Diversity and seasonal changes in carabid assemblages of a mature, secondary and plantation forest mosaic in the Zhangguangcai Mountains, North-eastern China

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Abstract: 1. While China is promoting the re-establishment of forests across the country on a globally unprecedented scale, the biodiversity harbored by the resulting secondary and plantation forests remains poorly understood. Here, we assess the carabid diversity at Zhangguangcai Mountains in north-eastern China that comprise a unique mosaic of mature forest remnants, secondary forests and forest plantations.

2. We located pitfall traps in five distinct forest types: mature conifer and mature mixed forest, secondary mixed forest, secondary broadleaved forest dominated by birch (*Betula platyphylla*) and poplar (*Populus davidiana*), and in larch plantations. We recorded 9,073 carabid beetles representing 42 species, with richness, abundance and diversity of ground beetles all peaking in secondary broadleaved forests. Assemblages sampled in larch plantations were least species rich, but species extrapolation curves indicate a potentially high overall species richness.

3. Carabid communities were clearly differentiated according to forest type, with larch plantations and secondary broadleaved forests containing beetle assemblages distinct from the other three forest types, while the mixed secondary and mature forest types harbored similar assemblages.

4. Carabid communities also showed a clear seasonality in all forest types, with the plantation forest communities remaining distinctly different from the clustered communities of the mature and mixed secondary forest types throughout the year. Broadleaved secondary forest assemblages occupy an intermediate position throughout the sampling season.

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Introduction

32 Mature forests across the globe have suffered significant declines in the second half of the 20th

33 century, chiefly linked to increasing demands for timber and cultivated land (FAO, 2001).

34 Furthermore, 'natural' forests account for only about a third of the total forest area (Morales-Hidalgo

35 *et al.*, 2015). Of these, 74 % are classified as 'other, naturally regenerated forests', while only 26%

36 are regarded as 'primary' or mature forests (FAO, 2015b). Particularly between 2010 and 2015,

37 losses of 'natural' forests (~7.6M ha y^{-1}) were partially offset by a combination of natural forest

38 regrowth on abandoned agricultural land (~2.2 M ha y^{-1}), and by forest plantations (~3.1 M ha y^{-1})

39 (FAO, 2015b; FAO, 2016). This highlights the increasingly important contribution of naturally

40 regenerating secondary forests and plantation forests towards global forest cover. Nonetheless, 80%

41 of terrestrial biodiversity are believed to be linked to mature forests, and the ongoing destruction of

42 these forests is seen as a key factor for the rapid biodiversity losses across the world and for the

43 threat of extinction faced by many plant and vertebrate species (Meng, 2006; Watson *et al.*, 2018).

44 Threats to the global species pool associated with the loss of mature forest ecosystems are therefore

45 of significant global concern (Potapov *et al.*, 2008).

46 China's government has launched globally unprecedented national forest rehabilitation and

47 afforestation programmes (FAO, 2016), chiefly aimed at reducing soil erosion and associated sand

48 and dust storms, as well as enhancing C sequestration and general improvement of environmental

49 conditions. The scale of these programmes are reflected by the fact that in 2015, China had naturally

50 regenerated secondary forest and forest plantation areas covering 1,180 M ha and 790 M ha,

51 respectively. This represents 56.5% and 37.9% of China's total forest area, respectively (FAO,

52 2015a). In addition to initiatives focusing on forest restoration, China's mature forests remnants are

53 now formally fully protected from logging, while significant parts of the plantation and naturally

54 re-growing secondary forests also benefit from strict commercial logging bans (Wang *et al.*, 2007).

55   Although naturally regenerated secondary forest and plantation areas are increasing rapidly in

56   coverage, and hence in their relative contribution towards China's forest estate, their potential role

57   in the conservation of biodiversity remains contentious. In contrast to mature forests, China's

58   plantation forests are commonly characterized by an evenly aged, homogenous stand formed by a

59   single species of conifer or by poplar clones (Chen *et al.*, 2014). The herbaceous plant communities

60   in their undergrowth and their nutrient and energy cycling also show distinct differences to mature

61   and secondary forests. Some studies focusing on implications of China's forest plantations for

62   biodiversity conservation have already indicated that these forests can make only limited

63   contributions towards the protection of China's rich biodiversity (Hua *et al.*, 2016; Yu *et al.*, 2002;

64   2006). At the same time, some plantation forests with low canopy closure appear to allow for a

65   relatively high species richness and density in understory plants (Lemenih *et al.*, 2004; Zou *et al.*,

66   2015). Furthermore, a comparison of secondary and plantation forest plots located across a wide

67   range of sites in Northeastern China has revealed a surprisingly high diversity in woody plants and

68   ground beetles in secondary and plantation forests (Zou *et al.,* 2019a), while comparisons of ground

69   beetle diversity and assemblage structure between areas dominated by plantation, secondary and

70   mature forest (Zou *et al.*, 2015) showed distinct trait differences, with secondary and particularly

71   plantation forests containing a high abundance and species richness of herbivorous carabids when

72   compared with mature forests. Nonetheless, these studies were conducted across sites that were

73   distributed across large geographic areas and accordingly differed also in their climatic conditions

74   and their history of arthropogenic interferences, while direct comparisons between plots of mature,

75   secondary and plantation forests from the same study region are currently lacking.

76   Furthermore, secondary forests commonly show distinct temporal shifts in their tree species

77   composition from early pioneer species like birch and poplar to a more diverse mixture of conifer

78   and broadleaved species. Nonetheless, the implications of these changes for their biodiversity, and

79   the resulting relative importance of mature, secondary and plantation forests for the conservation of

80   the local species richness remains poorly researched.

81   We are addressing persisting knowledge gaps, based on a forested landscape that forms part of

82   the south-eastern slopes of the Zhangguangcai Mountains in Heilongjiang Province on the boundary

83   to Jilin Province, Northeast China. In the past, large parts of the mature forests occupying this area

84   were logged, and larch plantations were subsequently established, while secondary forest growth

85   was also observed. Parts of the area are nonetheless still covered in mature forest remnants,

86   harboring trees aged up to at least 400 years, while the secondary and plantation forests were

87   established about 50 years ago. Logging is now banned, and the entire forested environment is

88   protected. The current patchwork of plantation, secondary and mature forests provides an ideal

89   setting to conduct research into the diversity patterns encountered within and between these forest

90   types. In our investigations of forest diversity, we are focusing on one of the most species-rich insect

91   taxa inhabiting these forests (Zou *et al.*, 2015), ground beetles (Coleoptera: Carabidae). With almost

92   40,000 described species (Carabidae of the World, 2018), ground beetles are highly sensitive to

93   environmental change and show strong habitat specificity (Brandmayr *et al.*, 2005; Lövei &

94   Sunderland, 1996). They are commonly used in studies of environmental change effects in the

95   context for example of forest management and of differences between forest habitats in the

96   temperate zone of the northern hemisphere (Gao & Fu, 2009). They are a popular study taxon not

97   least because they are susceptible to sampling using pitfall traps that generate a standardized

98   measure of the activity density of these beetles, and they are more easily identifiable than most other

99   mega-diverse insect taxa (Gnetti *et al.*, 2015; Kotze *et al.*, 2011).

100   Patterns in insect activity, diversity and community composition change with changes in

101   seasonality. Variations in these patterns are linked to differences in the habitat conditions

102   encountered by the respective insect communities. For example, the conditions and diversity of host

103   trees in different forest types have an immediate impact on the caterpillar abundance and the

104   potential occurrence of spring abundance peaks (Shutt *et al.*, 2019). In addition to direct climate-

105   related signals, phenological patterns in the vegetation including the development and seasoning of

106   foliage and reproductive organs trigger distinct seasonal changes in the insect community structure

107   (Cardoso *et al.*, 2007). Variations in these factors between distinctly different habitats might also

108   trigger distinct differences in seasonality patterns observed in insect assemblages. For ground

109   beetles that are predominantly predatory or omnivorous and hence often assumed to be less strongly

110   determined directly by the vegetation and its seasonal changes than strictly herbivorous taxa,

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111 seasonal patterns of species diversity have received limited attention (but see Gnetti *et al.*, 2015;

112 Dornelas *et al.*, 2013).

113 Here, we compared the abundance, species richness and assemblage composition of ground

114 beetles in the mosaic of mature forest, secondary forest and forest plantations at Zhangguancai

115 Mountains in 4 week-intervals between early June and late August 2016 to establish the variations

116 in species diversity and assemblage composition in the different forest types from early summer to

117 mid-autumn. In our paper, we will test the hypotheses that 1) in line with the proposed importance

118 of mature forests for biodiversity conservation, carabids diversity peaks in mature forest, followed

119 by secondary forests, with the plantations harboring species-poor, homogenous assemblages; that 2)

120 the carabid assemblage structure in larch plantations differs significantly from that in other forest

121 types; and that 3) there are distinct seasonal variations in beetle assemblages that consistently

122 differentiate the assemblages in mature, secondary and plantation forest types.

Material and methods

Study Site

125 The study was carried out in the temperate forests of Hailin City, Heilongjiang Province, in

126 northeastern China (N 44°24.2169' – 44°24.7459'; E 128°24.0576' – 128°24.8530', Fig. 1). The

127 study plots were located in a mountainous region with peaks exceeding 1650 m that experiences a

128 temperate continental monsoon climate. The average annual temperature is 2.6ºC, with daytime

129 temperatures commonly exceeding 20ºC in July and August. The average annual precipitation is

130 551mm, with most precipitation experienced in the summer months. In the study area, mature and

131 naturally regenerated secondary forests comprised of a mixture of coniferous and broad-leaved trees

132 cover about 92 % of the total forest area, with the rest being formed by plantation forests.

133 We selected a total of 20 plots across a small altitudinal range between 749 and 985 m

134 representing five distinct different forest types; larch plantation, secondary broadleaved forest

135 dominated by *Populus davidiana* and *Betula platyphylla*, mature mixed forests dominated by *Pinus*

136 *koraiensis*, *Abies fabri*, *Picea asperata*, *B. platyphylla*, *Tilia tuan*, *Ulmus pumila* and *Fraxinus*

137 *mandschurica*, mature conifer forests dominated by *P. koraiensis*, accompanied by *A. fabri* and *P.*

138 *asperata*, and secondary mixed forests dominated by a wide variety of broadleaved and conifer

139 species, including *P. koraiensis*, *B. platyphylla*, *T. tuan*, *U. pumila*, *F. mandschurica*, *Acer pictum*

140 and *Syringa reticulata*. Four replicate plots measuring 20 m×20 m were established within each

141 forest type to sample ground beetles. The distance between neighbouring plots was at least 50 m,

142 which can be considered independent as the ground beetles generally have small home range

143 (Loreau & Nolf, 1993; Digweed *et al.*, 1995), with all plots, located within homogenous patches of

144 the respective forest type to limit edge effects (Fig. 1).

Ground beetle sampling

146   A 10 m × 10 m beetle sampling plot was established, with a pitfall trap placed in each corner

147 of this sampling plot, leading to a total of 80 traps used in this study. Each pitfall trap was comprised

148 of a simple plastic cup of about 250 ml volume and a diameter of 7.5 – 8.0 cm, filled with saturated

149 salt (NaCl) water mixed with several drops of detergent to break the water surface tension. Salt

150 solution is considered odourless and not attracting specimens, thereby generating widely unbiased

151 samples (Kotze *et al.*, 2011). An aluminum roof was fixed about 6 cm above the trap to prevent rain

152 dilution and limit water evaporation. The traps were positioned with the top rim level with soil

153 surface. Carabids were sampled between late May and the end of August in 2016, cups being

154 emptied after 14 days. We collected the pitfall traps at four distinct times at monthly intervals around

155 June 7th, July 4th, August 2nd and August 30th, respectively, to analyze seasonal changes, with an

156 additional sample taken on June 21st. All traps were set and emptied within two days of each other

157 in order to keep sampling synchronicity.

Data Analysis

159   For subsequent analysis, data from all pitfall traps on each plot were pooled. For the seasonality

160 analysis, data from all 16 traps representing a forest type were pooled to account for the small

161 monthly sample sizes generated per trap (Devries *et al.*, 1999; Jos *et al.*, 2007), with samples

162 differentiated by the four distinct sampling events. We then used the packages "vegan" (Oksanen *et*

163 *al.*, 2019) in R (v3.6.1, R Core Team, 2019) to calculate the Chao 1 species richness estimator (Chao,

164 1984) as basis for diversity comparisons between different forest types.

165 We additionally used coverage-based rarefaction and extrapolation (R/E) sampling curves to

166 compare species richness patterns across the samples with varying sample sizes using the R package

167 "iNEXT" (Hsieh *et al.*, 2016), this method allows for standardized unbiased comparisons of the

168 relative species richness between communities (Chao & Lou, 2012) . We used this package to plot

169 the resulting rarefaction and extrapolation sampling curves for the three most widely used members

170 of the Hill number family (species richness, q = 0; Shannon's entropy index, q = 1; Simpson diversity,

171 q = 2) (Chao *et al.*, 2014). Extrapolations were standardized to 4000 individuals, representing about

172 four times the smallest sample size we recorded from an individual forest types.

173 For the analysis of species turnover patterns over the sampling season across the 20 plots, we

174 calculated chord-normalized expected species shared (CNESS) dissimilarity matrices (Trueblood *et*

175 *al.*, 1994), based on an open source R script (Zou & Axmacher, 2019b) to analysis data and create

176 the ordination plots. CNESS dissimilarity matrices can be calculated for different sample sizes via

177 changes of the sample size parameter *m*, with low values (extreme: *m* = 1) emphasizing the similarity

178 in dominant species, and large values of *m* providing an overview of overall changes in the

179 assemblages. In this study, we calculated the matrices for *m* = 1 and for *m* = 10 as the largest common

180 sample size of all samples.

181 Hierarchical Partitioning for Redundancy Analysis and Canonical Correspondence Analysis

182 were then used to analyze changes in the carabid assemblage composition in relation specifically to

183 habitat type and seasonality using the R package "devtools" (Wickham *et al*., 2019) and "rdacca.hp"

184 (Lai, 2019). In this context, the "rdacca.hp" package specifically allows calculations of the

185 respective proportion of every explanatory variable to the explained variance, based on the

186 Hierarchical Partitioning theory. Entities in the rdacca plot represent carabid species as response

187 variable, as well as study plots representing the different habitat types and sampling events as

188 explanatory variables. Due to the large number of '0' values in the data-set, the carabids data matrix

189 was Hellinger-transformed (Legendre & Gallagher, 2001).

190 ## Results

Species compositions

We caught 9073 ground beetle specimens representing 42 species in 18 genera. We were able to verify scientific species identities for 37 of the 42 species, with the remaining five morphospecies all securely identified to genus level. The total recorded species richness was highest in the secondary broadleaved forests (n = 33) (Fig. 2), but showed similar levels in the remaining four forest types, larch plantation (25), mature mixed forest (26), mature conifer forest (27) and secondary mixed forest (27). The species' activity density in the different forest types differed greatly, with traps in secondary broadleaved forests (1977 individuals) and mature mixed forest (2014 individuals) reflecting a significantly higher activity density of carabid beetles than the other three forest types, with mature conifer forest (1885) and secondary mixed forest (1860) forests samples showing intermediate activity densities, while larch plantations harbored the assemblages with the lowest recorded activity densities (n = 1337 specimens). The most dominant species in our samples belonged to the genus *Pterostichus*, with *Pt. silvestris*, *Pt. interruptus* and *Pt. adstrictus* contributing 18.1%, 16.9% and 16.5% of all individuals, respectively. *Pt. maryseae* contributed a further 10.4% and *Pt. bituberculatus* 9.9%. When comparing between forest types, there was a clear differentiation with regard to dominant species. *Pt. maryseae* and *Pt. adstrictus* dominated in the larch forest, where these two species accounted for 38% and 21.2% of all sampled individuals, respectively. *Pt. silvestris* dominated in the mature mixed forest (25.4%), while *Pt. silvestris* and *Pt. interruptus* dominated in both the mature conifer forest (25.5% and 21.9%, respectively) and the secondary mixed forest (20% and 25.1%, respectively).

In terms of the estimated species richness, Chao 1 estimates show that the larch plantation forest potentially contains a large number of species that we missed in our samples, leading to an overall highest estimated species richness of all forest types (Fig. 2). Nonetheless, the large confidence intervals indicate that with the exception of secondary broadleaved versus mature mixed forests, the estimated species richness was not significantly different between the forest types, despite a general trend for the mature forests to harbor a lower estimated species richness than secondary forests and the forest plantation plots.

218   The standardized extrapolated species richness (n = 4000 individuals) for each forest type

219   substantiates this pattern, with the five confidence bands not intersecting for species richness (q=0)

220   if coverage exceeds 50%, species richness in the secondary broadleaved forest and in the secondary

221   mixed forest were significantly higher than in other forest types for standardized sample covers

222   between 50% and 93% (Fig. 3, left panel). Nonetheless, only the species richness in mature conifer

223   forest and larch plantations showed statistically significant differences. In terms of diversity indices

224   that reflect, to increasing degree, the evenness as additional diversity component to species richness

225   (q = 1-Shannon diversity and q = 2-Simpson's diversity), results indicate that larch plantation

226   forests harbor a less diverse assemblage than the other forest types, with secondary broadleaved

227   forests showing the highest levels of diversity (Fig. 3, central and right panel). The differentiation

228   between larch plantations and the remaining forest plots increased with increasing Hill number,

229   indicating that plantation assemblages are strongly dominated by a small set of species.

230   *Seasonality and spatial turnover patterns in beetle assemblages*

231   In terms of the community composition of carabid assemblages, distinct changes occur both

232   according to habitat types and during the sampling seasons. When emphasizing dominant species

233   (CNESS m = 1, Fig. 4), assemblages in the two mature forest types and in the secondary mixed

234   forests show great similarities in their composition at each sampling event, assemblages in larch

235   plantations are dominated by a distinctly different set of dominant species, while the dominant

236   species in the assemblages of secondary broadleaved forest are in an intermediate position between

237   the plantation forests and the mature forest/mixed secondary forest assemblages at all times. Trends

238   for the similarity in overall assemblage patterns (CNESS m = 10, Fig. 4) showed a similar trend.

239   In addition to the clear habitat-specific clusters, there are also distinct seasonal variations in

240   the beetle assemblages that follow forest-type specific temporal trajectories. For both the turnover

241   patterns in carabid assemblages for both m = 1 and m = 10 (Fig. 4), species assemblages representing

242   the two mature forest types and the mixed secondary forest assemblages showed strong similarities

243   in their species composition throughout the four sampling times, resulting in four distinctive

244   temporal clusters for these plots with the exception of the mature conifer forest, where the beetle

community appears to remain fairly stable in late summer. The dominant species in the plantation forest assemblages in contrast remained almost constant between early June and July (CNESS $m = 1$, Fig. 4), with plantation forest assemblages always strongly differentiated from the mature and mixed secondary forest plots at all times and for both sample sizes. The secondary broadleaved forest assemblages occupied intermediate positions between the plantation forests and the other three forest types throughout the summer months, while again showing a very distinct seasonal variation.

Relative influence of forest type and seasonality on the composition of carabid assemblages

The occurrence of the 15 common carabid species that individually accounted for more than 0.7% of the overall number of individuals in this study area was strongly influenced by both habitat types and seasonality (Fig. 5A). Seasonality-linked factors could be linked to 49.9% of the observed variation, while 37.1% could be associated with forest type – specific factors. The 22 rare species that individually accounted for less than 0.7% of the number of individuals in our study were predominantly related to changes in seasonality (42.3% explained variance) (Fig. 5B). These species showed much less clear preferences for different forest types (5.6% explained variance).

Discussion

Species diversity and differentiation between different forest types

Based on our results, we can clearly reject the original hypothesis that mature forests harbor a higher carabid diversity than the other forest types. Our observations of species diversity peaking instead in the naturally regenerating, overall relatively tree species-poor, secondary broadleaved forest strongly dominated by birch (*B. platyphylla*) and poplar (*P. davidiana*) trees that represent two early-mid succession species (Zhou *et al.*, 2013) came as a big surprise, not least since this outcome is also inconsistent with previous studies from China's regenerating forests. Zou *et al.* (2015) for example reported a high alpha diversity in mature forest plots when compared to plots representing secondary forests, and Magura *et al.* (2003) and Yu *et al.* (2006) similarly report the

species richness and abundance of carabid assemblages to be higher in old-growth forests when compared to young, regenerating forests. Blanchet *et al.* (Blanchet *et al.*, 2013) also suggest that highly productive forests that are rich in tree species support more diverse ground beetle assemblages. The lowest diversity of carabids in larch plantations in contrast confirms a trend widely reported in the literature: that mono-dominant plantation forest types commonly harbor a lower carabids diversity than natural secondary and mature forests. This trend was for example also seen at forests on Dongling Mountain (Warren-Thomas *et al.*, 2014) and Changbai Mountain (Zou *et al.*, 2015). It also aligns with a number of studies outside China that report a reduced diversity of ground beetles in plantation forests compared to natural forests (Butterfield & Benitez, 1992; Butterfield *et al.*, 1995; Fahy & Gormally, 1998; Jukes *et al.*, 2001; Jung *et al.*, 2014; Oxbrough *et al.*, 2016). Nonetheless, a number of studies have provided more nuanced results in this context, with for example Yu *et al.*'s (2006; 2008) investigations of species diversity in plantations showing significant decreases in species diversity and abundance directly after reforestation of logged broad-leaved forests with larch plantations, while they eventually recorded more species and individuals in young conifer plantations than in older, naturally regenerated forests. A number of further studies have found greater or equal insect species abundance and richness in plantations in comparison to mature forests (Koivula *et al.*, 2002; Lawton *et al.*, 1998; Niemelä, 1993; Oxbrough *et al.*, 2012; Ramos, 2000). A wide range of factors have been proposed to explain this phenomenon, such as an overriding influence of climatic conditions, for example associated with altitudinal change, on the species distributions and hence diversity of insects(Axmacher *et al.*, 2004; Zhang *et al.*, 2009; Zou *et al.*, 2015), or a strong link of forest insect diversity to specific heterogeneity in microhabitats and microclimatic conditions of different forest types(Axmacher *et al.*, 2004; 2009; Warren-Thomas *et al.*, 2014; Yu *et al.*, 2008), with particular importance for carabids of the humidity in the litter layer (Koivula *et al.*, 1999; Magura *et al.*, 2005) and the degree of canopy cover (Fuller *et al.*, 2008).

Although it conforms to numerous other studies, the low diversity of carabids in the larch plantations in our study area is nonetheless somewhat surprising, given that this forest has been protected for 50 years and is characterized by dense herbaceous undergrowth. Furthermore, the altitude, and depth of the humus layer of the plantation forest plots was similar to both, the secondary

mixed forest and the mature mixed forest. Nonetheless, the undergrowth of the larch forests was more strongly dominated by grasses when compared to the herb-dominated vegetation in the other forest types, and the high vegetation density by these plants at ground level might impede the movement and hence also the hunting efficiency of ground beetles. It could also have a negative impact on the effectiveness of the pitfall traps. The results from both the rarefaction/extrapolation and species richness estimation that are specifically designed to account for such differences do furthermore raise the question if the recorded low diversity in the larch plantations is genuine or relates to a low sample completeness, and only a significant further sampling initiative could fully clarify the situation. What is nonetheless becoming very clear is that larch plantations vary greatly in the actual species assemblage present in these forests when compared to the other forest types. This difference could not only relate to the aforementioned different structure of the undergrowth vegetation, but also to differences in the herbivorous prey species composition associated with grass-dominated undergrowth that might preferentially benefit a specific set of predatory carabid species. Related to this, the predatory carabid larvae might also be affected by a different soil macro-fauna that results from the different nature of the needle litter produced by larch trees in comparison to other litter types, with Wu *et al*. (2006) reporting a distinctly lower abundance and richness of soil animals under larch plantations than under mature forests. We also observed that the canopy coverage of mature and secondary forests was higher than that in the larch plantations, which could also help to explain the differences in carabid communities between plantation forests and the other forest types. Yu *et al*. (2008) suggested that a high canopy cover as encountered particularly in the mature forests and the mixed secondary forest might be a prerequisite for the occurrence of forest specialists, and the similarity in assemblages in the latter forest types can be seen as supporting this hypothesis.

The diversity peak of carabids in secondary, birch (*B. platyphylla*) and poplar (*P. davidiana*)-dominated broadleaved forests could be related to micro-diversification in this habitat and its distinctiveness in habitat conditions when compared to the other studied forest types. The growth of birch and poplar during about 50 years can be seen as representing an advanced development of an early succession stage in the regional forest community, with these species likely to gradually

327 become replaced by hardwood species. This contrasts greatly to the structure of the mixed secondary

328 forest, where it is likely that saplings survived the logging about five decades ago or tree species

329 quickly regenerated from the seed-bank, hence triggering a regrowth of a tree species assemblage

330 that showed strong similarities to the mature forests, in effect eliminating the early successional

331 stages characterized by birch and poplar dominance. In terms of the intermediate disturbance

332 hypothesis (Connell, 1978), it could overall be argued that the 50 year-old broadleaved, birch- and

333 poplar-dominated secondary forest plots represent an intermediate stage of succession. The resulting

334 forest might hence allow for the persistence of a diverse carabid assemblage (Schirmel *et al.*, 2012;

335 Skłodowski, 2016) comprising of generalist species, of carabids adapted to early, open successional

336 stages, as well as of species more commonly associated with late successional stages once tree

337 canopies have closed and more shade-tolerant tree species start to emerge. The positioning of the

338 broadleaved secondary forest plots between the larch plantations and the remaining secondary and

339 mature forest plots further supports this theory. Additionally, the secondary broadleaved forest was

340 generally encountered in areas of high ground water table or near the local river, with the resulting

341 damp soil conditions potentially benefitting a subset of hygrophilous specialists or mesophilous

342 species within the regional species pool, with Worthen and Merriman (2013) reporting that many

343 carabid species prefer moist or mesic environments.

344 *Species turnover patterns and composition influenced by seasonality versus forest type*

345   While there was a very strong seasonality signal observable for each forest type, mature forests

346 and secondary mixed forests followed very similar turnover in their species assemblages, a result

347 contradicting our third hypothesis and indicating that these forests share a very similar species pool

348 throughout the seasons. We assume that this assemblage represents a local set of forest specialist

349 species that originally occurred in the native forest communities. The similarity of mature and

350 secondary mixed forest assemblages hence indicates the potential great value of secondary forests

351 that resemble mature forests in their tree species composition for the conservation and strengthening

352 of assemblages of forest specialist invertebrates, since they appear to provide similar habitat

353 conditions to both the mature conifer and mature mixed forests with not only similar tree species,

354 but also similar shrub and undergrowth vegetation(Yu *et al.*, 2008) and similar variations in canopy

355   density.

356   The pronounced seasonality in all carabid species assemblages, irrespective of forest type, can

357   be related to a number of know environmental determinants that influence the spatio-temporal

358   occurrence patterns of these beetles. At the beginning of June and the end of August, our study area

359   experiences great differences in key climatic factors like temperature and precipitation that also

360   greatly impact soil humidity. The increased temperatures and amounts of precipitation in our study

361   area in July and August could provide optimal positions for both, thermophilic and hygrophilous

362   carabid species, while xerophilous and mesic species will find more suitable conditions earlier in

363   summer, with the distinct climatic shifts in the weather patterns of our study area in our view

364   explaining the significant change in the community structure over the study period.

365   As pine plantation forests in Britain (Jukes *et al.*, 2001), in New Zealand (Brockerhoff *et al.*,

366   2005) and in northern China (Zou *et al.*, 2015) have previously been identified as potential habitats

367   of rare carabid species, plantation forests in the Zhangguangcai Mountains appear to support at least

368   distinct sets of carabid species, while the overall rarity of the respective species in the wider region

369   remains unknown. Species only encountered in the larch plantation and secondary broadleaved

370   forests include *Pterostichus maryseae*, Sun & Shi (Sun *et al.*, 2018), a newly described species that

371   is only known from these forests.

372   With regards to the pronounced and habitat-specific seasonality patterns observed in our study

373   area, previous studies have shown that asynchronous seasonal cycles and patterns can attribute to

374   the reduction of interspecific competition among carabid beetles (Tauber & Tauber 1981; Werner &

375   Raffa, 2003). Lundgren *et al*. (2009) similarly hypothesized that seasonal niche partitioning might

376   contribute to the maintenance of a diverse and abundant epigeal predator community.

377   Seasonal variations are associated with distinct changes in temperature and precipitation, two

378   key factors influencing general activity, flight and foraging behavior of carabid species (Saska *et al*.,

379   2010; Kotze *et al*., 2011). Locally rare species that responded chiefly to seasonal patterns, but

380   appeared less sensitive to habitat types, might have more specific temperature and precipitation-

381   related niche spaces, while the general importance of seasonality in both, rare and common carabid

species, shows how strongly the assemblage overall potentially responds to climatic changes in their ambient environment.

Conclusion

Overall, our study indicates that plantation forests and broadleaved secondary forests, with their distinct canopy tree species composition compared to mature forests, harbor ground beetle assemblages that are distinctly different to mature forest assemblages. In contrast, mixed secondary forests with a very similar canopy tree species composition to mature forests, despite their much younger age, were inhabited by remarkably similar assemblages in our study area. Our results furthermore indicate a very distinct seasonal signal in all carabid assemblages across the summer months, explaining large parts of the variation in assemblage compositions observed in our study.

In terms of the conservation of forest specialist species, our results suggest that forest plantations should be planted with a set of local species that also dominate potential mature forest plots in the respective area, and that secondary forests consisting predominantly of early pioneer species like birch or poplar could greatly benefit from additional planting of later successional species. Overall, we believe that the current approach of planting large-scale monocultures of often non-local species is detrimental to forest biodiversity, in turn also hampering ecosystem services like biological pest control that are associated with highly species-rich assemblages that contain a large proportion of specialist species. The most effective way to improve the future expansion of China's forest area would be to allow nature to take its course, while potentially speeding up successional processes by targeted, sparse planting of local, late-successional tree species in areas where secondary forests are dominated strongly by early successional trees.

Acknowledgments

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Zou, Y., Sang, W., Wang, S., Warren-Thomas, E., Liu, Y., Yu, Z., Wang, C. & Axmacher, J.C. (2015) Diversity patterns of ground beetles and understory vegetation in mature, secondary, and plantation forest regions of temperate northern China. *Ecology and Evolution*, **5**, 531–42.

Legend

Fig.1. Map showing the location of our study region and a detailed map showing the location of the 20 study plots representing the five forest types. LP: Larch plantation, SBF: Secondary broadleaved forest, SMF: Secondary mixed forest, MMF: Mature mixed forest and MCF: Mature conifer forest

Fig.2. Carabid species richness, estimated richness and abundance in five forest types (Error bars represent standard error of species estimated richness; LP: Larch plantation, SBF: Secondary broadleaved forest, SMF: Secondary mixed forest, MMF: Mature mixed forest and MCF: Mature conifer forest)

Fig.3. Coverage-based rarefaction (solid line segment) and extrapolation (dotted line segments) sampling curves with 95% confidence intervals (shaded areas) for the carabids data of five forest types (LP: Larch plantation, SBF: Secondary broadleaved forest, SMF: Secondary mixed forest, MMF: Mature mixed forest and MCF: Mature conifer forest), separately by diversity order: $q = 0$ (species richness, left panel), $q = 1$ (Shannon's entropy index, middle panel) and $q=2$ (the inverse of Simpson's concentration index, right panel). The five different icons represent the reference samples, the numbers in parentheses are the sample coverage and the observed Hill numbers for each reference sample

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Fig.4. Non-metric multi-dimensional scaling of carabid samples based on the CNESS dissimilarity
matrix for a minimum sample size (m = 1, Stress = 0.12) and the maximum common sample size (m
= 10, Stress = 0.07; LP: Larch plantation, SBF: Secondary broadleaved forest, SMF: Secondary mixed
forest, MMF: Mature mixed forest and MCF: Mature conifer forest

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Fig.5. Hierarchical partitioning for canonical correspondence analysis and redundancy analysis plots
showing the relationship between carabid species compositions, seasonality and forest type; (A)
represent common species (>0.7 % of the total number of individuals caught) and in (B) represent
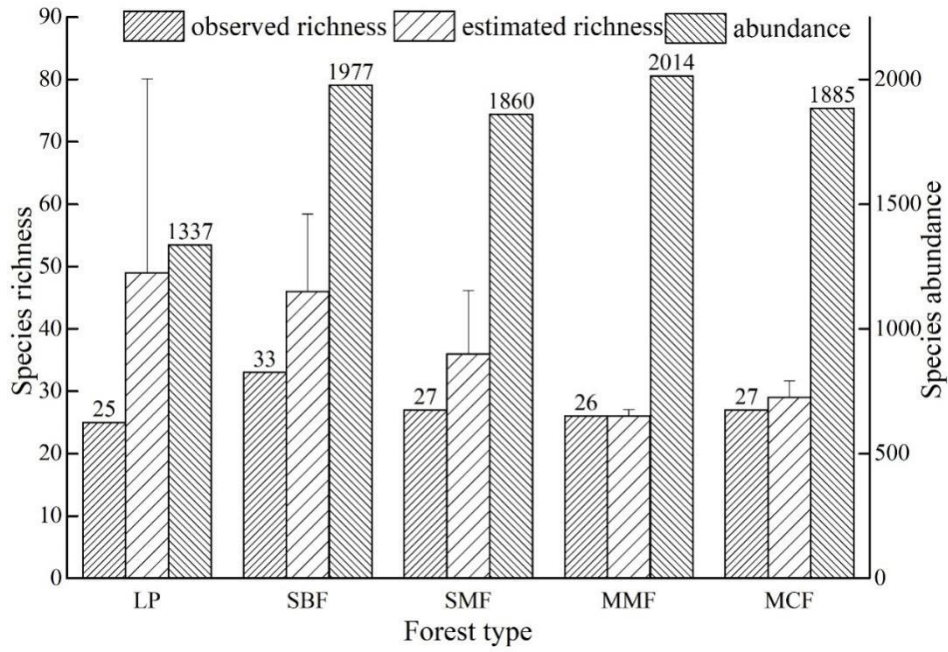rare species (<0.7 % of the total number of individuals caught)

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635   Fig.1
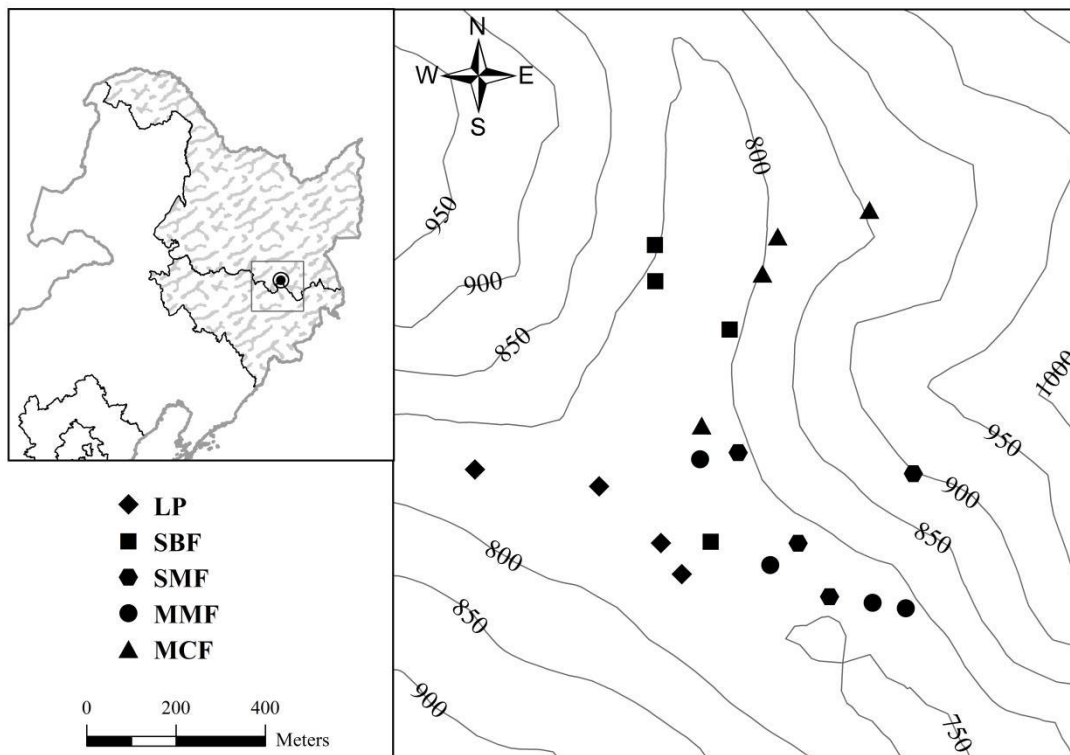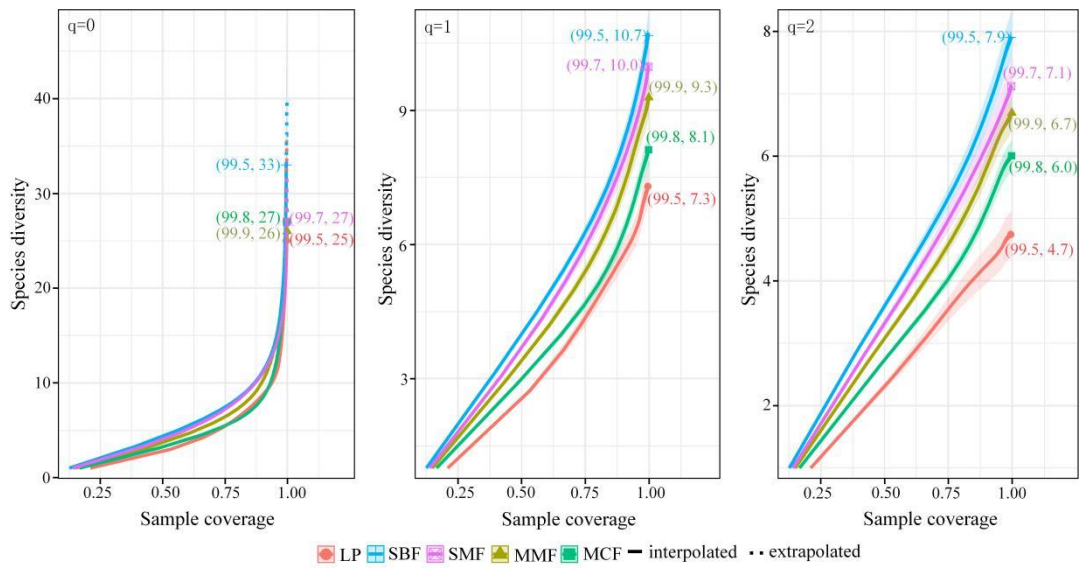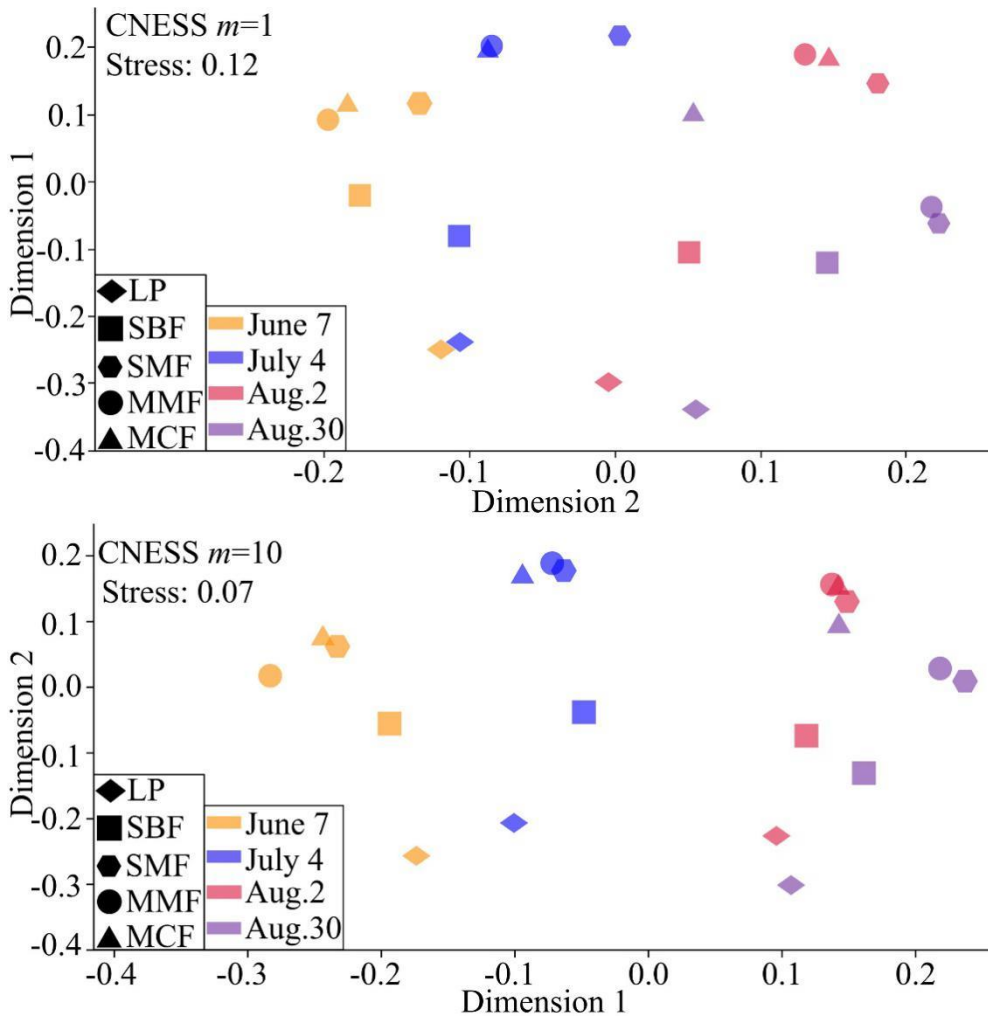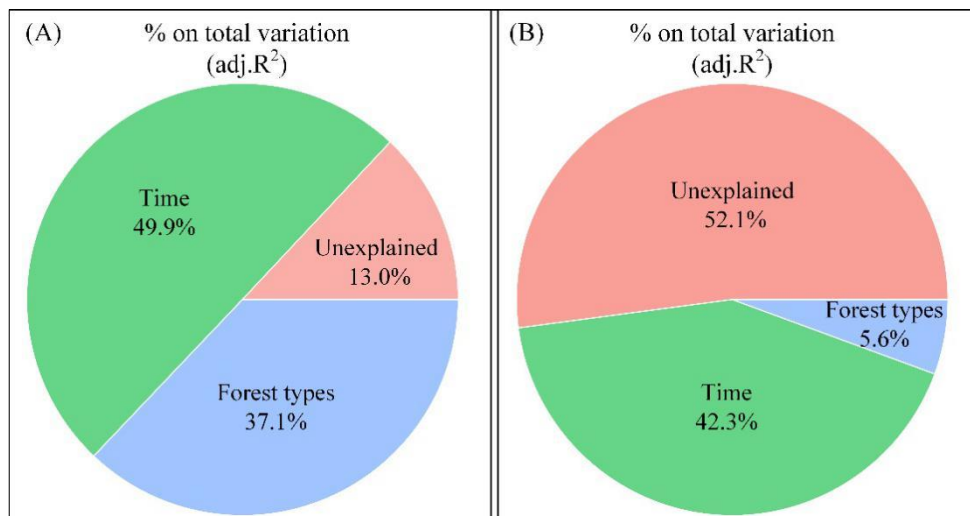

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