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Large-scale α-diversity patterns in plants and ground beetles (Coleoptera: Carabidae) indicate a high biodiversity conservation value of China's restored temperate forest landscapes

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Abstract

Aim: Following the near-complete destruction of China's forest ecosystems during the 20th century, recent reforestation programmes have created large-scale mosaics of protected secondary and plantation forests. These restored forests are often assumed to have limited biodiversity conservation value, but large-scale evaluations of their diversity are lacking. In our study, we compared α-diversity and species dissimilarity patterns of vascular plants and ground beetles (Coleoptera: Carabidae) in restored secondary and plantation forests to remnant mature forests across north-eastern temperate China. We also assessed functional traits of beetles and cross-taxon diversity links to evaluate differences in ecosystem functioning among forest types.

Location: . Northeast China.

Methods: Vascular plant and ground beetle assemblages were recorded in 159 temperate forest plots. The α-diversity and species compositional dissimilarity of these taxa and the functional traits of beetles were compared between plantation, secondary and mature forest ecosystems.

Results: Herbaceous plant species richness peaked in mature forests, while carabid and woody plant diversity did not differ between forest types. Species dissimilarity of carabids was lowest in mature forests and highest in plantation forests. Mature forest contained the highest proportion of carnivorous beetles and secondary forests of large-bodied carabids. Carabid diversity and woody plant species richness were positively correlated in mature forests, but not in secondary or plantation forests.

Main conclusions: While China's mature forests show a great conservation value in harbouring highly diverse herbaceous plant assemblages and an abundance of distinct invertebrate trait groups such as small predatory carabids, China's restored temperate forests also support a high diversity of woody plants and carabids. Overall, our findings offer an encouraging conservation message for biodiversity conservation in China and demonstrate the importance of policy measures that ensure effective long-term protection of both, China's remnant mature forests, but also its new forest ecosystems.

KEYWORDS

body size, carabids, feeding guild, forest plantation, mature forest, secondary forest, species composition

1 | INTRODUCTION

Mature forests harbour significant proportions of the global species pool, and their widespread destruction is a key driver of the ongoing global biodiversity crisis (Gibson et al., 2011; Watson et al., 2018). Plantation and secondary forests contribute substantially towards global forest cover and associated carbon stocks (Cunningham et al., 2014; Guo & Gifford, 2002; Tong et al., 2018). Nonetheless, these forests are commonly assumed to harbour less diverse species assemblages (Barlow et al., 2007; Gibson et al., 2011) dominated by more widespread and generalist species (Bremer & Farley, 2010; Brockerhoff, Ecroyd, Leckie, & Kimberley, 2003) compared to mature forest ecosystems.

In line with the global decline in mature forest cover over the last century (MacDicken et al., 2016), China's mature forests have suffered a dramatic reduction in area, with only small patches remaining (Zhang et al., 2000; Zhang & Song, 2006). In response to resulting environmental problems such as flooding and dust storms, the Chinese government has re-established forest ecosystems across the country, for example via the "Natural Forest Conservation Program" and "Grain for Green" project (Wang, Innes, Lei, Dai, & Wu, 2007). In combination with forest protection policies such as logging bans that apply to all forest ecosystems, these restoration projects have resulted in vast areas of protected forest plantations and naturally regenerated secondary forests (Li, 2004; Viña, McConnell, Yang, Xu, & Liu, 2016). This process has significantly increased the country's overall forest area and created a mosaic of distinctly different secondary forest and forest plantation types (MacDicken et al., 2016; Tong et al., 2018). These "new" forests are increasingly becoming connected as total forest area increases, and they have started to form ecological corridors linking previously isolated mature forest remnants (Dai, Zheng, Shao, & Zhou, 2006).

Although re-establishing forest cover across more humid parts of northern and north-eastern China has successfully decreased soil erosion, it remains unclear whether these new forests support species-rich assemblages of plants and animals (Macias-Fauria, 2018; Tong et al., 2018). In China, biodiversity and conservation assessments of forests commonly focus on plants and vertebrates (Tang, Wang, Zheng, & Fang, 2006), whereas mega-diverse invertebrate taxa are often ignored (You, Xu, Cai, & Vasseur, 2005; Zou, Feng, Xue, Sang, & Axmacher, 2011). At the same time, links between plant and invertebrate diversity patterns within forests are not always positive (Axmacher, Liu, Wang, Li, & Yu, 2011; Schuldt et al., 2011; Zou, Sang, Bai, & Axmacher, 2013). This means that policies and measures designed to protect areas of high plant diversity or enhance local plant species richness might have limited value for the conservation of invertebrate assemblages (Schuldt et al., 2015), and for the ecosystem services they provide. The implications of China's reforestation and afforestation initiatives for the conservation of invertebrates, in terms of α-diversity and assemblage composition, therefore, require urgent attention. There are already a small number of case studies assessing the insect biodiversity conservation value of individual forest areas (Zou, Sang, Wang, et al., 2015; Zou, Sang, Warren-Thomas, & Axmacher, 2016). Nonetheless, the small scale and lack of replicates in these studies mean that their results cannot be extrapolated across wider geographic areas. This leaves a key gap in our understanding of species richness and diversity patterns within China's new forests across the large geographic scales on which they occur.

When characterizing species assemblages, their functional traits, which affect ecological functions and the delivery of ecosystem services (Cadotte, Carscadden, & Mirotchnick, 2011; Tilman et al., 1997), form an important aspect to consider in addition to the assemblages' diversity patterns. Ecosystem functioning is understood to be particularly efficient and resilient to outside pressures, when the diversity of both species and functional traits within an ecosystem is high (Cardinale et al., 2012). Regional studies around the world suggest that the species composition of invertebrate assemblages in secondary and plantation forests differs from mature forest communities (Maeto & Sato, 2004; Magura, Tothmeresz, & Bordan, 2000), resulting in different trait spectra and associated ecosystem functions (Bihn, Gebauer, & Brandl, 2010; Bremer & Farley, 2010). However, patterns in the functional structure of ecological communities do not necessarily correlate with patterns in species richness or composition (Cadotte et al., 2011; Sattler, Duelli, Obrist, Arlettaz, & Moretti, 2010). Functional trait spectra should, therefore, be assessed separately when appraising the potential conservation value of ecosystems (Barnes et al., 2014; Flynn et al., 2009).

Body size and trophic guild are two functional traits that affect invertebrate response to environmental conditions (Ball, Woodcock, Potts, & Heard, 2015; Nolte, Schuldt, Gossner, Ulrich, & Assmann, 2017; Schweiger et al., 2005). Species at higher trophic levels and with larger bodies are assumed to have greater mobility and require larger habitat patches, than smaller bodied species at lower trophic levels (Gathmann & Tscharntke, 2002; Ritchie & Olff, 1999). This makes them potentially more extinction-prone in disturbed and highly fragmented landscapes (Davies, Margules, & Lawrence, 2000; Thies, Steffan-Dewenter, & Tscharntke, 2003; Tscharntke, Klein, Kruess, Steffan-Dewenter, & Thies, 2005). A mature ecosystem with high food web complexity usually contains a large proportion of species at high trophic levels (Finke & Denno, 2004; Polis, Myers, & Holt, 1989). It can, therefore, be inferred that younger, less complexed, ecosystems should contain a lower proportion of both predatory and large species. Evidence from selected sites in our previous studies suggests that secondary and plantation forests contain a smaller proportion of predatory carabid species than mature forests (Zou, Sang, Wang, et al., 2015). Nonetheless, this trend has not previously been tested at a wider geographic scale. In order to gain a more comprehensive understanding of the biodiversity conservation value of China's large-scale reforestation and afforestation schemes, it is crucial to assess both species diversity and functional trait spectra of invertebrates across multiple sites over a wide geographical area.

Our study aims to fill these research gaps by comparing ground beetle (Coleoptera: Carabidae) diversity and trait patterns, as well as vascular plant species diversity, among plantation forests, secondary forests and mature forest remnants across 500,000 km^2 of temperate forests in north-eastern China. We firstly aim to compare the differences between plantation, secondary and mature forests in α-diversity and functional traits of beetles as well as in the α-diversity of plants. Mature forests are less disturbed and commonly assumed to be characterized by more complex food webs. Therefore, we hypothesize that mature forests harbour greater carabid and plant species richness and a greater proportion of predatory and large-sized beetle species compared to forest plantations, with secondary forests occupying an intermediate position between these habitat types. Secondly, we aim to compare the species turnover rates of beetles and plants between plantation, secondary and mature forests. The widespread forest destruction will likely have resulted in the large-scale extinction of forest specialist species in deforested areas, resulting in an overall homogenization of communities in secondary forest habitats. We, therefore, hypothesize that mature forests harbour a greater species turnover rate than secondary and plantation forests. Finally, we aim to explore potential links between the diversity of plant species and carabid assemblages. We hypothesize that at large spatial scales, there is a positive link between plant species richness and species diversity in carabid assemblages.

2 | MATERIALS AND METHODS

2.1 | Study area

We established eight study areas across a region that ranges north-east from the city of Beijing towards the Chinese borders with North Korea and Russia, stretching over a distance of about 415 km from north–south, and for about 1,170 km from west to east, covering a total area of approximately 500,000 km^2 (Figure 1). The entire region falls within the Dwa and Dwb climatic zones according to the Koppen classification system, and it was originally covered by temperate mixed broadleaved and coniferous forests. In the 1950s and 1960s, the region was extensively deforested, leading to severe environmental degradation. In response, forests were re-planted and secondary forests allowed to recolonize large areas in recent decades under several large-scale ecological restoration programmes (Wang et al., 2007). In order to conserve water and soil, commercial timber logging was furthermore prohibited in the forests across the region.

We sampled beetles and plants in each of the forest types (mature, secondary and/or plantation) present in our eight study areas on a total of 159 sampling plots. The minimum distance between two neighbouring sampling plots was 50 m, and plots were located at least 10 m inside sampled forest patches, avoiding forest gaps and minimizing edge effects. In total, 41 mature forest plots, 62 secondary forest plots and 56 forest plantation plots were sampled (Figure 1). The original mature temperate forest ecosystems of the study region would generally have consisted of a mixture of broadleaved and conifer species (see an example in Appendix S1a), with coniferous species increasing in dominance with increasing elevation and latitude. Dominant trees in the studied mature forest remnants included Korean pine (*Pinus koraiensis*) and fir (*Abies nephrolepis* and *A. fabri*) as key conifer canopy species, with maple (*Acer* spp.) species common in the undergrowth. Naturally regenerating secondary

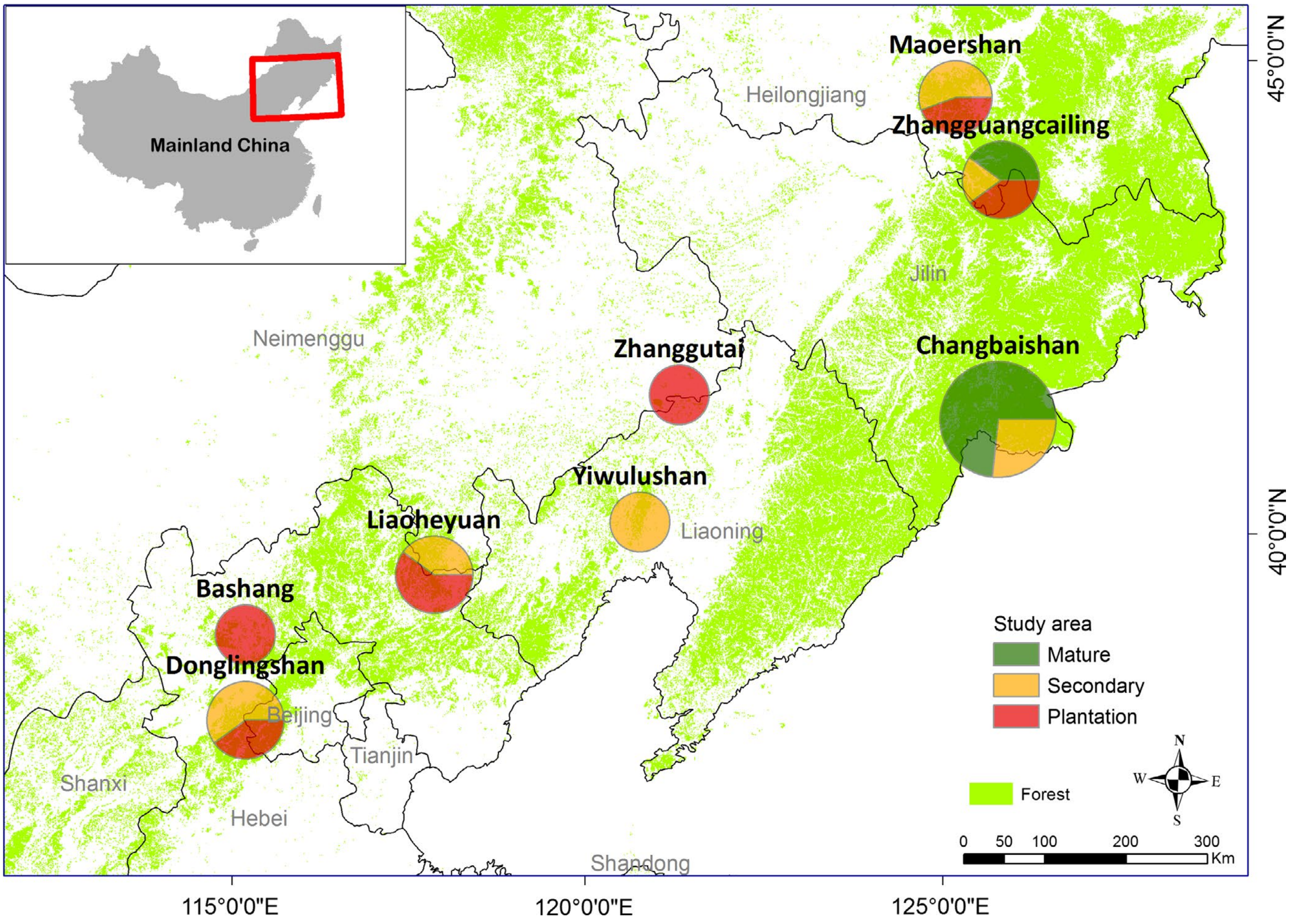

FIGURE 1 Location of study areas. Pie charts refer to the forest composition of sampling plots in each area; relative size of a pie indicates the number of sampling plots in each area

forests were very rich in tree species and often contained high proportions of oak (e.g., *Quercus mongolica* and *Q. wutaishanica*) and ash (*Fraxinus* spp.) in the canopy, with numerous species of maple (*Acer* spp.) again forming the undergrowth (Appendix S1b). Birch species (*Betula ermanii*, *B. platyphylla* and *B. davurica*) also commonly occurred in the canopy and represented typical pioneers in forest gaps. Typical forest plantations in the study region included planted monocultures of larch (*Larix gmelinii*, Appendix S1c), pine (*Pinus tabulaeformis*) and poplar (*Populus tomentosa* and *Populus canadensis*).

2.2 | Recording of vegetation and beetles

Vascular plant species were recorded as presence/absence data in plots measuring 20 x 20 m^2. Tree and shrub species were recorded across the entire plot. The plot was then further subdivided into four 10 x 10 m^2 sub-plots, and undergrowth herbaceous species were surveyed within a 1 m^2 quadrat in each of the sub-plots located at least 2 m away from the sup-plot edge, so that herbaceous plants were recorded from an area of 4 m^2 at each plot.

Carabids were collected over the summer months from late May/early June to late August/early September using pitfall traps located in the centre of each 10 x 10 m^2 sub-plot. In each area, sampling was conducted over a period of 1–2 years, with sampling starting in 2006 at the Bashang area and ending in 2016 at the Liaoheyuan area. The mean sampling effort per plot was 301 (*SE* = 9.2) trap-days. Carabid species were classified as "chiefly carnivorous" and "chiefly non-carnivorous" (e.g., granivorous and phytophagous), based on the wider literature (Harvey, Putten, Turin, Wagenaar, & Bezemer, 2008; Saska, Werf, Vries, & Westerman, 2008; Shibuya et al., 2015; Talarico, Giglio, Pizzolotto, & Brandmayr, 2016; Yu, 1980). For species where this information was missing, feeding classifications followed dominant feeding habits of species in the same genus. Body size was measured from the tip of the mandibles to the end of the abdomen with a precision of 1 mm. Measurements were taken from at least 20 individuals for species with abundance >20 specimens and from all specimens with <20 individuals.

2.3 | Data analysis

As the sample size differed among sampling plots, we selected sample size-independent diversity indices as indicators of carabid's α-diversity: rarefied species richness (standardized for 30 individuals) and Fisher's alpha. These two indices have been commonly used in studies of mobile insects that allow us to compare plots with different sample completeness and sample size (Axmacher et al., 2004; Beck & Schwanghart, 2010; Brehm, Süssenbach, & Fiedler, 2003; García-López, Micó, & Galante, 2011; Zou et al., 2016). In order to have a robust estimation of the α-diversity, plots with <30 carabid specimens (27 plots) were excluded from this analysis. For plants, the actual number of species recorded in the sampling plots (species richness) was used as an indicator of α-diversity.

Generalized linear mixed models (GLMMs) were used to compare diversity and trait composition of carabids, and the richness of plants, among plantation, secondary and mature forests. In all models, study area was set as random variable. In consideration of the elevation-related changes in environmental conditions (Zou, Sang, & Axmacher, 2015), we added elevation as an additional control variable.

We ran models with the following response variables:

1. Tree species richness (Poisson error distribution, logit-link function).
2. Shrub species richness (Poisson, logit-link).
3. Herbaceous species richness (Gaussian, identity-link).
4. Carabid abundance (Negative binomial, logit-link; log-transformed sampling trap X days was set as offset).
5. Carabid rarefied species richness (Gaussian, identity-link).
6. Carabid Fisher's alpha (Gaussian, identity-link).
7. Proportion of carnivorous specimens in the samples (binomial, logit-link).
8. Proportion of carnivorous species in the plot-specific species pools (binomial, logit-link).
9. Abundance-based Carabid average body size (Gaussian, identity-link).
10. Species-based Carabid average body size (Gaussian, identity-link).

To compare species composition changes in the different forest types, we calculated the "Jaccard" dissimilarity index for carabid and herbaceous plant samples within each forest type and each study area. We then compared the dissimilarity values in carabids and herbaceous plants between the forest types in a mixed model, with area set as random factor. As the species dissimilarity increases with the increase in spatial distance, we additionally included geographical distances and elevational differences as control variables.

Generalized linear mixed models were also used to investigate the relationships between carabid diversity and plant species richness. Rarefied species richness and Fisher's alpha-diversity of carabids were used as response variables. Tree, shrub and herbaceous plant species richness were included as explanatory variables, respectively, with study area again incorporated as random variable. Analyses were conducted separately for different forest types, followed by an analysis across all plots, with forest type included as additional explanatory variable.

All models were validated based on the residual distribution meeting normality and the homoscedasticity assumption, and no overdispersion was observed for the count data-based model (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). In addition, spatial autocorrelation of model residuals was checked using Moran's I coefficient (Gittleman & Kot, 1990); no significant spatial autocorrelation was found for any of the models (at $p < 0.05$). All analysis and modelling was carried out in R (v3.1.2, R Core Team, 2014), using the 'VEGAN' package (Oksanen et al., 2014) to calculate Chao1, rarefied species richness and Fisher's alpha-diversity, the 'nlme' package (Pinheiro, Bates, DebRoy, & Sarkar, 2014) to compute the mixed models for Gaussian error distribution, 'lme4' (Bates, Maechler, Bolker, & Walker, 2014) for the Poisson and binomial error distribution and 'BhGLM' (Yi, 2017) for the negative binomial error distribution. The 'ape' package (Paradis, Claude, & Strimmer, 2004) was used to calculate Moran's I index.

3 | RESULTS

3.1 | General results

We recorded a total of 667 vascular species, the vast majority of which were herbaceous (491 species). An additional 97 species were shrubs, and 79 were tree species. The most widely distributed tree species across the study region was larch, *Larix gmelinii*, recorded at seven of the eight study areas. This species is commonly used in plantation forests, so, although it is native to the region, its current range is likely to be at least partly the result of anthropogenic activity. Similarly, the poplar *Populus davidiana* commonly used in plantations was encountered at six areas. In contrast to the aforementioned tree species, the records of *Ulmus pumila* from six areas probably reflect the naturally large distribution range of this species (Appendix S2). The most widespread herbaceous species was *Rubia cordifolia*, occurring at five study areas. *Euonymus alatus*, *Lespedeza bicolor*, *Spiraea salicifolia* and *Ribes mandshuricum* showed the widest distribution of all shrub layer species, all occurring at four of our study areas.

The pitfall traps sampled 30,685 carabid individuals representing 162 species over a period of 47,896 trap-days. The most widely distributed species was *Carabus canaliculatus*, occurring at all study areas apart from Zhanggutai, although this species accounted for only 4.9% of all specimens (1,487 individuals). The most abundant species was *Pterostichus acutidens* (5,150 individuals, 17% of specimens), recorded at four areas (Changbaishan, Donglingshan, Liaoheyuan and Yiwulushan). A detailed species list can be found in Appendix S3.

3.2 | Diversity and traits

Plantation forests contained a mean species richness of 4.2 (*SE*: ±0.4) tree species per plot, while secondary and mature forest harboured 8.0 (±0.5) and 7.6 (±0.5) species, respectively, but these differences were not statistically significant from the model when considering the effect of elevation (Figure 2a, with all model results in Appendix S4). No significant differences were observed for shrub

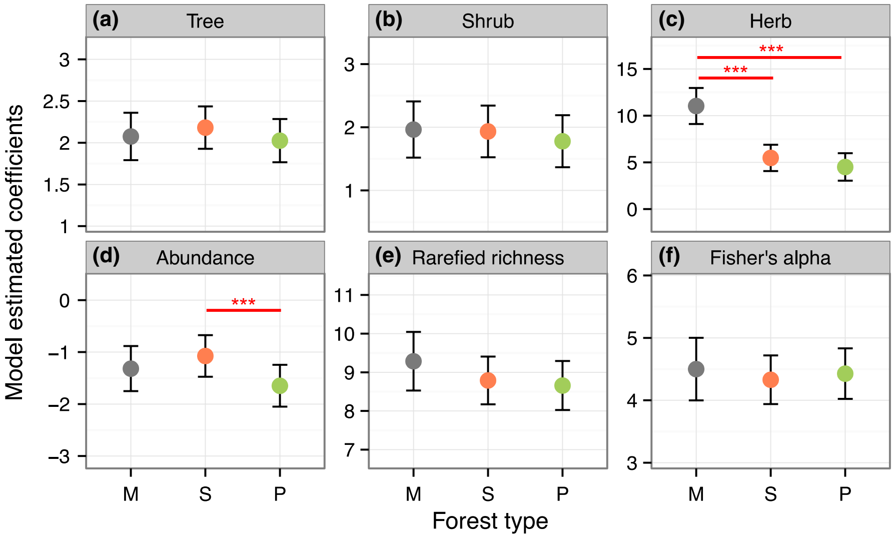

FIGURE 2 Estimated coefficients from generalized linear mixed models showing the differences between assemblages in different forest types (M: mature; S: secondary; P: plantation) with regards to species richness of tree (a), shrub (b) and herbaceous plant species (c), carabid abundance (d, number of individuals per trap-day), rarefied species richness (e) and Fisher's alpha (f); error bars refer to *SE* of estimates, and asterisks indicate a significant difference based on the models shown in Appendix S3 (*≤0.05; **≤0.01; ***<0.001)

species richness among different forest types (Figure 2b). Mature forests did contain a significantly higher species richness of herbaceous plants (14.1 ± 1.0) compared to secondary (8.7 ± 0.6) and plantation (7.8 ± 0.4) forests, with plantation forests harbouring the least diverse herbaceous vegetation (Figure 2c).

Secondary forests contained a higher abundance of carabids (Mean ± *SE* here and afterwards: 0.89 ± 0.11 per plot per trap-day) than plantation forests (0.63 ± 0.09). Abundance did not differ between mature (0.69 ± 0.09) and secondary or between mature and plantation forests (Figure 2d, with all model results in Appendix S4). Rarefied carabid species richness and Fisher's alpha was similar across all three forest types (Figure 2e,f).

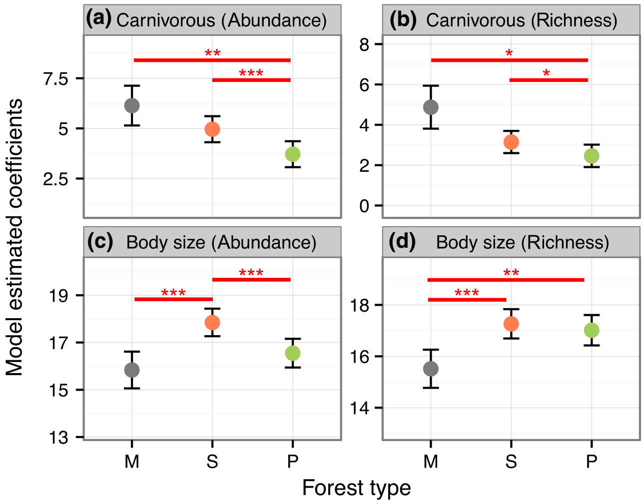

FIGURE 3 Estimated coefficients from generalized linear mixed models showing the differences between different forest types (M: mature; S: secondary; P: plantation) in the proportion of carnivorous species with regards to abundance (a) and richness (b), and in the mean body size based on abundance (c) and richness (d); error bars refer to the *SE* of estimates, and asterisks indicate a significant difference based on the models shown in Appendix S3 (*≤0.05; **≤0.01; ***<0.001)

Plantation forests contained a lower proportion of carnivorous carabid individuals (91.2 ± 2.1%) and species than mature (99.9 ± 0.04%) and secondary (99.2 ± 0.5%) forests, while differences between mature and secondary forest were not significant (Figure 3a,b, with all model results in Appendix S4). Mean carabid body size was larger in secondary forests (17.7 ± 0.3 mm) than in mature (15.2 ± 0.2 mm) and plantation forests (16.0 ± 0.4 mm) based on the abundance of all individuals (Figure 3c). When assessed using the mean body size per species for the overall species pools, mean carabid body size was also larger in secondary (16.9 ± 0.3 mm) than in mature (14.5 ± 0.2mm) and plantation forests (15.7 ± 0.3 mm; Figure 3d, Appendix S4). In addition, the abundance-based proportion of carnivorous species was positively correlated with the mean body size of carabid specimens (Appendix S4, Pearson r = 0.37, $p < 0.001$), indicating that assemblages with a high proportion of carnivorous individuals were characterized by a large mean body size (Appendix S5).

3.3 | Species dissimilarity

For carabids, mature forest assemblages were more homogenous (Jaccard distance 0.50 ± 0.04) than assemblages in secondary forests (0.55 ± 0.04), while beetle assemblages in plantation forests displayed the highest variation between individual sampling plots (0.64 ± 0.04, Figure 4a) according to results from the mixed model. For herbaceous plants, no significant difference between forest types was observed in their dissimilarity (Figure 4b).

3.4 | Relationship between plant diversity and carabid diversity

Mixed models showed that carabid Fisher's alpha was significantly positively correlated with tree species richness in mature forest

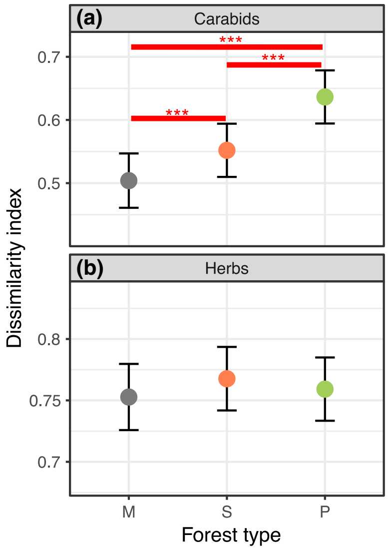

FIGURE 4 Mean pairwise "Jaccard" dissimilarity index within assemblages of the same forest type (M: mature; S: secondary; P: plantation) for carabids (a) and herbaceous vascular plants (b); Error bars show the *SE*, and asterisks indicate the significance based on the linear mixed models (***<0.001)

($\hat{\beta}$ = 0.19, t = 3.656, p < 0.001; Figure 5a). Although there was no significant relationship recorded in plantation and secondary forests when analysed separately, there was a positive correlation between the overall carabid rarefied species richness and tree species richness across all forest types ($\hat{\beta}$ = 0.11, t = 2.64, p = 0.009, Figure 5a). Marginally significant positive relationships were found between Fisher's alpha of carabids and shrub species richness in mature forests ($\hat{\beta}$ = 0.10, t = 1.98, p = 0.055) and across all forest types ($\hat{\beta}$ = 0.09, t = 2.25, p = 0.03, Figure 5b). There was no significant correlation between Fisher's alpha of carabids and the number of herbaceous plant species in any of the forest types, or for all forest plots combined (Figure 5c). Carabid rarefied species richness showed very similar relationships with tree and herbaceous species richness to the relationships with carabid Fisher's alpha (Appendix S6).

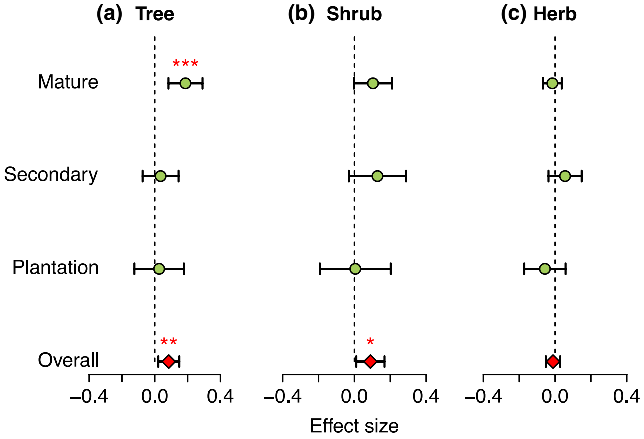

FIGURE 5 Estimated coefficients of the relationship between carabid Fisher's alpha and the number of tree, shrub and herb species in different forest types. Effect size refers to the estimated coefficients from the generalized linear mixed models. Error bars represent the 95% confidence intervals and asterisks indicate the significance of the estimated coefficients (<0.1; *≤0.05; **≤0.01; ***<0.001)

4 | DISCUSSION

The first finding of this study is that secondary and plantation forests harbour a similar level of shrub and tree species richness when accounting for the effect of elevation, suggesting the establishment of a diverse woody plant species assemblage within these new forests. It must be noted that herbaceous plant species richness in contrast was significantly lower in plantations than the other forest types, with maximum herbaceous plant diversity observed in mature forest. The similarity of tree and shrub species richness between secondary and primary forests is in line with a recent meta-analysis reporting a significant recovery of woody plant species richness in the protected secondary forests of China (Liu, Liu, Skidmore, & Garcia, 2017). The low herbaceous plant species richness in plantation forest corroborates existing findings that establishing plantations within climatically semi-arid areas commonly results in a species-poor understorey vegetation cover, because herbaceous plants native to these areas are generally maladapted to the shaded conditions under forest canopies (Cao, Chen, & Yu, 2009).

The similar levels of carabid species diversity in mature, secondary and plantation forest types contrast studies in temperate regions of Europe that reported a lower carabid diversity in non-native, monoculture plantation forests in comparison to secondary or mature forests of native trees (Elek, Magura, & Tóthmérész, 2001; Fahy & Gormally, 1998; Magura, Elek, & Tóthmérész, 2002). The difference could be related to plantation forests in Europe harbouring a much lower tree species richness than plantation forests in our study region. In fact, our results also correspond with patterns previously reported for geometrid moths in secondary and mature forests from two of our study areas, Changbaishan and Donglingshan, where recently established forests were shown to harbour similar levels of α-diversity to mature forests (Zou et al., 2016). In addition, our results are in line with a recent study from south-central China by Hua et al. (2016), who reported general positive impacts of species-rich mixed forests on regional biodiversity. Although further studies of large-scale biodiversity patterns for other taxa in the long-term protected secondary and plantation forests in temperate China are currently missing, our results already clearly indicate that these new forests supported the regeneration of native woody species, and they should not be regarded as "green deserts" (see e.g., Appendix S1). In China's large-scale reforestation schemes, it is therefore very important to restore the highly diverse local native forest vegetation (Hua et al., 2016).

Naturally regenerating woody plant species in plantation and secondary forests might have benefitted strongly from the long-term ban on logging that is being enforced for these forests across the country. The regeneration of native plant species could benefit carabid species (Magura et al., 2000). The long-term protection for newly establishing forest ecosystems appears to also have provided suitable conditions for the establishment of a high diversity of carabids. This might be linked to the resulting high structural diversity and heterogeneity (e.g., dense leaf litter, Koivula, Punttila, Haila, & Niemelä, 1999) associated with natural regrowth and a lack of significant human interventions following the initial planting of the plantation forests. The structural heterogeneity can also partly explain the high heterogeneity in carabid assemblages observed in the new forest types. Alternatively, the high carabid diversity in plantation forests could be the result of a diverse species pool existing in the area prior to the establishment of the plantations. For example, in the Bashang region, the plantations were established on previously untouched steppe vegetation. These grasslands contain a high species richness and similar carabids assemblages to the forest plantations (Liu, Axmacher, Wang, Li, & Yu, 2012). We acknowledge that the observed high diversity of carabids across the different forest types could be a taxon-specific trend. Referring to beetles, taxa that rely strongly on resources widely available in mature forests, but not in younger secondary or plantation forests, such as saproxylic species with their close link to dead wood, are for example highly likely to show a much greater diversity in the mature forest remnants of our study region, mirroring results observed in temperate regions of Europe and the United States (see review in Grove, 2002), and in the temperate-subtropical transition zone of south China (Wu, Yu, & Zhou, 2008).

The forest destruction-regeneration processed could be expected to have caused the extinction of a large number of forest specialist species (Brandmayr, Pizzolotto, Colombetta, & Zetto, 2009), with the large-scale forest destruction during the 20th century creating a relatively homogeneous open landscape that favoured highly mobile generalist species. In turn, the dominance of habitat-generalists in the wider landscape could also result in a lower turnover rate (low dissimilarity) within secondary forests than mature forests. However, our results did not provide evidence for such a pattern. On the contrary, we found the lowest dissimilarity in mature forests. Such results are in line with previous studies of both geometrid moths and carabid beetles in one of our study areas, at Donglingshan, where species dissimilarity was higher than in the mature forest at Changbaishan (Zou, Sang, Wang, et al., 2015; Zou et al., 2016). The relatively high dissimilarity in beetle assemblages within secondary and plantation forests suggests that they are not strongly dominated by generalists. Instead, it appears that the carabids in these assemblages are highly sensitive to the small-scale heterogeneity in environmental conditions encountered in the newly establishing forests. In this context, we encourage further comprehensive studies to establish in more detail structure of carabids community of different forest types in China's reforested landscapes.

Our results partly support our hypothesis that mature forests harbour the greatest proportion of predatory carabids species, indicative of a stable complex food web in this forest type. In terms of the body size, however, results indicate a hump-shaped relationship between forest structural complexity and carabid body size: secondary forests (of middle complexity) contained a high proportion of large-bodied species, while plantation (low complexity) and mature forests both contained a higher proportion of small species. Species with larger body sizes are believed to be more mobile (Andresen, 2003; Den Boer, 1990), and a higher mobility of species is also often associated with a high trophic level (i.e., carnivorous behaviour), because actively hunting predatory species requires access to large patches of habitat to find sufficient prey (Thies et al., 2003). This means that carnivorous carabid species tend to have a large body size, which was supported by our observation of a positive correlation between the proportional abundance of carnivorous species and their body size. Nonetheless, there are also a number of large-bodied species that are not strictly carnivorous, for example the large-bodied genera *Amara* and *Harpalus*, and some carnivorous species in the genera *Synuchus* and *Pterostichus* are relatively small. This explains the observed differences in species' functional compositions between mature and secondary forests, with mature forests containing a higher proportion of small-bodied, carnivorous species, while secondary forests contain more large-bodied, non-carnivorous species. The high proportion of large-bodied species in secondary forest might relate to the Intermediate Disturbance Hypothesis (Grime, 1973), as secondary forests could be seen as relatively complex ecosystems that have widely recovered from heavy disturbance due to several decades of strict protection. After the clearance of primary forests, the newly generated forests may not return to pre-disturbance conditions for many decades or even centuries, but could have matured to become functioning forest ecosystems that differ in their species composition from the original mature forests (Guariguata & Ostertag, 2001; Norden, Chazdon, Chao, Jiang, & Vílchez-Alvarado, 2009; Zhu, Mao, Hu, & Zhang, 2007). Results from our study suggest that secondary forest ecosystems are suitable habitats in particular for the population development of mobile, large-bodied species.

The significant positive relationship between carabid diversity and tree species, especially in mature forests, could relate to a greater diversity of leaf litter and microclimatic conditions at ground level due to different crown densities and structures in more tree species-rich mature forests. Increased structural complexity could result in greater niche space diversity, which is likely to promote a greater diversity of carabids (Koivula et al., 1999; Niemelä, Spence, & Spence, 1992). These findings are consistent with Basset et al. (2012), who reported that tree species richness is a strong predictor of arthropod diversity in tropical forests, although strong links in temperate mature forests might be highly dependent also on the respective spatial scales considered (Schuldt et al., 2011; Zou et al., 2013). Furthermore, our observed positive effect of woody plant (tree and shrub) species richness on carabid diversity was limited to old-growth forests, but not secondary and plantation forests. This may be related to the age of the forest ecosystem having a further confounding effect on the carabid species composition (Oxbrough, Irwin, Kelly, & O'Halloran, 2010; Taboada, Kotze, Tárrega, & Salgado, 2008; Vehviläinen, Koricheva, & Ruohomäki, 2008). The average tree age of mature forests in our study was about 200 years, while tree ages in secondary and plantation forests varied from approximately 30–60 years. Decaying wood is known to provide heterogeneous habitats that can support specific species pools of carabids and other invertebrates (Braccia & Batzer, 2001), but this resource was limited within secondary and plantation forests in our study area, as the trees are not old enough. It can therefore be inferred that mature forests are inhabited by a greater proportion of small-bodied carnivorous species, as well as more diverse assemblages for example of saproxylic taxa (Stenbacka, Hjältén, Hilszczański, & Dynesius, 2010), when compared to secondary and plantation forests, with the larger amount of woody debris in mature forests providing suitable habitats particularly for these species.

Our study provides important insights into the implications of China's forest protection policies and reforestation measures for forest biodiversity. We show that China's restored forests have great potential to support a high species richness in vascular plants and carabids. Nonetheless, mature forests were shown to be irreplaceable, since they not only support highly diverse assemblages of both herbaceous plant and carabid species, but also strongly benefit distinctive trait groups such as small predatory beetles. Policies targeting the strict protection of the remnant primary forests are crucial in order to conserve both biodiversity and the unique species and trait groups encountered in these forests. In order to comprehensively evaluate the potential biodiversity conservation value of China's existing and newly created forest types, we encourage more studies that cover a wider range of taxa, representing a greater diversity of functional groups and a wider range of climatic zones.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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