Ground beetle assemblages in Beijing's new mountain forests

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A R T I C L E  I N F O

Article history:
Received 28 July 2014
Received in revised form 15 September 2014
Accepted 18 September 2014
Available online 7 October 2014

Keywords:
Carabidae
China
Plantation
Regeneration
Temperate forest

A B S T R A C T

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.

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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., 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
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 invertebrates 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 understood (Lövei and Sunderland, 1996; Kotze et al., 2011) and known at least in temperate areas, their ecology is relatively well understood (Lövei and Sunderland, 1996; Kotze et al., 2011) and understood (Lövei and Sunderland, 1996; Kotze et al., 2011) and understood (Lövei and Sunderland, 1996; Kotze et al., 2011) and understood (Lövei and Sunderland, 1996; Kotze et al., 2011) and understood (Lövei and Sunderland, 1996; Kotze et al., 2011) and understood (Lövei and Sunderland, 1996; Kotze et al., 2011) and understood (Lövei and Sunderland, 1996; Kotze et al., 2011) and understood (Lövei and Sunderland, 1996; Kotze et al., 2011) and understood (Lövei and Sunderlan

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.

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 an 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-dominant (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 (Sukaczew) 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.

Plot locations 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.
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 m² 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 m² quadrats placed either side of a 2 m line drawn between the two pitfall traps. Leaf litter samples were collected from a 0.25 m² 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 m² quadrat centred on each plot. This large quadrat was then subdivided into four 10 m² squares where the presence of all herb species was recorded in one 1 m² 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).
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 than beetle assemblages in mixed and oak forest as well as pine plantations.

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-
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 menziesii (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 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.

<table>
<thead>
<tr>
<th>Species</th>
<th>Stress: 0.15</th>
<th>Dimension 2</th>
<th>Dimension 1</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pine</td>
<td>1.5</td>
<td>-0.5</td>
<td>0.5</td>
</tr>
<tr>
<td>Oak</td>
<td>1.0</td>
<td>2.0</td>
<td>1.5</td>
</tr>
<tr>
<td>Larch</td>
<td>0.5</td>
<td>1.0</td>
<td>2.0</td>
</tr>
<tr>
<td>Birch</td>
<td>0.0</td>
<td>1.5</td>
<td>2.0</td>
</tr>
</tbody>
</table>

4. Discussion

Table 1

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

<table>
<thead>
<tr>
<th>Forest type</th>
<th>Leaf litter (dry weight, g)</th>
<th>Ground cover (%)</th>
<th>Shrub cover (%)</th>
<th>Max. shrub height (cm)</th>
<th>Canopy cover scores</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mixed</td>
<td>49.7 ± 30.4</td>
<td>13.7 ± 12.2</td>
<td>32.9 ± 25.5</td>
<td>82.2 ± 62.1</td>
<td>3.3 ± 0.7</td>
</tr>
<tr>
<td>Pine</td>
<td>80.3 ± 18.4</td>
<td>14.3 ± 9.1</td>
<td>40.3 ± 20.8</td>
<td>93.4 ± 36.7</td>
<td>8.6 ± 3.2</td>
</tr>
<tr>
<td>Oak</td>
<td>50.0 ± 26.9</td>
<td>16.0 ± 9.8</td>
<td>36.9 ± 26.1</td>
<td>111.6 ± 48.6</td>
<td>5.3 ± 3.6</td>
</tr>
<tr>
<td>Birch</td>
<td>58.1 ± 30.5</td>
<td>4.7 ± 4.3</td>
<td>43.1 ± 31.2</td>
<td>128.4 ± 54.5</td>
<td>5.4 ± 2.6</td>
</tr>
<tr>
<td>Larch</td>
<td>98.8 ± 2.9</td>
<td>33.1 ± 23.6</td>
<td>50.9 ± 27.3</td>
<td>96.6 ± 47.3</td>
<td>4.9 ± 1.0</td>
</tr>
</tbody>
</table>

* Measured using a 25 point moosehorn improved according to Brown et al. (2000); ratio score out of 25.
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. vladimirsxkyi 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-Waldeheim, 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).
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 example was 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 contain the highest 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.

Acknowledgements

This study was facilitated by the support and generous funding of the Chinese Academy of Sciences Fellowship for International Scientists (Fellowship Number 2011T2S18), the “111 Program” from the Bureau of China Foreign Expert – Ministry of Education (contract no. 2008-B08044) and the National Science Foundation of China (no. 31270478). Eleanor Warren-Thomas was also supported by a NERC Masters Studentship. We are very grateful to Professor Liang Hongbin and Liu Ye from the Institute of Zoology, Chinese Academy of Sciences, who assisted in identification of a number of difficult species. Duan Meichun provided valuable assistance with specimen preparation. Professor Yu Xiao-Dong kindly provided reprints of his papers that were not available in the UK. Sincere thanks also go to the staff at Beijing Forest Ecosystem Research Station for their hospitality and to two anonymous reviewers for their helpful comments.

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.

References


