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Ground beetle assemblages in Beijing's new mountain forests

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ABSTRACT

Mature forests have been almost completely destroyed in China's northern regions, but this has been followed by large-scale reforestation in the wake of environmental degradation. Although future forest plantations are expected to expand over millions of hectares, knowledge about the ecology and biodiversity of China's replanted forests remains very limited. Addressing these knowledge gaps, we recorded ground beetle (Coleoptera: Carabidae) communities in five secondary forest types: plantations of Chinese Pine (*Pinus tabulaeformis*) and Prince Rupprecht's Larch (*Larix principis-rupprechtii*), Oak (*Quercus wutaishanica*) and Asian White Birch (*Betula platyphylla*) woodlands, and naturally regenerated mixed forest. Species richness peaked in mixed forests, while pine and oak woodlands harboured discrete communities of intermediate species richness. Oak, pine and mixed forest habitats also showed high levels of species turnover between plots. Canopy closure was an important factor influencing ground beetle assemblages and diversity, and a number of forest specialist species only occurred in pine or oak forests. We believe that some forest specialists have survived earlier deforestation and appear to be supported by new plantation forests, but maintenance of secondary native oak and mixed forests is crucial to safeguard the overall species pool.

1. Introduction

Global declines of mature forests render secondary forests and forest plantations increasingly important for the conservation of forest biodiversity (Brockerhoff et al., 2008). Global forest area declined by 5.6 million ha per year from 2005 to 2010 (FRA, 2010) with only 36% of global forest area classified as primary forest, and 53% as modified natural forests in 2005 (FAO, 2006). While forest plantations account for around 3.5% of global forests, large-scale plantations are planned in many regions of the world, and global plantation forest area expanded by approximately 14 million ha from 2000 to 2005 (FAO, 2006). Enhancing understanding of biodiversity patterns in planted and secondary forests is therefore of paramount importance to optimise their potential conservation value.

In China, forests cover approximately 195 million ha (Jia et al., 2011), but estimates suggest only 30% of this area comprises mature forest (Li, 2004). Loss of mature forest ecosystems in China has been accompanied by the extinction of at least 200 plant species and severe habitat loss for large mammals (López-Pujol et al., 2006; Sang et al., 2011); meanwhile, impacts on the species-rich insect fauna are widely unknown (You et al., 2005). The 32% decline in China's mature forest cover from 1950 to 2005 was accompanied by an increase in the proportion of land area covered by forest plantations, from 5.2% to 16% (FAO, 2006). Forest plantations are commonly established to protect watersheds and reduce soil erosion (Zhang et al., 2000), but their role in supporting biodiversity has been widely ignored. It is generally assumed that these plantations have inferior ecological functioning (Li, 2004), not least due to widespread use of tree monocultures even in ecological restoration programmes, like the Natural Forest Conservation Programme and "Grain to Green" projects (Cao et al., 2011; Lü et al., 2011). Accordingly, the net gain in China's forest cover of approximately 4 million ha annually from 2000 to 2005 (FAO, 2006) is

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believed to have had little influence on forest biodiversity (Lü et al., 2011).

China's temperate forest zone has been heavily depleted of mature forests, with widespread forest plantations and secondary forests becoming integral in supporting the region's biodiversity. The forested landscape currently comprises a mosaic of patches occupied by native and exotic, broadleaved and conifer tree species (Ma and Fu, 2000), providing a unique setting for investigations into biodiversity patterns in different secondary and plantation forest types. These patterns are poorly understood, especially in relation to highly species-rich invertebrate taxa like ground beetles (Coleoptera: Carabidae). In Europe and North America, carabids have been commonly used to compare the ecology of pristine forests and exotic conifer plantations (Magura et al., 2000; Elek et al., 2001), different conifer species plantations (Jukes et al., 2001; Finch, 2005) and in relation to plantation management (Magura et al., 2002; Fuller et al., 2008). Carabids are taxonomically well known at least in temperate areas, their ecology is relatively well understood (Lövei and Sunderland, 1996; Kotze et al., 2011) and they are sensitive to environmental change, showing strong habitat specificity and low inter-patch dispersal rates (e.g. Butterfield et al., 1995; Barbaro et al., 2005; Pearce and Venier, 2006; Work et al., 2008; Koivula, 2011). With over 35,000 described species (1573 species known from China) and new descriptions reaching 100 species per year (Lorenz, 2005; Kotze et al., 2011), they are a mega-diverse taxon.

In comparison to Europe and the US, carabid assemblages in northern China currently remain poorly understood. Yu et al. (2010) suggest that in temperate China, native pine (*Pinus tabulaeformis* (Carr.)) plantations support fewer carabid species and individuals than natural oak (*Quercus wutaishanica* (Mayr)) forests, while *Carabus* spp. appear to be more abundant in mixed broadleaf forests and larch plantations than in oak forests (Yu et al., 2004). However, little else is known.

Our study therefore addresses the urgent need for a better understanding of changes in ground beetle communities between different temperate forest types in China. We aim to assess the relative contribution of different plantation types and naturally regenerated forests towards α- and γ-diversity of ground beetles, while also assessing the contribution of environmental factors towards observed diversity patterns. Our findings have implications for the future planning, management and restoration of secondary forests and plantations in the temperate forests of China.

2. Material and methods

2.1. Study area

The study was conducted at the Beijing Forest Ecosystem Research Station (BFERS), 114 km west of Beijing city centre (40°00′N, 115°26′E, Fig. 1) in the transitional zone between the North China Plain and the Mongolian altiplano. The area around the BFERS has an altitudinal range of 800–2300 m and experiences a cool-temperature monsoon climate, with an average annual temperature of 4.8 °C (January −10.1 °C, July 18.3 °C). Average annual precipitation reaches 612 mm, with 78% of rainfall occurring between June and August (Sang, 2004).

The oak-dominated (*Q. wutaishanica*) forests originally covering most of the study area were destroyed during extensive deforestation in the 1960s (Li, 2004; Yu et al., 2010). Subsequent soil erosion and flooding stimulated the establishment of widespread non-extractive forest plantations. Unlike many exotic conifer plantations found across the globe, the plantation tree species are chiefly native to the wider region, although they naturally occur in mixed forests rather than monoculture, and often at different elevations to the current plantations (Zhang et al., 2009). The resulting reforested landscape is highly fragmented, with a mosaic of different forest and scrub types, farmland and settlements (Ma and Fu, 2000).

The area surrounding the BFERS is dominated by secondary *Q. wutaishanica* woodland, while stands of the native birch species *Betula platyphylla* (Sukaczev) and *B. dahurica* (Pall.) have become established, especially at higher elevations. Natural regeneration has also led to the establishment of a mixed forest of broadleaved and conifer species, while non-extractive pine (*P. tabulaeformis*) and larch (*Larix principis-rupprechtii* (Mayr.)) plantations cover significant areas. *P. tabulaeformis* is a popular plantation species naturally co-occurring with *Q. wutaishanica* at elevations of 1200–2000 m, whereas *L. principis-rupprechtii* grows naturally at elevations between 1610 and 2445 m in northern China (Zhang et al., 2009), although larch monocultures are commonly encountered at lower altitudes.

We selected study sites in the five dominant forest types: larch, pine, mixed, oak and birch forest. These all harbour a well-developed and diverse understory of subdominant trees, shrubs and herbs. All study sites were located on steep slopes of 15–39° between 1165 m and 1410 m, with larch and birch forest sites located on north-exposed slopes in accordance with their general distribution, while sites representing the other forest types varied in their exposition. Following exploration of forest type boundaries on the ground, four plots were selected in each forest type to survey vegetation and sample ground beetles. Plots were positioned at least 50 m away from each other to ensure sample independence (Digweed et al., 1995). A distance of at least 15 m was kept to any path or open space to minimise edge effects. This was deemed sufficient since carabids do not respond strongly to edge effects in forest landscapes (Heliölä et al., 2001). Plots were located in areas that appeared representative of the overall forest structure, and plot locations were recorded using GPS. In the centre of each plot location, two pitfall traps were set two metres apart, giving a total of eight traps per forest type. Plots were necessarily grouped relatively closely together due to the small patch size of each forest type and the need to avoid transitional zones. Plot locations were selected to provide distinct results in relation to the specific carabid assemblages supported by each forest type.

2.2. Ground beetle sampling

Sampling occurred over ten weeks between July and August 2011 and over thirteen weeks between June and September 2012, to coincide with peaks in carabid activity reported from the same area (Yu et al., 2006). Plastic cups with a diameter of 7.5 cm and a depth of 10.2 cm were used as pitfall traps, protected by a metal roof positioned ~6 cm above the cups. Traps were filled with 100–150 millilitres of a super-saturated salt water solution (>300 g salt/L) with a small amount of detergent added to break the surface tension. Salt solution has the advantage of being odourless and not attractive to particular species, thereby minimising bias in the species composition within samples (Kotze et al., 2011). For the same reason, we did not use bait in the pitfall traps. Traps were emptied at least fortnightly throughout the sampling period, and no disturbance of traps by animals or people was observed during the sampling period. Reliance on pitfall trapping for assessments of carabid communities is associated with known problems, including overrepresentation of large-bodied species (Work et al., 2002), but field testing of alternative methods including light trapping and litter sampling yielded very low capture rates. Pitfall trap samples represent activity densities rather than "true" densities (Baars, 1979; Spence and Niemelä, 1994); therefore, 'abundance' in this paper always refers to 'activity density' rather than true abundance patterns.

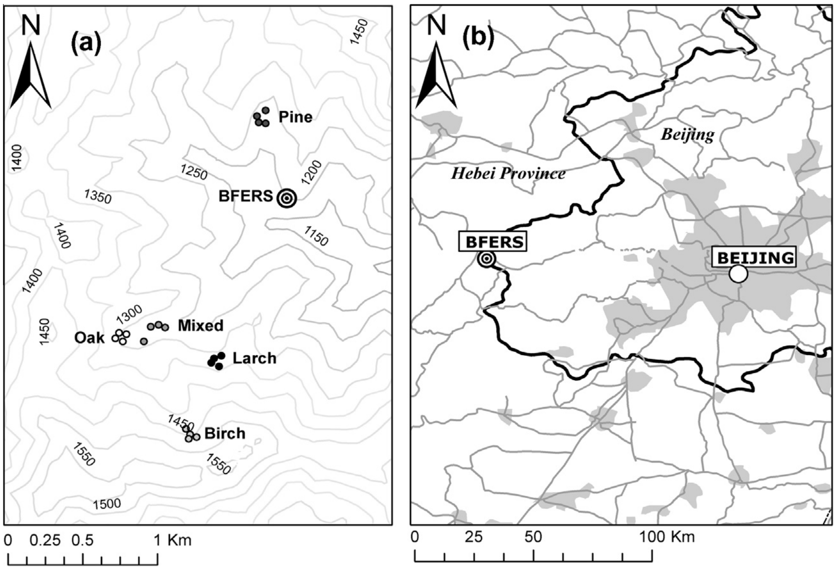

Fig. 1. Map of the study area, showing (a) the location of the four plots within each forest type in relation to the Beijing Forestry Ecosystem Research Station (BFERS) and (b) the location of the study site in a regional context (roads are shown as grey lines, urban areas as grey shading and provincial boundaries as a solid black line).

All specimens were identified using reference collections at the China Agricultural University and the Chinese Academy of Sciences, as well as online references (Berlov, 2002; Anichtchenko et al., 2011). They have subsequently been deposited at the Chinese Academy of Sciences.

2.3. Environmental data

A number of environmental parameters were recorded within a 2 × 2 m quadrat centred on the two pitfall traps of each plot. Canopy cover density was measured using the canopy scope method (Brown et al., 2000). Shrub, ground and leaf litter cover were estimated using four 1 × 1 m quadrats placed either side of a 2 m line drawn between the two pitfall traps. Leaf litter samples were collected from a 0.25 × 0.25 m quadrat, clearing everything down to the humus layer (Spence and Niemelä, 1994), dried at 60 °C and weighed. Shrub and ground vegetation height were also recorded. Aspect and slope were measured using an inclinometer, and altitude was measured using a barometric altimeter.

The presence of all tree and shrub species were recorded in a 20 × 20 m^2 quadrat centred on each plot. This large quadrat was then subdivided into four 10 × 10 m^2 squares where the presence of all herb species was recorded in one 1m^2 plot randomly located in each square. The resulting species lists were used as a measure of plant species richness for each forest type.

2.4. Data analysis

All carabid specimens collected from individual traps were pooled at plot level for analysis. Differences in species richness between habitats was investigated using the rarefaction–extrapolating method (Chao and Jost, 2012; Colwell et al., 2012), which we calculated using iNEXT (Hsieh et al., 2013). A standardized extrapolated sample size of 600 individuals was selected as basis for the species richness comparisons between different forest types. This number represents four times the smallest total sample size recorded from an individual forest type.

To investigate changes in the species composition and turnover between plots and habitats, non-metric multidimensional scaling (NMDS) of the Chord-Normalised Estimated Species Shared (CNESS) Index (Trueblood et al., 1994) was computed for the maximum common sample size of the plot samples (five). The CNESS index was calculated using COMPAH96 (Gallagher, 1998), and the non-metric multidimensional scaling plot was created using PASW Statistics 18. Redundancy Analysis (RDA) was subsequently used to establish links between environmental factors and the turnover within the carabid assemblages using ECOM version 1.37 (Pisces Conservation Ltd.). Species abundance data was CHORD transformed prior to the RDA, and multi-collinearity within the *z*-transformed environmental data was insignificant.

3. Results

3.1. Carabid abundance and diversity

A total of 1191 ground beetles comprising 23 species were collected in the pitfall traps (Appendix 1). Carabid abundance was notably higher in birch and larch forest than in the other forest types (Fig. 2a). Three species (*Carabus smaragdinus*, *Harpalus bungii* and *Panagaeus davidi*) were represented by only one individual in our overall samples and a further species (*Asaphidion semilucidum*) was represented by only one individual within both oak and mixed forests, respectively, while 12 species were represented by at least ten individuals. *Pterostichus acutidens* (Fairmaire, 1889) was by far the most common species, accounting for 44.4% of the total catch (531 individuals), with highest abundances recorded in larch (representing 64% of all individuals, Fig. 2f) and birch forests (representing 64% of all individuals, Fig. 2e), but also accounting for 57% of all individuals caught in mixed forests (Fig. 2b). *Carabus crassesculptus* (Kraatz, 1881) made up 16.3% of the total catch (195 individuals), being more evenly distributed across all five forest types with a particularly high dominance (41% of sampled individuals) in pine forest (Fig. 2c). *Carabus manifestus* (Kraatz, 1881) and *Pterostichus adstrictus* (Eschscholtz, 1823) made up 8.6% and 6.9% of the total catch, respectively, and both species were most abundant in birch forest, where they represented 16% and 14% of all individuals, respectively (Fig. 2e). Finally, *Carabus vladimirskyi* (Dejean, 1930) represented 6.2% of the total catch (74 individuals), with more than 85% of its specimens collected in oak forest plots, where *C. vladimirskyi* accounted for 42% of caught individuals (Fig. 2d).

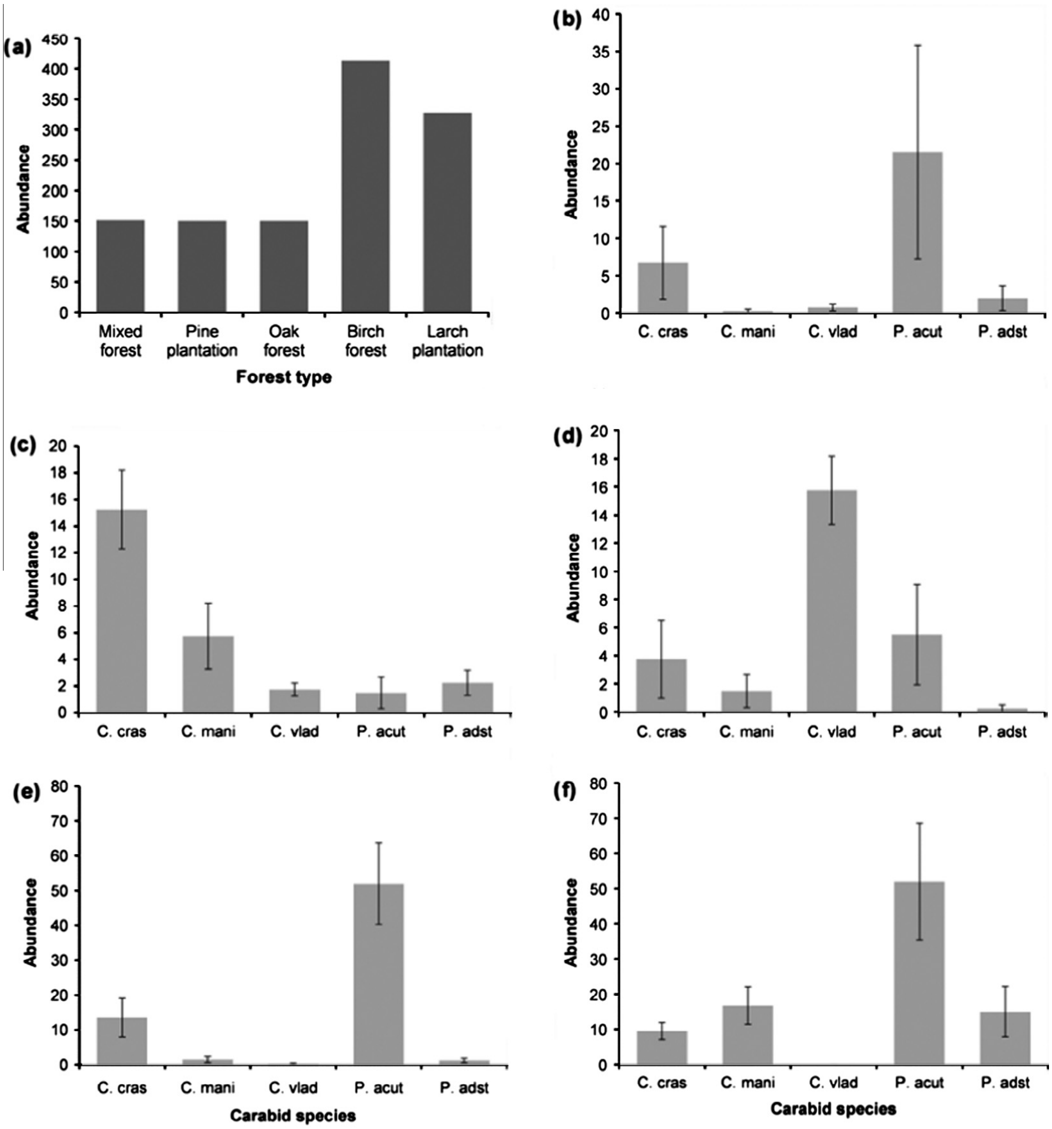

Fig. 2. Abundance of all carabids across forest types (n = 1191) (a) and mean abundance of the five most dominant carabid species (total $n > 50$) in mixed forest (b), pine plantation (c), oak forest (d), birch forest (e) and larch plantation (f) (Error bars represent standard error of the mean; *Abbreviations:* C. crass = *Carabus crassesculptus*, n = 195; C. mani = *Carabus manifestus*, n = 103, C. vlad = *Carabus vladimirskyi*, n = 74, P. acut = *Pterostichus acutidens*, n = 530, P. adst = *Pterostichus adstrictus*, n = 83).

Recorded total species richness was highest in mixed forest (n = 18) and lowest in larch and birch forest (n = 13 for each) (Fig. 3). The estimated extrapolated species richness (n = 600 individuals) for each forest type substantiates this pattern, with mixed forest containing a significantly ($P < 0.05$) higher estimated species richness than all other forest types, while pine and oak forests showed intermediate diversity levels, followed by larch and finally birch forests. The extrapolated species richness of larch forest assemblages was furthermore significantly lower than the species richness in pine plantations, whereas birch forest assemblages were significantly less species-rich then beetle assemblages in mixed and oak forest as well as pine plantations.

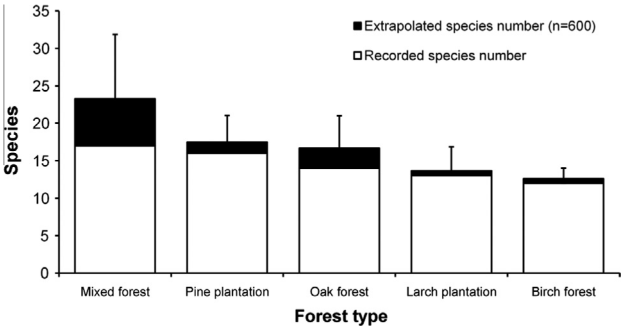

Fig. 3. Measured and estimated carabid species richness harboured by the five forest types (error bars show upper confidence intervals).

In relation to plant species (Fig. 4), average and total herb and tree species richness were both highest in pine plantations (in total 31 and 11 species, respectively), followed by mixed forests (in total 26 and 10 species, respectively), while average and total shrub diversity was highest in birch (in total 6 species) forests. The lowest vascular plant species richness in all three layers both on average and in total was recorded in oak forests (in total 19 herb, 2 shrub and 4 subdominant tree species).

3.2. Beetle community composition

Analysis of the community composition of carabid assemblages (Fig. 5) reveals that the pine plantation and oak forest harbour dis-

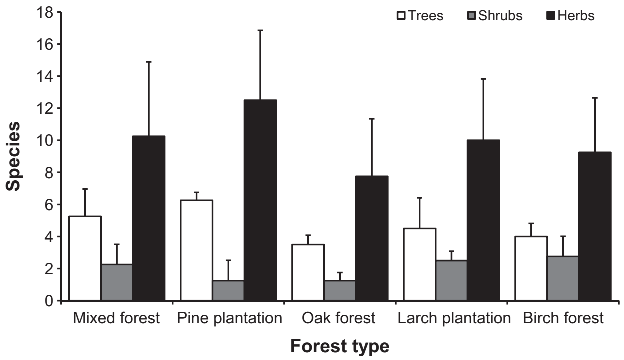

Fig. 4. Average plant species richness recorded on the plots representing the different forest types (bars indicate standard deviation).

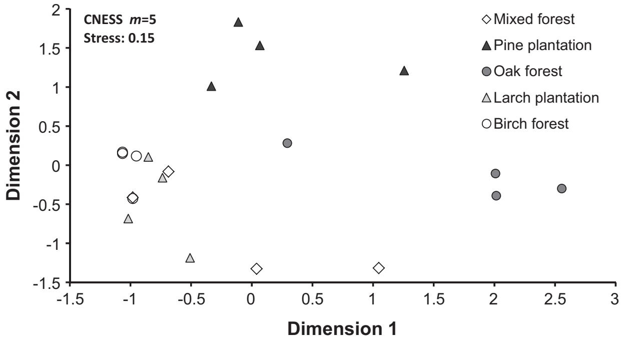

Fig. 5. Non-metric multi-dimensional scaling of the CNESS dissimilarity matrix (Sample size parameter $m = 5$, Stress = 0.15).

tinct communities relative to the other forest types. Furthermore, it is apparent that oak, pine and mixed forests show greater heterogeneity in community composition and therefore a higher species turnover between plots than the other forest types. By contrast, birch and larch forest plots show relatively little variation in the species composition.

The environmental parameters investigated in this study (Table 1) exerted only a limited amount of control over the beetle distribution patterns, with the first two RDA axes explaining only 16.2% and 5.9% of species variation, respectively.

Both canopy cover and dry weight of the litter layer exerted some influence, with larch and birch forests being characterised by a high amount of litter and open canopies (Fig. 6). Oak and pine forests were both characterised by closed canopies, but oak forest litter had a lower relative dry weight. Mixed forests were most heterogeneous in relation to environmental parameters, mirroring the high levels of heterogeneity observed in carabid species composition between samples in this forest type.

Most carabid species are clustered towards the centre of the RDA plot. The abundances of some of these species are likely too low to result in a clear environmental response pattern, while other species may be unaffected by the recorded variables or prefer intermediate environmental settings. However, all five dominant species are clearly associated with distinct habitat conditions. *C. vladimirskyi* associates strongly with high canopy cover and low leaf litter mass that characterises oak forest samples, while *C. crassesculptus* also associates strongly with high canopy cover, but only intermediate leaf litter mass and low ground cover. By contrast, *P. acutidens* has a strong association with open canopies and a high leaf litter mass. *P. adstrictus* and *C. manifestus* associate with intermediate values of these parameters. Furthermore, *Synuchus* sp. and *Harpalus coreanus* (Tschitscherin, 1895) are notable due to their association with higher ground vegetation cover values.

4. Discussion

4.1. Carabid abundance, diversity and community composition in different forest types

The carabid diversity recorded from our study area is similar to the species richness reported from northern Europe, where 16 species were recorded in native oak woodland and six in Sitka spruce (*Picea sitchensis*) plantations in Ireland (Fahy and Gormally, 1998), while in a managed forestry landscape in Belgium, 23 species were recorded in even-aged conifer (Norwegian spruce *Picea abies* (L.) Karst and Douglas fir *Pseudotsuga menzienzii* (Mirb.) Franco) plantations, 30 species in even-aged oak, and 24 species in mixed regenerated conifer-oak stands (de Warnaffe and Lebrun, 2004). The carabid species richness we observed at Donglingshan is also only marginally lower than that of assemblages in one of the few remaining primary temperate forest ecosystems of northern China, Changbai Mountain, where 47 species were encountered in mature forest habitats along an altitudinal gradient from 700 to 2000 m, while only 20 of these species were found between 1100 and 1500 m in native mature mixed coniferous forest which corresponds to the altitudinal range of our site (Zou et al., 2014). Our recording of 18 species within secondary mixed forest might therefore suggest that these forests support a considerable proportion of the native forest carabid fauna, although a comparison with the species composition reported from Changbai Mountain shows considerable faunal differences, which might suggest that a substantial proportion of the Donglingshan carabid fauna consists of more generalist species.

In contrast both to studies from North America and Europe that report highest carabid α-diversity in native deciduous woodlands relative to plantations (Fahy and Gormally, 1998; Elek et al., 2001; Magura et al., 2003; Finch, 2005), and to Yu et al. (2010) who report significantly higher diversity in oak forests than in pine plantations in northern China, our results suggest that the native oak-dominated forest harbours a similar diversity to pine plantations, while carabid species richness in these habitats was clearly surpassed by the mixed forests. Despite the natural dominance of oak in the study area, mature pristine forests in this region generally contain a mixture of tree species; high beetle diversity in mixed forest may therefore be a consequence of greater habitat similarity with natural forest that formerly covered the area. Mixed

Table 1
Environmental parameters recorded within carabid sampling plots; values represent mean and standard deviation for each forest type.

	Leaf litter (dry weight, g)	Ground cover (%)	Shrub cover (%)	Max. shrub height (cm)	Canopy cover scores[a]
Mixed	49.7 ± 30.4	13.7 ± 12.2	32.9 ± 25.5	82.2 ± 62.1	3.3 ± 0.7
Pine	80.3 ± 19.4	14.3 ± 9.1	40.3 ± 20.8	93.4 ± 36.7	8.6 ± 3.2
Oak	50.0 ± 26.9	16.9 ± 9.8	36.9 ± 26.1	111.6 ± 48.6	5.5 ± 3.6
Birch	58.1 ± 30.5	4.7 ± 4.3	43.1 ± 33.2	128.4 ± 54.5	5.4 ± 2.6
Larch	98.8 ± 2.9	33.1 ± 23.6	50.9 ± 27.3	96.6 ± 47.3	4.9 ± 1.0

[a] Measured using a 25 point moosehorn improved according to Brown et al. (2000); ratio score out of 25.

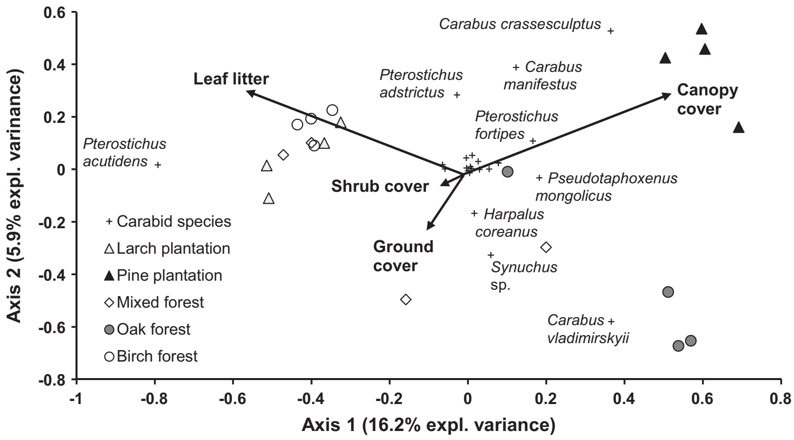

Fig. 6. RDA ordination plot of environmental variables and carabid species (icons represent samples and italicised names represent species, species names are abbreviated to the first three letters of each part of the binomial name, arrows indicate environmental variables (Leaf litter: dry weight (g), ground and shrub cover: % cover of the respective layer, canopy cover: canopy cover score).

forests also represent a low contrast matrix among other forest types, providing heterogeneous ground cover and leaf litter conditions that can provide microhabitats suitable for a wide variety of carabid species, including species using them chiefly as corridors.

We suggest that the strong differences in canopy cover among forest types is an important factor explaining observed differences in beetle species richness and composition. Canopy cover influences ground beetles indirectly through changes in microclimatic and soil moisture conditions, as well as shaping the density and composition of the understory vegetation layer (Fuller et al., 2008). Our observation of higher carabid diversity in mixed forest, despite comparatively low canopy cover, seems to contrast earlier findings (Niemelä and Spence, 1994; Humphrey et al., 1999; Elek et al., 2001; Finch, 2005; Fuller et al., 2008; Yu et al., 2008, 2009; Oxbrough et al., 2010). However, pine and oak forests, characterised by high canopy cover, contained distinct carabid assemblages within our study region, with high canopy cover thought to be a prerequisite for the occurrence of forest specialists (Niemelä and Spence, 1994; Jukes et al., 2001; Mullen et al., 2008; Yu et al., 2008; Oxbrough et al., 2010).

Our finding that larch plantations harboured slightly less species-rich and much more homogeneous carabid assemblages than pine plantations, is coherent with observations from Europe and North America that report differences in beetle assemblages among different conifer plantations. Such differences are again linked to shifts in environmental variables and associated microclimatic conditions (Humphrey et al., 1999; Ings and Hartley, 1999; Finch, 2005). In our study, three factors may be relevant: (1) larch forest specialists are unlikely to occur in the study area, due to *L. principis-rupprechtii* naturally occurring at much higher elevations than the study area (Zhang et al., 2009), (2) the uniformly lighter canopy of larch in comparison to both native oak and pine forests, which exhibit greater heterogeneity in canopy cover, might render larch forests less suitable for the local forest carabid species pool, favouring a smaller range of more generalist species, and (3) humification of larch litter is reportedly about a third slower than pine litter and two to three times slower than birch leaf litter (Vedrova, 1997), which leads to distinct differences in epigeic conditions that may also affect prey densities. The first two factors can also be assumed to be at work within birch forests, with the observed homogeneity and overlap in carabid species composition within and between these two forest types further supporting this assumption.

Niemelä et al. (1992, 1996) argue that a high density of ground vegetation potentially inhibits the movement and prey capture of forest carabids, whereas Elek et al. (2001) state that increased ground cover can lead to an enhanced abundance of potential prey. Nonetheless, the influence of the ground vegetation density appears limited in our study, since birch forests had much less dense undergrowth, but yielded very similar samples, both in abundance and assemblage structure, to larch forests with their distinctly denser undergrowth. The homogeneity and similarity in the beetle assemblages in larch and birch forests could be partly attributable to the comparatively cold and exposed conditions of these forests due to their northern exposition, potentially allowing only a limited beetle species pool to thrive in these locations.

4.2. Forest type specialists

Very little information is currently available about the ecological preferences of individual carabid species in northern China, but the results of this study have identified some patterns in habitat preference at least for the locally dominant species. The scarcity of primary oak forest in the whole of northern China suggests that some specialist species in these forests might have been lost before detailed recordings of ground beetles began (Yu et al., 2006). In our study area, two different ground beetle communities appear to be associated with high canopy density, which we assume might represent remnants of woodland specialist communities once existing in the area. One of these communities is linked to the native oak woodland, the second to pine plantations. This differentiation has also been recorded in previous studies comparing oak and pine forests (Day et al., 1993) and is further supported by the comparison of these two forest types in the same geographical area (Yu et al., 2010). It also corroborates studies in Europe that show the existence of closed canopy specialists which are restricted to forests dominated by particular tree species (Elek et al., 2001). Our results indicate that *C. vladimirskyi* could represent such a specialist, showing a distribution chiefly limited to dense native oak forests. Further species appear to be widely restricted to either, pine or oak forests, but their overall low abundances do not provide sufficient proof how close these links are. Our results nonetheless suggest that these closed canopy specialists contribute significantly towards the carabid diversity in both pine and secondary oak forests.

On the other side of the specialization spectrum, *C. smaragdinus* (Fischer-Waldheim, 1823), *H. bungii* (Chaudoir, 1844) and *A. semilucidum* (Motschulsky, 1862) represent habitat generalists, since they are also commonly encountered in agricultural fields, orchards and lawns in the agricultural landscape (Liu et al., 2010). *P.*

acutidens, the most dominant species in our samples, was highly abundant in birch and larch forests, and substantially rarer in oak and pine forests. Yu et al. (2006, 2010) also found few individuals of this species in pine forest, but recorded it in a wide range of forest types and under a wide variety of environmental conditions. However, *P. acutidens* has not been reported from nearby agricultural landscapes (Liu et al., 2010), suggesting that this is a forest generalist species with a potential preference for open forest canopy conditions.

Some species appear to undergo very high inter-annual variations in population sizes, leading to substantial shifts in resulting α- and β-diversity patterns. *C. crassesculptus* for example was one of the most dominant species in our samples, whereas Yu et al. (2004, 2006) recorded high abundances of this species in only a single year during a three-year sampling period. Similar patterns emerge for *C. manifestus,* which was highly abundant only in birch forest during our study period, while Yu et al. (2004) found a high abundance of this species in larch forests. Finally, *C. vladimirskyi* was highly abundant in oak forests in 2012, but rarely encountered in 2011 samples. While no detailed records detailing the larval development of Carabus species in China are currently available, some Carabus spp. in Europe are known to live for several years and reproduce more than once, and an individual's development can take more than one season in poor environmental conditions or when food availability is low (Lövei and Sunderland, 1996). Such characteristics could partly explain the observed inter-annual variations.

5. Conclusion

Overall, this study provides important insights into the different carabid communities found in plantations and secondary forests in northern China. Despite the history of widespread deforestation in the 1960s, forest specialist species preferring closed forest canopies appear to have persisted, presumably in remote, small pristine forest islands in the mountainous landscapes, from where they successfully re-colonised the newly-establishing secondary forests and forest plantations. Different forest types furthermore clearly support distinct assemblages, with north-exposed birch and larch forests harbouring highly abundant, species-poor and homogeneous ground beetle communities, while secondary mixed forests contain the highest α-diversity in ground beetles, hence contributing significantly to γ-diversity. At the same time, mixed forest beetle assemblages are distinctly different to both, pine and oak forests. The high degree of spatial aggregation exhibited by many carabid species and their low overall abundances support our assumptions that they are chiefly limited to small, distinct habitat patches. The most appropriate restoration strategy for carabid beetle diversity and the potential associated control of invertebrate pest species across this forest landscape therefore needs to involve the maintenance of both within-stand and between-stand heterogeneity, with particular emphasis on variations of canopy closure. Future forest plantations should be developed with a strong focus on locally native species to further support the colonisation of remnant populations of forest specialists into China's new forests.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2014.09.022.

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