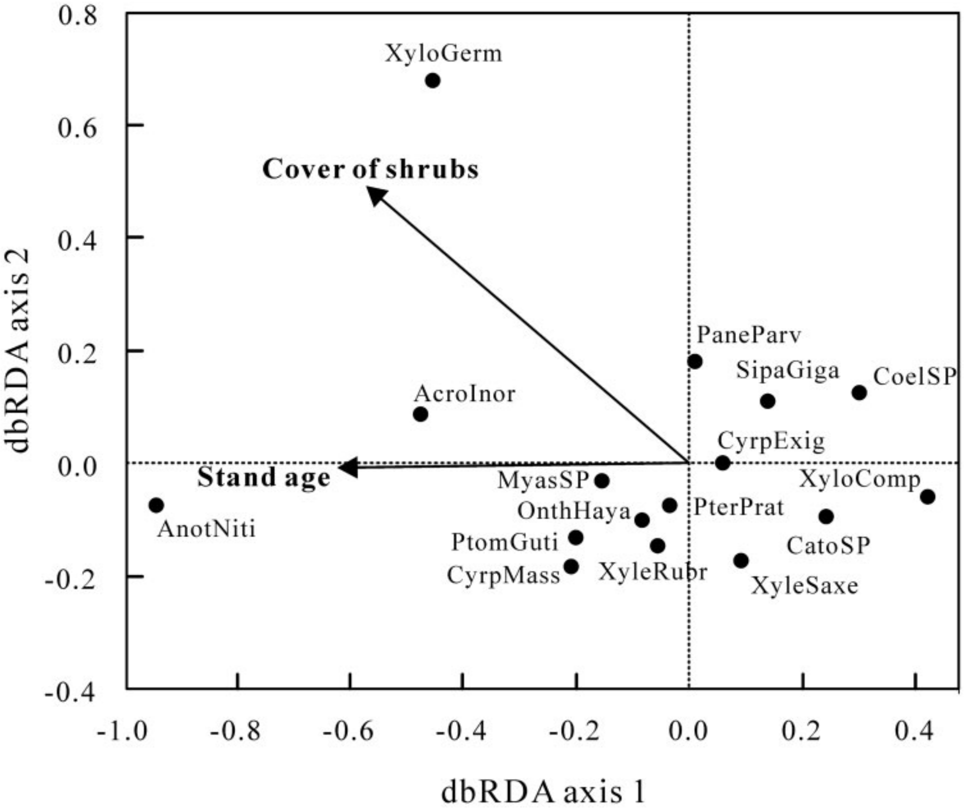

Fig. 3. DbRDA showing species–environment relationships for ground-dwelling beetle species in relation to dominant gradients of variation in stand age and cover of shrubs. Only species with >1% of the total catch (17 individuals) are presented. The beetle species are annotated with genus and species abbreviations (e.g., *Anotylus nitidifrons* = AnotNiti); see Supp Appendix 1 (online only) for details.

ranged from 40–270 m^2 and were just at the smallest size level of previous studies (e.g., Shure and Phillips 1991, Wermelinger et al. 2002, Koivula and Niemelä 2003, Bouget 2005a). Small sizes of forest openings led to a relatively high proportion of shadiness compared with the larger gaps, and thus most forest species could survive in these small gaps (Table 1). Moreover, small size of forest gaps resulted in a diffuse amount of light flecking and limited light intensity. Thus, these small gaps might not support open-habitat species, opposing the general rule that rapid population increases due to open habitat species aggregation should be observed in the disturbed sites (e.g., Niemelä et al. 1993; Spence et al. 1996; Koivula 2002a,b). Patrick et al. (2012) also found no significant differences in litter ant assemblages between small treefall gaps (only 0.008 ha) and intact forests in a tropical montane cloud forest.

Phytophagous species appear to favor young leaves from seedlings and saplings, which are often more abundant in light-rich canopy gaps (Norghauer et al. 2008). However in our study, we found that shrubs composed of a lot of saplings were more abundant in the shaded intact forests than in the forest gaps (Supp Appendix 2 [online only]), resulting in an increase in abundance of phytophagous species in the shaded plots in mature stands (Table 1).

Interactive Effects Between Gap Phase and Stand Age

The interaction between gap phase and stand age had a significant effect on the abundance of all beetles, fungivorous and phytophagous species groups, and two abundant species (i.e., *Cryphalus massonianus*, *Coelosternulum* sp.). In mature stands, the abundances of these groups or abundant species were much higher in the shaded understory, whereas in young regenerating stands, there were no significant differences among the three plot types. Moreover, stand age seems to play an important role for ground-dwelling beetles. Nearly all groups and abundant species responded significantly to stand age, corroborated with our previous studies (e.g., Yu et al. 2006a,c, 2008). These findings suggest that beetle assemblages in early successional stands might be dominated by disturbance-tolerant species, and therefore a new ice storm-induced gap might have little influence on species composition. By contrast, there might be more disturbance-intolerant species in the mature forests and therefore treefall gaps might have a larger effect.

The small size of gaps should be considered in caution in this study. The sample sizes are relatively small, which might be seen to limit the interpretive value of the work. However, there are significant trends for the more abundant taxa, and the fact that gap effects are most pronounced in the mature forest stands also makes good biological sense. In addition, because the older stands are further from human settlements, mature stands and regenerating stands are completely spatially separated in the study area. This leads to spatial autocorrelation of the stand-age treatment effect, and inference about stand age is therefore limited by this problem. Normally this type of problem could negate the conclusions of a manuscript, but in this case because the same gap-phase sampling design was deployed at all locations, it would have a bearing on the main findings about gap-phase effects, or the interaction between gap-phase and stand age.

In total, our results suggest that beetle responses to gap-phase dynamics in early successional forests are generally weak, and that effects are more discernible in the mature stands in a subtropical forest in East China, perhaps due to the abundance responses of forest-specialist species.

Supplementary Data

Supplementary data are available at *Environmental Entomology* online.

Acknowledgments

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