



Regional sets of diverse, specialized ground beetle and plant assemblages recolonise China's restored temperate forest landscapes

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ABSTRACT

Following the historic destruction of China's forests, large protected forest landscapes have been reestablishment across the country in recent decades. Currently, the species assemblages inhabiting these landscapes remain widely unknown. Here, we aim to establish whether the new temperate forest landscapes in Eastern China, composed of plantation, secondary and remnant mature forest patches, are dominated by widely distributed habitat generalists, widely distributed habitat specialists, or by sets of highly localized forest habitat specialist species, using vascular plants and ground beetles as case studies. We sampled plants and ground beetles on 159 plots representing different forest types distributed across ten study regions. The Chord-normalized expected species shared (CNESS) dissimilarity for beetles and Jaccard dissimilarity for plants were calculated to establish species' turnover patterns, while we used structural equation and multiple regression models for dissimilarity matrices to establish the relative importance of location, elevation and biotic interactions in explaining large-scale distribution patterns of species assemblages. Both taxa showed highly regionalized recruitment, with plant communities responding strongly to latitude, and to geographic location in general, while the composition of ground beetle communities appeared strongly governed by both the composition of the vegetation and study plot location. Both assemblages showed a distinct lack of widespread habitat generalists. Our results demonstrate for the first time that local assemblages of forest specialist species appear to have survived last century's deforestation in unknown refugia before successfully re-colonizing China's restored forest ecosystems. We argue that restored forest landscapes can play a significant role in the conservation of temperate China's biodiversity at both local and regional scales.

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1. Introduction

Land-use change represents the main driver of global terrestrial biodiversity declines (IPBES, 2019, Newbold et al., 2020), chiefly through loss and fragmentation of natural habitats (Dirzo et al., 2014, WWF, 2016). Losses of mature forests around the world that harbour significant proportions of the global species pool are particularly concerning (Morales-Hidalgo et al., 2015, Watson et al., 2018). Forest ecosystem losses are also linked to increased flood risks (Sahin & Hall, 1996, Costa et al., 2003), soil erosion and, particularly in semi-arid areas, amplification of dust storms (Li, 2004, Wei et al., 2020). Carbon emissions from deforestation represent an additional global concern (Pan et al., 2011). Restoration of forests could reverse some of these processes to deliver multiple benefits, but the outcomes of forest restoration programmes are highly context dependent (Chazdon & Brancalion, 2019).

In China, clear-felling of forests in the twentieth century greatly decimated the mature forest cover, with only very few, small and highly isolated mature forest patches remaining by the beginning of the 1970s. Associated increases in flooding, soil erosion and dust storms prompted China's central government to initiate forest protection projects, targeting both remaining mature forest remnants and secondary forests that had begun to regenerate on logged land (Wang et al., 2007). In addition, China started reforestation projects on globally unprecedented scales (Zhang et al., 2000, Cao, 2011). These measures have resulted in mosaics of different forest types covering large, expanding and increasingly interconnected areas (Li, 2004), with the associated greening also easily detectable in satellite imagery (Tong et al., 2018). These forests appear to have successfully reduced flooding, soil erosion and dust storms (Liu et al., 2008). However, the biodiversity value of the newly establishing forested landscapes has been questioned (Yu et al., 2006, Barlow et al., 2007, Niemelä et al., 2007, Bremer & Farley, 2010, Gibson et al., 2011), with reforestation efforts commonly using a very limited selection of tree species that poorly represented the locally dominant flora (Cao et al., 2010).

Scepticism about benefits of China's reforestation projects for biodiversity conservation is also partly based on the many studies from around the world that report reduced plant and animal species richness in secondary and plantation forests compared to mature forest ecosystems, with widespread species sharing generalist traits widely replacing forest specialists (see e.g. Makino et al., 2007, Gibson et al., 2011, Johansson et al., 2016). A recent global review (López-Bedoya et al., 2021) of beetle diversity patterns in forestry plantations with strong geographic foci in Europe and the tropics also emphasized a general negative impact of forest plantations on beetle diversity when compared to natural forests that was particularly severe in exotic tree plantations. However, several studies have reported that old plantation forests can support invertebrate communities resembling assemblages of mature forests, with corresponding levels of species richness (for carabid beetles, see e.g. Martínez et al., 2009 or Irwin et al., 2014).

This trend has also been recorded by initial studies from temperate China, where newly establishing mosaics of secondary forests and forest plantations support plant, ground beetle and geometrid moth assemblages with a comparable species richness to mature forest remnants (Zou et al., 2015b; Zou et al., 2016; Zou et al., 2019). These studies nonetheless indicate that assemblages in new forest ecosystems differ significantly in their species composition and functional trait spectra from mature forests, potentially reflecting the aforementioned shift from forest specialist to widespread habitat generalist species. A key limitation of previous studies comparing the composition of forest species assemblages across temperate China is their restriction to only a small number of study sites, located at significant geographic distances from each other. This has made it difficult to ascertain whether observed assemblage variations are related to differences in forest type, forest age or vegetation composition, or whether they are instead chiefly a function of large-scale spatial turnover. The role widely distributed

generalist species play in beetle and plant communities of China's newly establishing forests, and the overall recruitment pattern of plants and invertebrates at wider (i.e. regional) spatial scales, has so far remained poorly understood, too.

Here, we address these knowledge gaps for the first time. We sampled ten distinct regions in the forested landscape of temperate Eastern China to investigate regional-scale patterns in vascular plant and carabid beetle assemblages in secondary and plantation forests, and in mature forest remnants at two regions where these very rare habitats still remain (Fig. 1).

The understanding of plant and invertebrate recruitment patterns our study provides can not only help in establishing the role these forests play for biodiversity conservation in China's temperate landscapes, but also illustrates potential biodiversity benefits of restoration projects targeting heavily degraded temperate forest ecosystems globally. In particular, our study helps illuminate whether biogeographic trends observed in the well-studied, comparatively impoverished invertebrate fauna and flora of Europe can be easily transferred to other, much more diverse temperate forest regions, such as Eastern Asia.

We set out to test the following three alternative hypotheses:

The 'widespread generalist'-hypothesis. Based on trends described for European secondary and plantation forests (e.g. Fahy & Gormally, 1998, Coote et al., 2012), this hypothesis predicts that assemblages of both, vascular plants and invertebrates, will be similar across secondary and plantation (restored) forest types throughout the entire study area, indicating that these taxa recruit from a common species pool composed of widespread, habitat generalist species.

The 'widespread habitat specialist'-hypothesis. This hypothesis predicts that across our study area, assemblages of both taxa will be clearly differentiated into mature, secondary and plantation forest communities. Assemblages may be further subdivided into broad-leaved and mixed-forest communities. This hypothesis is based on niche theory, such that differences in niche requirements of specialist species restrict them to specific types of forest. Under this hypothesis, we would expect strong similarity between assemblages encountered in plots of the same forest type across the different study regions.

The 'local recruitment' hypothesis. This hypothesis predicts that the newly forming forests recruit species from highly localized species pools, where forest habitat specialist species might have survived the forest destruction of the last century in small wooded refugia. Assemblages in restored forests would be primarily determined and differentiated by the specific location of the sampling site, rather than by the forest type, with few species showing a widespread distribution across the different study regions. The main differentiation of assemblages would be by region, not by forest type.

Our investigations focus on plant and ground beetle assemblages in planted and secondary forest ecosystems, while the two regions containing mature forest remnants provide important background information to contextualize the observed patterns in view of our hypotheses. The resulting imbalance in the spread of forest types across the investigated regions also reflects the great scarcity of mature forests in north-eastern China. Findings from mature forests are analysed and discussed with full reference to this limitation.

2. Material and methods

2.1. Study regions

We selected ten study regions in the forested, mostly mountainous, temperate landscapes between 39.95°N and 45.41°N, stretching from Beijing to China's borders with Russia and North Korea, with the longitude varying from 114.95°E to 128.41°E (Fig. 1). We aimed to select study sites at slightly higher elevations in the southern parts of our

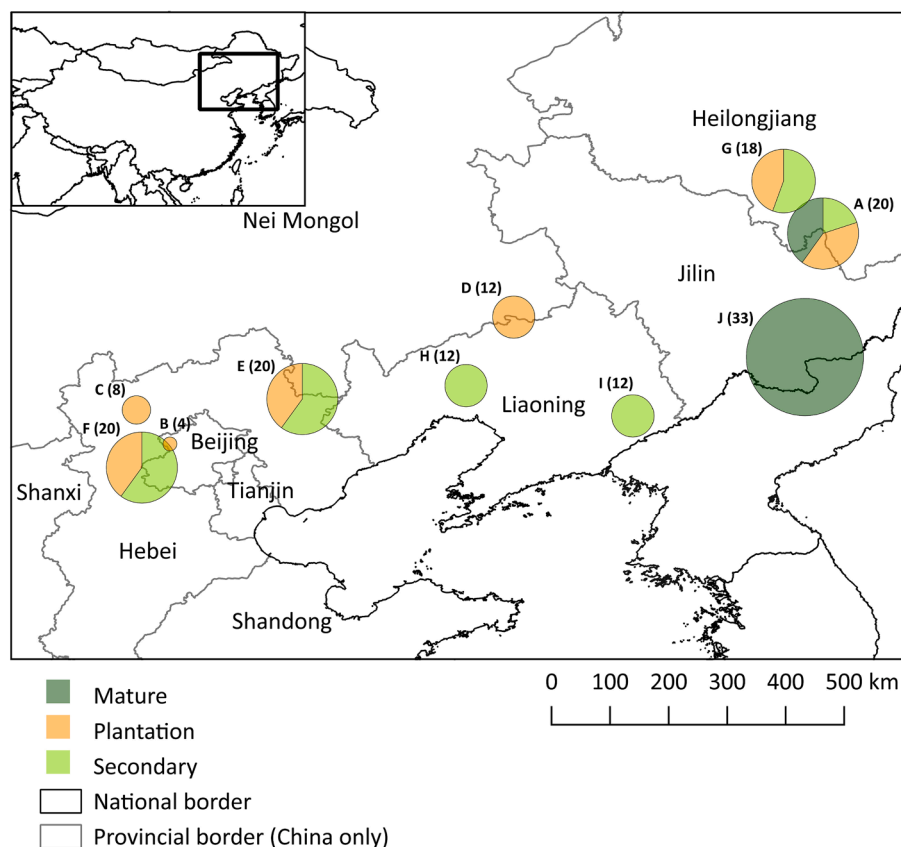


Fig. 1. Map of the study area, showing the locations of the individual study regions. Letters indicate the study region (see Table 1), numbers in parentheses indicate the total number of plots investigated at each region, and the size of the circle is proportional to the total number of plots. The different colours within each circle represent the proportion of plots within each main forest type category; mature, secondary and plantation.

study area (Table 1) to account for potential climatic differences associated with changes in latitude, although the choice of specific sampling locations was also strongly determined by logistical concerns regarding the accessibility of sites, the availability of representative, densely forested landscapes, and by the age of the studied forest ecosystems.

All sampled landscapes fall within the humid continental temperate climate zone (Dwa/Dwb according to the Köppen classification system). At each study region, sampling was conducted in several replicates of the dominant forest types encountered, encompassing, wherever present, mature forests that contain specimens >100 years of age, naturally regenerating secondary forests, and forest plantations dominated by

broadleaved and conifer species (Table 1). The selected secondary and plantation forests were between 30 and 60 years old.

Sampling occurred on 159 plots measuring 20 m × 20 m each. In the mixed agricultural-forested landscapes of Zhanggutai and Bashang, where distinct patches of homogenous forest were surrounded by agricultural fields and grassland, we selected no more than two plots in each forest patch. The continuously-forested landscapes of the other eight study regions comprised a complex matrix of different forest types and ecotones. In these landscapes, we randomly placed plots in homogenous sections of distinctly different forest types. In all cases, plots were positioned at minimum distances of 50 m from each other, and located

Table 1

Number of plots selected at each study region, further subdivided into broadleaved (BL) or mixed (M) forests and broadleaved or conifer (C) plantations, elevational ranges of plot locations, number of plant and beetle species recorded and mean sample completeness per plot with standard deviation for ground beetles (based on the bias-corrected Chao 1 estimator) in each of the ten regions.

Study region	Number of plots for each forest type					Elevation (m)		Number of species recorded		Mean (SD) of beetle sampling completeness per plot (%)	
	Plantation	Secondary	Mature			Min	Max	Plants	Beetles		
A Zhangguancailing	4	4			8	712	985	86	41	78.2 (15.4)	
B Bashang (low)	4					521	526	83	17	59 (22.7)	
C Bashang (high)	1	7				1412	1681	217	33	74 (15.5)	
D Zhanggutai	6	6 (5)				243	256	34	24	83.7 (22)	
E Liaoheshan	4	8				1000	1640	106	39	86.6 (14)	
F Donglingshan		8	11	1		1160	1410	91	23	75.2 (20.4)	
G Maoershan		8	7	3		383	444	105	48	85.2 (10.1)	
H Yiwulushan			3	9 (8)		335	460	52	24	77.3 (11.3)	
I Changbaishan – Baishilazi			3 (2)	9		552	772	72	21	78.9 (9.9)	
J Changbaishan – CNR					3	30	770	2000	178	45	86.5 (13.8)
Total	15	41 (40)	36 (35)	26 (25)	3	38			667	162	81.4

BL: broadleaved, C: conifer, M: mixed, min: minimum, max: maximum, numbers in brackets: plot number of vegetation plots.

at least 10 m inside the respective forest patch, to limit edge effects. The surveyed plots comprised 41 mature forest plots, 62 secondary forest plots and 56 forest plantation plots. Mature and secondary forests were further differentiated into mixed (conifer and broadleaved) and broadleaved forests, while plantations were classified as broadleaved or conifer plantations based on the planted tree species. The dominant planted conifer species was *Larix gmelinii*, while *Pinus koraiensis* and *P. tabuliformis* were also regularly cultivated. Broadleaved plantations were dominated by poplar (*Populus* spp.). The secondary broadleaved forests were often dominated by birch or oak, while ash was an important component of broadleaved and mixed forests. The lower canopy of the different forest types was commonly dominated by a range of *Acer* spp. as well as by *Corylus heterophylla*. While beetles were sampled on all 159 plots, vegetation data was only available from a subset of 156 plots (Table 1).

2.2. Recording of vegetation and ground beetles

All tree and shrub species were recorded across the entire 20 m × 20 m plot. To record herbaceous vegetation, plots were subdivided into 10 m × 10 m quarters, and all herbaceous species were recorded in 4 m² sample subplots randomly located within each of the quarters. All plant species were recorded as presence/absence data, with data being combined across all strata and for all species encountered on the entire plot.

Ground beetles were sampled over the summer months from late May/early June to late August/early September, using pitfall traps with a diameter of 7.5 – 8 cm, filled with saturated salt water (see Warren-Thomas et al., 2014 and Zou et al., 2015; Zou et al., 2019 for detailed information) and positioned in the centre of the 10x10m² quarters mentioned above, with a mean resulting sampling effort per plot of 301 (SE = 9.2) trap-days. In each region, sampling was conducted over a period of 1–2 years, starting in 2006 at Bashang and ending in 2016 in the Liaohueyan region. Beetles were identified by the taxonomic experts in our team, based on substantial reference collections at the Chinese Academy of Sciences, the Beijing Forestry University and the China Agricultural University.

2.3. Data analysis

To analyse changes in the composition of the vegetation and beetle assemblages, we calculated distance matrices describing the dissimilarity in species assemblages between plots. For beetles, we calculated assemblage dissimilarities based on the Chord-Normalized Expected Species Shared (CNESS) (Trueblood et al., 1994), a probability-based dissimilarity measure that estimates the probability that two samples were taken from the same species pool, i.e. looking at the number of species expected to be shared between randomly taken samples. We calculated the CNESS based on a slightly modified version introduced by Zou and Axmacher (2020):

$$CNESS_{ij|m} = \sqrt{1 - \frac{ESS_{ij|m}}{\sqrt{ESS_{ii|m} \times ESS_{jj|m}}}}$$

where

$$ESS_{ij|m} = \sum_{k=1}^S \left[1 - \frac{\binom{N_i - N_{ik}}{m}}{\binom{N_i}{m}} \right] \times \left[1 - \frac{\binom{N_j - N_{jk}}{m}}{\binom{N_j}{m}} \right]$$

$CNESS_{ij|m}$ and $ESS_{ij|m}$ represent the (Chord-Normalized) number of Expected Species Shared between site i and j for a randomly drawn sample of m individuals, where S is the total number of species, while N_i and N_j are the total numbers of individuals at sites i and j , and N_{ik} and N_{jk} represent the abundances of the k^{th} species at sites i and j , respectively.

The CNESS dissimilarity allows for the comparison of assemblage

similarities among samples of different sizes by standardizing the sample size parameter m . This index is an improved version of the Morisita index (Morisita, 1959) and the ‘Normalized Expected (number of) Species Shared’ index (Grassle & Smith, 1976). For small values of m , the CNESS measure describes the probability that the same species dominate in both assemblages, whereas for larger values of m , the resulting matrix reflects the overall similarity in the assemblage composition. The CNESS measure has been widely used in studies of mobile insect biodiversity (Axmacher et al., 2004, Beck & Vun Khen, 2007, Hilt & Fiedler, 2008, Liu et al., 2010, Zou et al., 2014, Duan et al., 2016). For our analysis, we calculated CNESS dissimilarity values of the beetle assemblages for an intermediate sample size of $m = 25$, as well as the dissimilarity in dominant species by setting $m = 1$.

Since vegetation data was recorded as presence/absence only, we calculated the Jaccard dissimilarity that is particularly robust for incidence data (Magurran, 2004) to show the turnover in plant species between our sampling plots.

We then used Non-Metric Multidimensional Scaling (NMDS) as an ordination technique to visually represent the relative position of individual sampling plots based on the dissimilarity in their species composition for both carabids (CNESS dissimilarity) and plants (Jaccard dissimilarity). Two dimensions were extracted to represent the variability in the original data, with resulting low stress values (<0.13) in all cases.

We subsequently calculated Multiple Regression of Distance Matrices (MRM)-models (Legendre et al., 1994, Lichstein, 2007) to specifically investigate the strength of potential non-linear, but monotonous effects linking changes in the vegetation, distance between sampling plots, and elevation to changes in carabid assemblages. This modelling was based on Spearman rank correlations and included the CNESS dissimilarity matrix of carabids for either $m = 1$ or $m = 25$ as response variable. We calculated models that included different sets and combinations of our explanatory variables, namely the dissimilarity matrix for plants, and distances represented by geographic coordinates and changes in elevation.

Finally, we used structural equation models (SEMs) to calculate the strength of overall links between beetle and plant species turnover and the differences in geographic locations and altitude between individual plots. While NMDS ordination plots at low stress create a highly realistic representation of the similarities between species communities that is not bound by linearity constraints, the cloud of plots can be rotated, and the actual NMDS axes values are hence poorly suited for use in SEMs. We therefore used multi-dimensional scaling based on a Principal Coordinate Analysis (PCoA) of our dissimilarity matrices in this context. Here, plots are located along the two respective dimensions (axes) in a way that specifically optimizes the spread of plots along these axes to represent the main turnover shown in the dissimilarity matrices. In contrast to NMDS, PCoA uses a linear underlying model. We then based our SEMs on the axis values of the two dimensions generated by a PCoA for both beetles and plants. We included the two beetle PCoA axis scores as independent response variables in two separate models for the CNESS dissimilarities of $m = 1$ and $m = 25$, respectively. We then used the two plant PCoA axis scores in addition to the latitudinal, longitudinal and elevational change between the plots as explanatory predictor variables. We also incorporated predictions of the two plant PCoA axis scores based on the geographic distances and elevational change in the models. To ensure that we used true distances, geographical coordinates were transformed into UTM coordinates. All variables were standardized prior to the analysis, and model estimates were based on 1000 bootstrapping operations. A detailed description of the structural equation model is provided in the [electronic appendix S1](#). Calculations of sample completeness were based on comparisons between observed and estimated species richness, calculated using the bias-corrected formula for the Chao 1 species richness estimator.

We used the ‘ecodist’ package to calculate the MRM models (Goslee & Urban, 2007), the ‘lavaan’ package for structural equation models

(Rosseel, 2012), and the ‘vegan’ package for remaining multivariate analyses (Oksanen et al., 2014), all in R (R Core Team 2014).

3. Results

3.1. General data structure

We collected 30,685 carabid beetle individuals representing 162 species in 37 genera from the 159 forest plots across the ten study regions (Table 1). Of these, 141 species were identified to species level, while the remaining 21 species represent morpho-species identified to genus level – with two *Pterostichus* spp. being new to science (Sun et al., 2018). None of the species were encountered at all the study regions. The most widespread species, the predatory *Carabus canaliculatus*, was recorded from eight regions, including the mature forests of Changbaishan and Zhangguancailing. One species, *Poecilus fortipes*, occurred at seven study regions; this species was missing from the two sites associated with the Changbaishan mountain range and from Zhangguancailing. *Trichotichnus coruscus* occurred at six study regions. All other carabid species (n = 159) were limited to five or less of the study regions. Furthermore, 89 species (55 %) were encountered in only one of the ten regions. Mean sample completeness per plot, estimated using the bias-corrected formula of the Chao 1 estimator, was 81.4 %, with no apparent region-specific bias in sample completeness.

Across the 156 vegetation plots distributed over the ten study regions (Table 1), we recorded 667 plant species in 349 genera. Of these, 491 were herbaceous species. In addition, we recorded 97 shrub and 79 tree species. Again, no plant species was encountered at all study areas. The most widely distributed vascular plant species were six tree species: *Larix gmelinii*, *Ulmus pumila* (seven regions, each), *Acer pictum*, *Betula platyphylla*, *Populus davidiana* and *U. laciniata* (six regions each). Of this group, *U. pumila* was the only species not recorded from the mature forest region of Changbaishan. Two of the widely distributed tree species, *L. gmelinii* and *P. davidiana*, are commonly used in reforestation campaigns, so that their wide distribution might at least partly be attributable to anthropogenic planting, in addition to reflecting their natural re-colonization. Of the herbaceous species, *Rubia cordifolia* and *Spodiopogon sibiricus* were the most widely distributed, occurring in half of the study regions, while none of the shrub species occurred at five or more study regions. In total, 443 species (66.4 %) were only recorded from a single study region.

3.2. Overall turnover patterns

The overall distribution patterns of both taxonomic groups (Fig. 2) show clustering according to individual study regions, reflecting the large proportion of both carabid beetle and plant species recorded at a single study region. This pattern was more pronounced for overall carabid assemblage composition ($m = 25$, Fig. 2b) than for dominant species ($m = 1$, Fig. 2a), with some overlap occurring in the carabid study-region clusters, particularly between Donglingshan, Yiwulushan and Liaoheyuan in the centre of the two ordination plots. These three study regions were all dominated by secondary forests and positioned in the Eastern part of our overall study area (Fig. 1).

The differentiation of the vegetation into distinct clusters representing individual study sites (Fig. 2c) was very strong, with each study area, with the exception of broadleaved secondary forests at Baishilazi and the two regions in the mountain ranges associated with the Bashang plateau, forming distinct regional clusters. Within individual study region clusters, there was no consistent sub-clustering by forest types, with plots representing mature, secondary and plantation forests at least partially mixed within some of the study regions. The ordination plot furthermore indicates that both, plant and beetle assemblages at Zhangguancailing, the only study area where we encountered plantation, secondary and mature forests in relatively close proximity, were very homogenous when compared with most of the other study regions.

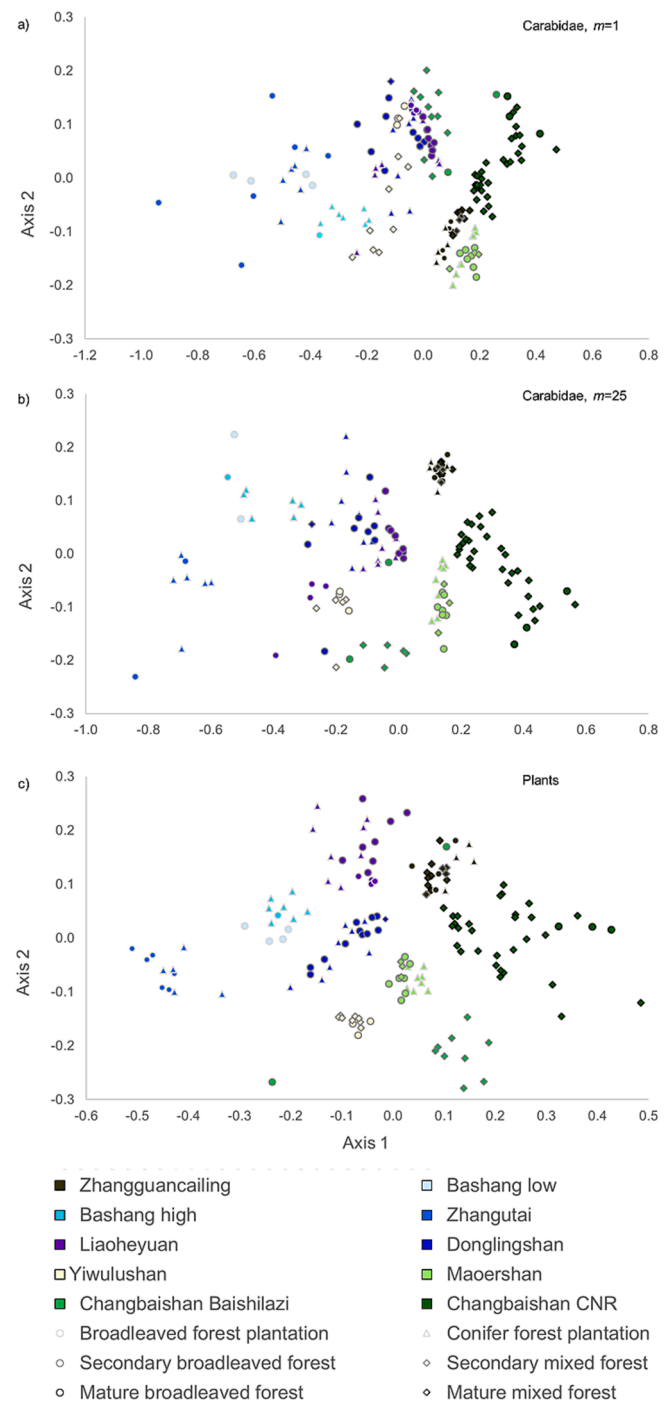


Fig. 2. NMDS ordination plots based on the CNESS dissimilarity matrix for ground beetle assemblages for a) a standardized sample size of $m = 1$, b) $m = 25$ and c) Jaccard dissimilarity for the vegetation. Different colours represent different study areas, different symbol shapes represent different forest types and different symbol lines differentiate between mature, secondary and plantation forests.

3.3. Links between carabid and plant assemblages and their spatial settings

Differences in species assemblages of ground beetles (Fig. 2) were strongly associated with both, geographic distance and changes in the vegetation composition. With view of the relative importance of these parameters, the non-parametric MRM models (Table 2) show strong differentiations between individual models. For turnover in dominant

Table 2

Model coefficients and R^2 of the multiple regression on distance matrices for models with different combinations of explanatory variables (MRM; *: $P \leq 0.05$; **: $P \leq 0.01$; ***: $P < 0.001$; -: variable was excluded from the respective model).

Reasonable variable dissimilarity matrix	Explanatory dissimilarity matrices			Model R^2
	Vegetation	Geographical distance	Altitudinal change	
Carabids, $m = 1$	0.482**	0.088**	0.008	0.205
	0.484**	0.090**	–	0.205
	0.499**	–	0.027	0.198
	0.507**	–	–	0.197
	–	0.159**	0.089**	0.041
Carabids, $m = 25$	0.548***	0.084***	0.007	0.263
	0.550***	0.086***	–	0.263
	0.566***	–	0.027	0.257
	0.573***	–	–	0.256
	–	0.176***	0.092***	0.049

beetle species ($m = 1$), but particularly for overall changes in beetle assemblages ($m = 25$), vegetation exerts the strongest influence ($P < 0.001$), while the influence of geographic distances is lower, albeit still being significant ($P < 0.01$) in all cases. In contrast, changes in altitude had a much smaller effect on beetle turnover that only became statistically significant once effects related to the vegetation composition were excluded from the models.

The strong links between turnover in vegetation and beetle assemblages, and the poor direct links especially between overall beetle assemblages and altitude, were further corroborated by the structural equation models (Fig. 3). This analysis indicates that the overall vegetation composition, as well as the distribution of dominant ground beetles (Fig. 3a) is heavily influenced by the location of the respective study plot and especially by the latitude of the study plots, while particularly changes in the overall beetle community (Fig. 3b) can chiefly be explained by changes in the plant communities in addition to changes in location, where longitude became an important predictor. In turn, vegetation changes are strongly determined by changes in location and, to a much lesser degree, elevation. This pattern emphasizes the significant determining power of both the vegetation and location on the species composition of the ground beetle communities across our study area, resulting in a strong regionalization of the species pools of both, beetle and plant communities.

4. Discussion

Based on the distribution patterns of both ground beetle and vascular plant species across the different mature, secondary and plantation forests in our study area, we can clearly reject our first, ‘widespread generalist’-hypothesis. According to this hypothesis, we would expect to see widely homogenous assemblages of both plants and beetles in the recently established forests, resulting in two distinct clusters in the ordination plot – one containing all new forest samples and one the mature forest samples. Instead, our results reflect a lack of widespread beetle or plant species found across the different restored and reforested sites that would represent such generalists.

The lack of widespread generalist species in either taxon in plantation forests, but also in secondary forests, might be surprising given that such patterns have been regularly reported in European epigeal beetle studies (Fahy & Gormally, 1998, Magura et al., 2002, Fuller et al., 2008, Martínez et al., 2009, Johansson et al., 2016, O’Callaghan et al., 2017). The observed differences could be related to distinct biogeographical and historical differences between Europe and China.

In contrast to the naturally highly impoverished European fauna and flora that suffered significant declines during the Pleistocene (Birks &

Tinner, 2016), China’s Eastern provinces remained widely ice-free and are likely to have provided suitable migratory routes for temperate species moving from colder conditions towards China’s main Pleistocene refugia in southern mountain ranges (López-Pujol et al., 2011), as well as to microrefugia closer to species’ current ranges (Bao et al., 2015). This may have resulted in a much higher number of temperate plant and carabid species surviving glaciation at the regional scale, including many forest specialist species with distinct niche requirements that were able to escape unfavourable environmental changes by shifting their distributions without impediment from major geographic barriers. This theory is further supported by the high levels of diversity in our study area for example in tree species when compared with the tree diversity of central Europe. While the native flora of central Europe contains five species of maple (*Acer* spp.), four birch species (*Betula* spp.) and eight members of the Pinaceae, our 156 study plots alone contained 12 maple and seven birch species, as well as 12 members of the Pinaceae. Floristic diversity levels in our study area were therefore more similar to levels recorded in the forests of the Eastern US (USDA, NRCS, 2019). Nonetheless, our data contains only highly localized plot-based records that represent only a fraction of the overall regional diversity in north-eastern China, highlighting the generally very high phytodiversity levels in this northernmost part of China.

The contrast between the patterns we report here with patterns widely described particularly in European studies in our view highlights potential problems in transferring ecological ‘principles’ established in the well-studied, but species-poor temperate European environments to other temperate regions of the world. It could well be that the highly varied assemblages of both forest beetle and plant species in temperate China is a singularity. Nonetheless, it could also be the case that the naturally impoverished, widely anthropogenic landscapes of Europe represent a singularity, too, and further research will be needed to clarify the general role forest plantations and naturally regenerated forests can play in the conservation of the biodiversity of temperate areas around the globe.

In addition to surviving the Pleistocene, highly biodiverse temperate forest species assemblages surprisingly also appear to have survived the widespread anthropogenic obliteration of China’s forest ecosystems, subsequently re-colonizing today’s regenerating and replanted forests. Thus, instead of the existence of a limited number of generalist species able to spread across the newly establishing forest landscapes, a much more diverse species pool has persisted. This has allowed for much stronger regional-scale differentiation in species assemblages colonizing the newly establishing forest landscapes.

Next, we need to consider whether the resulting differentiation of species assemblages occurs along the lines of habitat differences or spatial differences, in support of either our second, ‘widespread habitat specialist’ hypothesis, or our third, ‘local recruitment’ hypothesis. Previous investigation of assemblages at Donglingshan, one of the study regions in this analysis, has highlighted that at the local level, there is strong forest-type specific differentiation of both plant and beetle assemblages (Warren-Thomas et al., 2014). The results of this new analysis also supports these findings: the highly significant influence of the vegetation composition on ground beetle species composition, even when differences in altitude and spatial patterns are accounted for, clearly suggests that habitat specialists are contributing to differentiations of newly establishing ground beetle assemblages. The observed links between plants and ground beetles can be explained since, from the perspective of predatory invertebrates, the vegetation composition strongly determines the physical structure and microclimatic conditions of their habitat, as well as impacting on the composition of available prey species (Maleque et al., 2009). Furthermore, the vegetation is indicative of abiotic factors like humidity and nutrient status of the respective site. Previous studies have highlighted that humidity, the composition of the litter layer and crown density – factors all highly dependent on the forest type – are crucial determinants for the structure of carabid assemblages in Europe (Fuller et al., 2008; Taboada et al.,

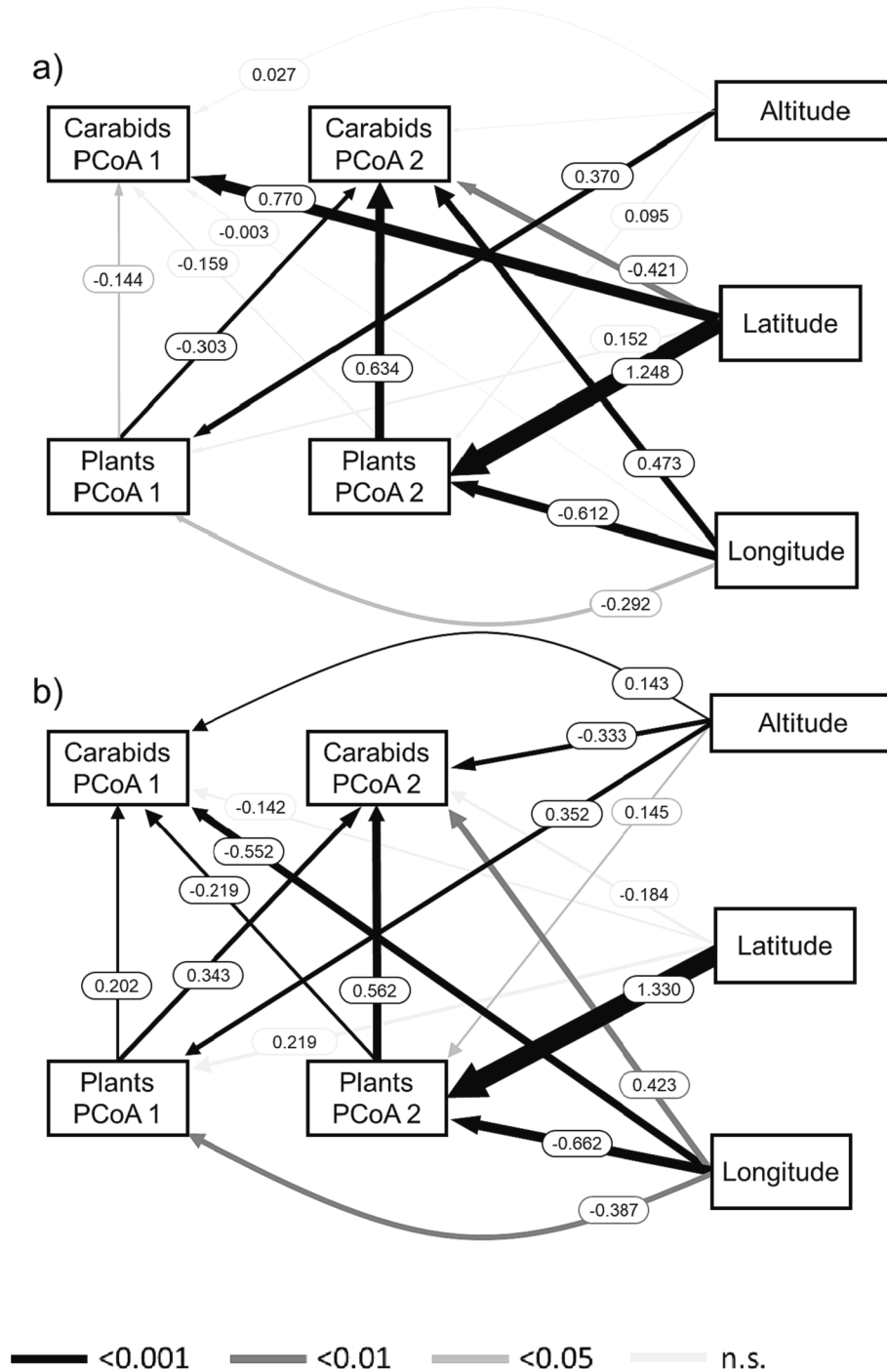


Fig. 3. Links between the location of the study plots (altitude, latitude, longitude) and the assemblage composition (two ordination axes resulting from Principal Coordinates Analysis of dissimilarity matrices) for beetles and plants, focusing on the turnover in dominant beetle species (CNESS, $m = 1$, 3a) and in the overall composition of ground beetles (CNESS, $m = 25$, 3b). Width of arrows and numbers indicate relative estimated slope parameter (β) of the respective relationships, with the grey scale of the arrows indicating significance levels.

2008; Lange et al., 2014; Negro et al., 2014; Spake et al., 2016) and China (Yu et al., 2006, Warren-Thomas et al., 2014).

Nonetheless, the significant influence of the vegetation across our large geographic study area is somewhat surprising, given results of smaller scale studies in the same area. Previous studies within our study area covering intermediate spatial scales have shown much weaker links between plant and invertebrate diversity, both for species richness (Axmacher et al., 2011; Zou et al., 2015a,b) and species composition (Zou et al., 2015b; Duan et al., 2016). Instead, these studies have shown that changes in elevation, which are strongly linked to changes in

climatic factors like precipitation, temperature and radiation, appear to be the main driver of species turnover at these intermediate scales. However, in this larger-scale analysis, we show that vegetation composition is a key predictor of carabid species turnover. This may be due to an increasing impact of large-scale biogeographic differentiations affecting both taxa in similar ways. Overall, our results provide strong evidence that the spatial context of studies investigating forest biodiversity is absolutely crucial; biodiversity response patterns are not only highly complex, but conclusions drawn from studies of a specific spatial setting cannot be easily generalized across spatial scales.

Our second, 'widespread habitat specialist' hypothesis does not only propose the existence of habitat-specific assemblages, but also postulates that respective habitat-specific assemblages occur over large geographic scales. We show that the distinct local habitat specialization in some study regions is much less pronounced than in others, and it clearly does not result in the presence of widespread habitat specialist assemblages that occur within a forest type across the entire study area. Instead, our results demonstrate that in neighbouring forest regions, even when there are no apparent dispersal barriers between them as they are connected by widely continuous forest ecosystems, assemblages are highly location-specific. The high regional turnover in the understorey vegetation in this context acts as a key predictor of the high spatial turnover in ground beetle assemblages. These patterns provide strong support for our third, 'local recruitment' hypothesis. At the large spatial scales we investigated here, the recolonization of China's newly establishing forests is therefore based on the existence of regional species pools of both, undergrowth vegetation and ground beetles.

Such a highly regionalized re-colonization pattern, additionally confounded by habitat-specific, and, in the case of carabids, vegetation-specific response patterns, strongly suggests that local forest species persisted in small microrefugia scattered across the entire study area when it experienced widespread forest destruction by the 1960s. The small size of carabids and herbaceous plants dominating the undergrowth vegetation could have strongly aided the survival of these species in times when large, unfragmented forests were lacking across our study area (Mosblech et al., 2011). A confounding factor in the case of ground beetles could relate to their relatively poor dispersal ability. Unfortunately, while detailed information on the proportion of brachypterous beetles in NE China is missing, we were unable to further investigate this aspect.

A further factor aiding the local survival of both plant and beetle species can be seen in the relative brevity of the time between the near-complete destruction of China's forests in the 1950s and 60s and the subsequent re-establishment of secondary forest ecosystems and forest plantations, with the latter strongly accelerating in the 1990s (Feng et al., 2005). It is well established that even small habitat islands initially contain, and can temporarily support, high levels of species richness once becoming isolated. Resulting extinction debts (Kuussaari et al., 2009), i.e. the time-frame for species pools in newly-isolated habitat patches to reach an equilibrium species number through the extinction of significant proportions of their initially species assemblage, often lasts for very significant time-frames (Gorman, 1979). It therefore appears that the forest regeneration and replanting occurred in time for the extinction debt associated with the severe forest destruction of the last century to have been widely avoided at least for ground beetles and understorey plants.

The significant environmental heterogeneity across the mountainous study area in terms of precipitation and elevation represents a further factor potentially aiding the highly regionalized recruitment of assemblages to the newly created forests. Remaining mature forest remnants, but also most secondary forests and forest plantations are encountered on land that is sub-optimal for agricultural production and located on mountain slopes, while the valleys and plain areas remain under intense agricultural use. Forest plant and beetle species will therefore encounter steep environmental gradients along relatively short geographic distances – conditions benefitting the creation and maintenance of a large, highly spatially differentiated regional species pool (Beck et al., 2013).

There is, to our knowledge, no reliable survey data available for invertebrates or plants in this area that would be suitable to establish pre-deforestation biodiversity across our study area, and it is therefore impossible to directly assess how many species, and how many forest specialist species in particular, have been lost during the deforestation of the last century. Nonetheless, previous research has shown that the overall species richness of ground beetles (Zou et al., 2015b; Zou et al., 2019) and geometrid moths (Zou et al., 2016) is currently not

significantly higher in the mature forest remnants than in at least some of the reforested areas considered in this research. This might indicate that overall species losses have been relatively minor, with most local forest species somehow surviving in the aforementioned refugia. Nonetheless, previous studies also showed strong differences for example in feeding trait spectra of beetle assemblages between newly established and mature forests (Zou et al., 2015b; Zou et al., 2019). Such differences could indicate that more generalist species, and particularly more herbivorous species, become established in secondary and plantation forests compared to mature forests. Further research into trait spectra will be needed to provide a clearer indication how assemblages differ between new and mature forests, and to assess implications of these variations for forest ecosystem functioning.

5. Conclusion

We conclude that the ongoing reforestation of large, strongly interconnected parts of temperate China has not resulted in the establishment of a homogenous assemblage of generalist understorey plants or beetles. Instead, the resulting forested landscape has been colonized by localized species assemblages that show a surprisingly high spatial turnover in their composition. There are also strong indications that these localized assemblages contain a significant number of forest specialist species, as suggested by both the small-scale differentiation of beetle and plant assemblages into different forest types at local scales in some of the study regions, and by the observed strong link between the composition of the vegetation and the beetle assemblages. China's extensive reforestation and forest protection measures therefore appear likely to strongly promote the long-term survival of forest species pools across the restored temperate forest landscapes. Since carabids are playing significant roles in the biological control of many pest species, the high ground beetle diversity can also be seen as a potential safeguard for the forest ecosystems against the establishment of pest species. These findings illustrate a globally-relevant lesson for wider forest restoration efforts globally – namely the importance of acting to restore forests in landscapes before extinction debts have been repaid.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2023.121479>.

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