Resilience of insect assemblages to climate change in mature temperate mountain forests of NE China

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ABSTRACT

The turnover patterns in species assemblages along gradients of abiotic or biotic conditions are indicative of the assemblages' sensitivity to changes in these conditions. Studies of such gradients allow an evaluation of the degree of habitat specialization in different taxa, which will strongly affect their ability to react to changes in climatic conditions. Our study was carried at one of the largest mature temperate forests in northeastern China, Changbai Mountain. We establish how strongly shifts in the assemblages of two mega-diverse insect families, ground beetles and geometrid moths, are associated with changes in the vegetation that are indicative of the degree of habitat specialization, in comparison to altitudinal change that is linked to changes in both temperature and precipitation. Overall, altitudinal change exerted a substantially stronger influence on insect species turnover patterns than vegetation changes, with elevation being particularly strongly linked to turnover in carabid and dominant geometrid species. Significant links were recorded between changes in the vegetation and turnover in both insect taxa, but Partial Mantel Tests reveal that the observed links with the vegetation are partly indirect. The results indicate that many species in both taxa are habitat generalists able to thrive in a wide range of plant species assemblages and vegetation structures. This will facilitate climate change-induced shifts in their distribution ranges. Conservation efforts should therefore be strongly focused on the smaller groups of habitat- and host-plant insect specialists, as well as on assemblages associated with mountain top habitats that will be unable to shift their ranges further upward.

Key words: Altitude; β-diversity; Carabidae; Geometridae; vascular plants

INTRODUCTION

Changes in species assemblages along environmental gradients may indicate their sensitivity to fluctuations in land-use patterns, climatic and other environmental conditions, as well as to historical factors (Condit *et al.*, 2002, McKnight *et al.*, 2007). Currently, our understanding of the drivers determining spatial variations in species assemblages remains limited, despite of their importance for ecosystem functioning, the effective conservation of biodiversity and for the sustainable management of ecosystems in times of rapid changes in climatic conditions.

Factors determining distribution, diversity patterns and sensitivity to climate change are particularly poorly understood with regard to most insect taxa (Andrew *et al.*, 2013, Butchart *et al.*, 2010, Schuldt *et al.*, 2012). This is highly problematic since insects account for the majority of multicellular organisms on our planet and play key roles in the provision of ecosystem services like pollination and pest control. Studies of species' altitudinal distribution patterns can help us to understand their climatic change responses (Sanders & Rahbek, 2012, Stevens, 1992), since changes in elevation are strongly associated with changes in both temperature and precipitation. Studies of altitudinal gradients both in tropical (Axmacher *et al.*, 2009, Rodríguez-Castañeda *et al.*, 2010) and temperate regions (Hawkins & Porter, 2003, Zou *et al.*, 2013) have highlighted changes in elevation and their associated shifts in climatic conditions to be key determinants of changes in insect assemblages. It nonetheless often remains unclear if the observed altitudinal turnover relates directly to climatic changes or is influenced by vegetation or habitat changes (Axmacher *et al.*, 2009, Carneiro *et al.*, 2014). In this context, ecological niche theory suggests positive links between the composition and diversity of plant assemblages and the respective patterns in both herbivorous and predatory taxa. These links are believed to be based on changes in the composition of available food resources provided by the vegetation and on the influence of vegetation structure on habitat features such as shelters and breeding sites. Consequently, changes in the local plant species composition may result in shifts in assemblages of herbivorous insects, which in turn affect the composition of prey species available to predatory insects (Rzanny *et al.*, 2012, Schaffers *et al.*, 2008). While links between changes in the species composition of plants and herbivorous insects have been investigated in tropical forests (Brehm *et al.*, 2003, Heimonen *et al.*, 2013), observations from temperate forests are limited, and information on insect taxa representing higher trophic levels are generally scarce.

In this study, we investigate factors underlying the turnover patterns in two insect families - carabid beetles (Coleoptera: Carabidae) and geometrid moths (Lepidoptera: Geometridae). They represent two of the most species-rich families on the planet, with more than 40,000 species of ground beetles and more than 35,000 species of geometrid moths currently known to science (Carabidae of the World, 2014, Lövei & Sunderland, 1996, McLeod *et al.*, 2009). Both taxa are also widely distributed and sensitive to changes in environmental conditions, making them good indicators of environmental change (Holloway, 1985, Rainio & Niemelä, 2003). In addition, they represent distinctly different trophic levels, with carabid beetles chiefly classed as predators or omnivores, while geometrid moths are chiefly herbivorous insects.

We provide insights into the changes of the species assemblage structure in these two insect taxa in relation to shifts in altitude and plant species composition. According to the bottom-up control theories, the plant species composition will affect arthropods that directly feed on these plants, with knock-on effects for arthropods at higher tropic levels such as predators and parasitoids (Schaffers *et al.*, 2008, Schuldt *et al.*, 2010, Sobek *et al.*, 2009). Nonetheless, the species composition of both plants and arthropods will also be affected by the change of environmental factors in relation to shifts in elevation. The first aim of our research is to identify whether the links between the turnover in plant species and in the two insect assemblages exceeds the strengths of links between the insect taxa and altitude. In addition, given the potential direct links between geometrid moths and the vegetation via herbivory and pollination (Macgregor *et al.*, 2015, Robinson *et al.*, 2010), while the link between predatory carabids and vegetation is more likely indirect, we hypothesize that species turnover patterns in this taxon are more strongly influenced by changes in the vegetation than the turnover in carabids. Overall, we aim to establish if the insect assemblages in the largest remaining mature forest environment of temperate China at Changbaishan show a high degree of habitat specialization – reflected in a strong link with the vegetation – as a potential barrier to climate-change induced shifts in their distribution ranges.

MATERIALS AND METHODS

Study area and sampling plots

This study was conducted along an altitudinal gradient on the northern slopes of Changbai Mountain, Jilin Province in northeast China (N 41°41' to 42°51' and E 127°43' to 128°16'). This region is dominated by cool-temperate moist forests. On the northern slopes of Changbai Mountain, an area of ~20,000 ha forming one of the most pristine large-scale forested environments in China has been protected in a national nature reserve.

Distinct zonal forest types are observed with increasing altitude on Changbai Mountain. Zonal forests range from mixed coniferous and broad-leaved forest (MCBF) below 1000m, Korean Pine forest (KPF) between 1000 and 1100m, mixed coniferous forest (MCF) from 1100 to 1500m and sub-alpine mixed coniferous forest (SMCF) at 1500 to 1800m to birch forest (BF) forming the upper forest boundary at 1800 to 2100m (Chen *et al.*, 1964, Sang & Bai, 2009, Zou *et al.*, 2014). We established 25 $20\times20\text{m}^2$ sampling plots covering all main forest types along our altitudinal transect from the mountain base at 700m asl to the upper forest boundary at 2000m asl (electronic appendix S1). The minimum distance between neighbouring plots was 60m.

Insect sampling and vegetation surveys

Automatic light traps consisting of a 12V, 20W, 60cm UV mercury light tube, a metal rain cover and three glass vanes mounted on top of a collection box that also contained the device's battery were located in the centre of each plot to sample geometrid moths. These traps were operated between 19:30 and 22:30, when geometrid moths were most active.

Carabids were sampled using pitfall traps. The 400m^2 plots were divided into four 100m^2 subplots, and a plastic cup with an open diameter of 7.5cm and a volume of 250ml was buried in the centre of each subplot. An aluminium roof of 10x10cm^2 was placed about 7cm above the cup. As the study area experienced high levels of precipitation during the sampling period, the roof was seen as essential to protect the killing solution from dilution by rain and litter contamination. The use of roof may reduce the capture rate (Spence & Niemelä, 1994), but any related bias will similarly affect all samples, as roofs were placed above all traps. Saturated saltwater was used as solution to kill and preserve the specimens in the traps, as this cost-effective solution also minimizes attractant bias (Kotze *et al.*, 2011).

Pitfall trap sampling was conducted between early July and early August in 2011, and from late June to late August in 2012, with traps continuously operated and being emptied and re-set in ten day-intervals. Consequently, plots were sampled over 22-34 days in 2011, and for 42-65 days in 2012, as it was impossible to carry out sampling on the same day across all traps placed in such a large study area. Light trap sampling was carried out once a month on each plot in July and August 2011 and in June 2012.

The main insect collections are kept in the Institute of Zoology, Chinese Academy of Sciences, Beijing, and identification of carabids was greatly aided by the taxonomic experts at this institute. Geometrids were sorted with help from experts at the same institute, and samples representing most morpho-species were sent to the Canadian Centre for DNA Barcoding (CCDB) to confirm identifications. Species were subsequently delimited based on a sequence divergence threshold of 2%.

For the vegetation surveys, plants were separated into three layers: a tree layer including all woody plants exceeding

2m in height; a shrub layer comprising all woody plants with a height between 0.4m and 2m, and an undergrowth layer including all woody plants with the height of less than 0.4m and all herbaceous species. Species in tree and shrub layers were recorded in each of the four 10m×10m sub-plots, while the undergrowth was recorded on four plots measuring 1m^2, with one plot randomly located within each of the sub-plots.

Data analysis

We used two analytical approaches to link the species turnover of insects to changes in elevation and the vegetation; canonical ordination and Mantel Tests of distance matrices, with both approaches accounting for different aspects of species composition change (Tuomisto & Ruokolainen, 2006). Data analysis followed two distinct pathways. First, to avoid bias from abundance-based information for vegetation, plant importance values (IV) were calculated based on the relative contributions (abundance, frequency and dominance) of plant species according to different vegetation layers (see Zou *et al.*, 2013). Principal Components (PCs) based on a Principal Components Analysis (PCA) combining elevation data with the importance values of individual plant species were calculated to condense the data. Redundancy analysis (RDA) was then used to analyse changes in the insect species composition in relation to these Principal Components. As the insect data matrix contained a lot of zero values, it was transformed using a Hellinger transformation (Legendre & Gallagher, 2001) prior to analysis. A stepwise regression approach with forward selection was chosen for this RDA. Selection was stopped based on the reduction of the Akaike information criterion (AIC). The significance ($P<0.05$) of the individual predictor contributions was also considered in the selection of the best model. If the AIC difference between a model entering all ‘significant’ variables and the model with the minimal AIC value was small (<1%), then the former model was selected. Otherwise, the model with the smallest AIC value was selected as final model. Monte Carlo permutation tests (n=999) were used to establish the significance of contributions by individual PCs.

For the second analytical pathway, three sets of dissimilarity matrices were firstly computed –dissimilarity matrices indicating change in the plant species assemblages, changes in the insect composition and differences in elevation between plots. The dissimilarity matrix for plants was calculated based on the Jaccard index using presence-absence data, with this index being particularly robust in measuring incidence data (Magurran, 2004). The Chord-Normalized Expected Species Shared (CNESS) index (Trueblood *et al.*, 1994) was selected to compute the dissimilarity patterns of carabid and geometrid assemblages between plots. This index has been widely used in relation to insect samples as it is widely independent of differences in sampling size and sampling effort (e.g. Beck & Vun Khen, 2007, Liu *et al.*, 2010). For our calculations, we selected both the minimum sample size (*m*=1) to focus on the similarity in dominant species and the maximum shared sample size of all plots (*m*=47 for carabids and *m*=87 for geometrids) to investigate overall assemblage changes. Mantel tests were subsequently used to analyse the correlation between the species turnover matrices of insects and plants, and between insects and elevation. Considering the auto-correlation between vegetation zonation and elevation along the altitudinal gradient, partial Mantel tests were then used to analyse the independent influence of plants and elevation on species turnover of insects, respectively, setting the other predictor variable as control parameter.

The CNESS index was calculated using COMPAH (Gallagher, 1998). All other statistical calculations were conducted in R (R Development Core Team, 2011), using the ‘vegan’ package (Oksanen *et al.*, 2012). R-values in correlations represent Pearson Correlation Coefficients.

RESULTS

A total of 3723 carabid beetles representing 46 species, 8231 geometrid moths representing 131 species and 161 plant species representing 56 families were recorded from the study area. The tree layer contained 32 tree species representing 12 families, the shrub layer was comprised of 38 species in 14 families, and the undergrowth consisted of 100 species representing 42 plant families.

Main gradients in vegetation composition and altitudinal change

The plant assemblage structure in the study area in conjunction with altitudinal change could be condensed to 24 principal components (PCs). PC1 and PC3 were strongly linked to both changes in altitude and plant species, while the remaining PCs explained further components of vegetation change (electronic appendix S2). The first ten of these (PC1 – PC10) accounted for over 2/3 (67.1%) of the original variance, with each of these PCs individually explaining more than 4% of the original variance. PC1, which was strongly correlated with altitude change, individually accounted for a 14.5% of the explained variance. This was much higher than the variance explained by all subsequent PCs, where the variance fell very gradually from 8.9% for PC2 to 4.1% for PC10. Consequently, we decided to focus all subsequent analysis on these ten PCs, with electronic appendix S1 providing detailed information on these PCs and on the taxa and parameters strongly associated with them, while Table 1 provides an overview of the explained variance represented by each PC and its links to altitude and parameters describing the overall plant species richness.

Influence of environmental factors on insect assemblages

Changes in carabid assemblages were significantly linked ($P<0.05$) to PC1, PC3 and to a much smaller degree to PC7 (Fig. 1a). The resulting model explained 52% of the beetle species variance and had an AIC value of -60.7. The first axis was highly correlated with PC1 ($r=0.85$, $P<0.001$), which individually already explained 42% of the original variance ($F_{1,21}=16.6$, $P=0.001$), while the second axis was significantly correlated with PC3 ($r=-0.84$, $P<0.001$) that represented a further 8% of the variance ($F_{1,21}=3.5$, $P=0.02$). PC7 finally explained an additional 2% ($F_{1,21}=2.7$, $P=0.05$) (Table 2).

Carabid assemblages encountered at the low-elevation forest types MCBF, KPF and at some MCF plots showed some similarities, forming a relatively clear aggregation pattern in the ordination plot, while species assemblages from habitats at higher elevations were more heterogeneous in their composition (Fig. 1a). Ten of the 17 most common species whose individuals accounted for more than 0.5% of all the specimens were clustered towards the centre of the plot, indicating that the distribution patterns of these species were not strongly influenced by the principal components generated by both elevation and plant species changes. Meanwhile, *Carabus aurocinctus* Motschulsky and *Pterostichus comorus* Jedlicka were positively associated with increases in values of PC1 (Fig. 1a), indicating their clear preference for SMCF and high-elevation plant assemblages, respectively. The three *Pterostichus* species *Pt. adstrictus* Eschscholtz, *Pt. orientalis* Motschulsky and *Pt. vladivostokensis* Lafer in contrast showed a clear preference for low-elevation, MCBF plant assemblages.

Similar to the carabid assemblage structure, species composition changes in geometrids were again significantly linked to PC1, PC3 and PC7, while PC9 and PC2 were included as additional components in the selected model with an AIC value of -66.5. The total explained variance in the geometrid moth assemblage composition in this model also reached 52%. In this model, PC1 contributed 25% ($F_{1, 21}=9,8$, $P=0.001$), PC3 11% ($F_{1,21}=.4.4$, $P=0.001$), PC7 6% ($F_{1,21}=2.1$, $P=0.042$) , PC2 5% ($F_{1,21}=2.0$, $P=0.047$) and PC9 5% ($F_{1,21}=2.1$, $P=0.043$), respectively (Table 2).

The first RDA ordination axis was again significantly positively correlated with PC1 (r=0.9, P<0.001), while the second axis was negatively correlated with PC3 (r=-0.68, P<0.001) and positively with PC9 (r=0.43, P=0.029). These two axes together explained 42% of the variance.

The overall structure of the geometrid assemblages was more strongly differentiated by habitat than that of the carabid assemblages. While MCBF and KPF assemblages were located closely together, assemblages in all forest types formed individual clusters (Fig. 1b). The majority of the 32 most common geometrid species that individually accounted for more than 0.5% of all individuals were again grouped in the plot centre. Of the remaining common species that had relatively high loadings on the ordination axes, most were positioned towards the positive side of the PC1, such as *Venusia cambrica* Curtis, *Hydriomena impluviata* Denis & Schiffermüller and *Alcis medialbifera* Inoue, indicating that those species were positively linked to the plant species and altitudinal changes underlying this component (Fig. 1b).

Cross-taxon similarities in species turnover patterns

Mantel Tests showed that the assemblage similarity patterns between plots in both carabids and geometrids (based on CNESS index values) were significantly correlated with the species assemblage structure of vascular plants (based on Jaccard dissimilarities), with similar trends observed both for dominant species (*m*=1; carabids: r=0.63, P<0.001; geometrids: r=0.69, P<0.001) and the overall assemblage structure (carabids *m*=47, r=0.66, P<0.001; geometrids *m*=87, r=0.69, P<0.001). In contrast to the resulting linear relationships observed between changes in insect and plant species compositions (Fig. 2), the highly significant positive relationship between the turnover in all three taxa and altitudinal change followed a logarithmic trend (Fig. 2, P<0.001 in all cases).

Even when setting plant dissimilarity as a control variable, Partial Mantel Tests showed a highly significant link between the turnover of the two insect taxa and altitudinal change (Table 3). When controlling for altitudinal changes, a much lower r-value in the Partial Mantel Tests indicated that the altitude-independent components of the relationships in species turnover between plants and both insect families were much weaker, although they remained highly statistically significant (Table 3).

DISCUSSION

Factors governing changes in species composition – altitude or vegetation?

The decrease in temperature and increase in precipitation with increasing elevation observed in our study area (Bai *et al.*, 2011) appears to strongly govern the turnover in both carabids and geometrids. Although we also observed significant links between the species turnover of both insect taxa and the turnover in the vascular plant assemblages, the overall variance in the insect assemblage composition explained by plant components was much weaker than that directly linked to altitudinal change. Both spatial Mantel Tests and the RDA reflect this pattern, indicating that a large proportion of the observed positive links between insect turnover and the complex of altitude and altitudinal vegetation zonation is actually related to the former. The relative weakness of direct links between changes in moth and plant assemblage composition, particularly once altitude was used as control parameter, could be seen as indicative for the existence of a regional geometrid moth community containing predominantly host-plant and habitat generalists. While our understanding of the detailed ecology and feeding habits of geometrid moth species in the study regions is extremely limited (Robinson *et al.*, 2010), the limited direct effects changes in the plant species composition have on the observed turnover of the moth assemblages strongly support this assumption.. The sensitivity of geometrid moths to changing temperature and precipitation regimes along the slopes of Changbai Mountain concurs with investigations of Brehm *et al.* (2003) and Rodríguez-Castañeda *et al.* (2010) from South America and by Axmacher *et al.* (2009) from Africa, which all identified elevation as the dominant factor in determining the composition of geometrid species assemblages.

Nonetheless, in view of the strong altitudinal zonation of the vegetation in our study area, it must be acknowledged that in models fully controlling for the influence of altitude, the remaining, independent links between plant species turnover and insect assemblage composition are likely to underestimate the existing strengths in these relationships, and even under these conditions, the links were still highly significant. This supports the assumption that at least some of the geometrid and carabid species show high degrees of habitat specialization and, in response to climatic change, might only be able to adapt their distribution range slowly, if at all, following the gradual, slow shift in the vegetation composition in these forest ecosystems (Bai *et al.*, 2011).

Since plots in this study followed an altitudinal gradient on the northern slopes of Changbai Mountain, altitudinal changes in this context are also correlated with horizontal distance. It could be suggested that parts of the observed altitudinal turnover patterns of insects are reflective of dispersal limitations that result from geographical dispersal barriers. However, the entire study area is covered by continuous forests, with no obvious physical dispersal barriers present. We therefore expect that demographic stochasticity effects related chiefly to evolutionary patterns that may potentially affect species composition (Hubbell, 2001) will be negligible in this relatively small area. The influence of altitudinal change on insect turnover are likely to be fully attributed to related changes in abiotic environmental factors, of which temperature and precipitation are seen as particularly important (Stevens, 1992).

Taxon-specific differences in response patterns

Both the higher variance explained by the altitude-related PCs PC1 and PC3 for carabids in comparison to geometrids and the larger regression coefficient in Partial Mantel Tests for large carabid sample sizes indicate that ground beetles are more sensitive to the climatic changes occurring along the altitudinal gradient. This in turn confirms our second hypothesis, predicting a stronger link between the turnover of geometrids and the vegetation. Carabids are already known to respond highly sensitive to changes in microclimatic conditions like humidity levels (Gillingham *et al.*, 2012, Koivula *et al.*, 1999, Niemelä *et al.*, 1992), which in our study area strongly relate to changes in elevation. The stronger turnover of carabids in response to environmental change might also be related to their comparatively weak dispersal abilities (Den Boer, 1970, Lövei & Sunderland, 1996). In addition, the predominantly carnivorous and omnivorous traits of ground beetles are associated with an increased metabolic rate in comparison to herbivores (Townsend & Hughes, 1981), again rendering them potentially more sensitive to environmental change compared to geometrid moths or other representatives from lower trophic levels (Voigt *et al.*, 2003).

The significant amounts of variance explained by the remaining PCs that mainly reflect changes in the vegetation and the substantially higher regression coefficient in Partial Mantel Tests for large sample sizes when controlling for altitudinal change in geometrids in comparison to carabids, also aligns well with the underpinning ecological theories, indicating strong bottom-up effects from the vegetation to herbivores, which then become weaker at higher trophic levels. Nonetheless, it must be noted that links with the vegetation were always substantially weaker for both insect taxa than links with altitude.

Lessons for biodiversity conservation

Our results show that, similar to trends reported for the turnover of plants and insects in tropical forests, the changing abiotic conditions associated with changes in altitude are key drivers of changes in plant, carabid and geometrid assemblages in the highly diverse, mature temperate forest ecosystems of Eastern Asia. On one hand, the very pronounced sensitivity of insect assemblages to changes in climatic conditions could be interpreted as forming a very substantial threat posed by climate change, particularly when seen in conjunction with habitat fragmentation and land-use change (Axmacher *et al.*, 2009, Axmacher *et al.*, 2011, Axmacher *et al.*, 2004).

On the other hand, the indicated weak direct links with the vegetation observed in our study indicate that many insect species might be able to react to climate change via vertical or lateral range shifts, subsequently utilizing alternative host plants and habitats, since plant distribution shifts in response to climate change are commonly slower than will be required by insects in order to stay within their climatic niches (Samways, 2005). Nonetheless, fast adaptations of distribution ranges will not be an option for host plant specialists that are therefore potentially severely threatened by climate change, particularly when they occupy a relatively limited climatic niche (Beck *et al.*, 2011, Wilson & Maclean, 2011), although shifts in caterpillar food plant ranges in response to climate change as observed in butterflies (Pateman *et al.*, 2012) might offer a potential solution. Nonetheless, even species utilizing a wider range of host-plants might be threatened by the complete disappearance of entire sets of plant species from the study area, where some very significant shifts in the undergrowth plant species composition have been observed in the last fifty years (Bai *et al.*, 2011). For the vegetation itself, new threats might arise from new encounters with herbivorous insect species that rapidly adjust their distribution range in response to climate change (Bale *et al.*, 2002, Hódar & Zamora, 2004, Lindner *et al.*, 2010), with potential further knock-on effects for food-plant specialists relying on the affected plant species. A further group of insects under strong threat by climate change are high-elevation specialists which are limited in their occurrence to the highest proportion of mountain ranges (Chen *et al.*, 2009). These species will be restricted to increasingly smaller areas in their distribution ranges under warming temperatures and will therefore also require specific conservation attention.

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Tables

Table 1 Explained variance and loading of altitude for principle components, and Pearson correlations coefficients between principle components and plant diversity/density factors (bold text represents significant correlations; *: P≤0.05, **: P≤0.01, ***: P≤0.001)

PCs	Explained variance	Altitude (m)	Tree species richness	Shrub species richness	Herb species richness	Woody species richness	Total plant species richness	Tree density	Shrub density	Herb density
PC1	14.5%	0.849***	-0.36	-0.29	0.51**	-0.66***	-0.14	0.44*	-0.16	0.54**
PC2	8.9%	0	-0.25	-0.06	-0.07	0.1	0.69***	-0.34	-0.33	-0.39
PC3	7.7%	-0.45**	0.21	-0.03	-0.23	0.5*	0.13	-0.44*	-0.46*	0.02
PC4	7.1%	0	0.07	0.26	-0.21	-0.21	-0.03	-0.09	-0.12	0.22
PC5	5.8%	-0.11	0.14	0.19	-0.27	0.1	-0.26	0.05	-0.03	-0.44*
PC6	5.4%	0.13	-0.27	-0.41*	0.24	-0.01	0.01	-0.03	0.32	0.17
PC7	4.9%	0.12	-0.19	0.21	0.28	0.16	0.28	0	0.41*	0.28
PC8	4.4%	0	0.3	0.13	0.21	-0.25	-0.32	-0.1	-0.16	-0.12
PC9	4.3%	0.07	0.40*	0.17	0.04	-0.18	-0.3	-0.27	-0.17	-0.17
PC10	4.1%	0.03	0.04	-0.02	0.21	-0.04	-0.02	-0.03	-0.04	0.02

Table 2 RDA results for carabid and geometrid assemblages using principal components (PC) that were computed based on the combination of altitude and plant species importance value as explanatory variables (*: PC strongly associated with both, altitudinal and plant composition changes; NS: not selected in the model)

Species composition	**Model AIC**	**Total explained variance**	**Unbiased total explained variance**	**Variance explained by first two RDA ordination axes**	**Variance explained by principal components**				
					***PC1**	**PC2**	***PC3**	**PC7**	**PC9**
Carabid beetles	-60.7	52%	45%	50%	42%	NS	8%	2%	NS
Geometrid moths	-66.5	52%	39%	42%	25%	5%	11%	6%	5%

Table 3 Partial Mantel Tests r value showing links between the dissimilarity patterns of insects and altitudinal difference (using plant dissimilarity as control variable) and plants (using altitudinal difference as control variable); P <0.001 in all cases, based on Monte Carlo permutation tests (n=999)

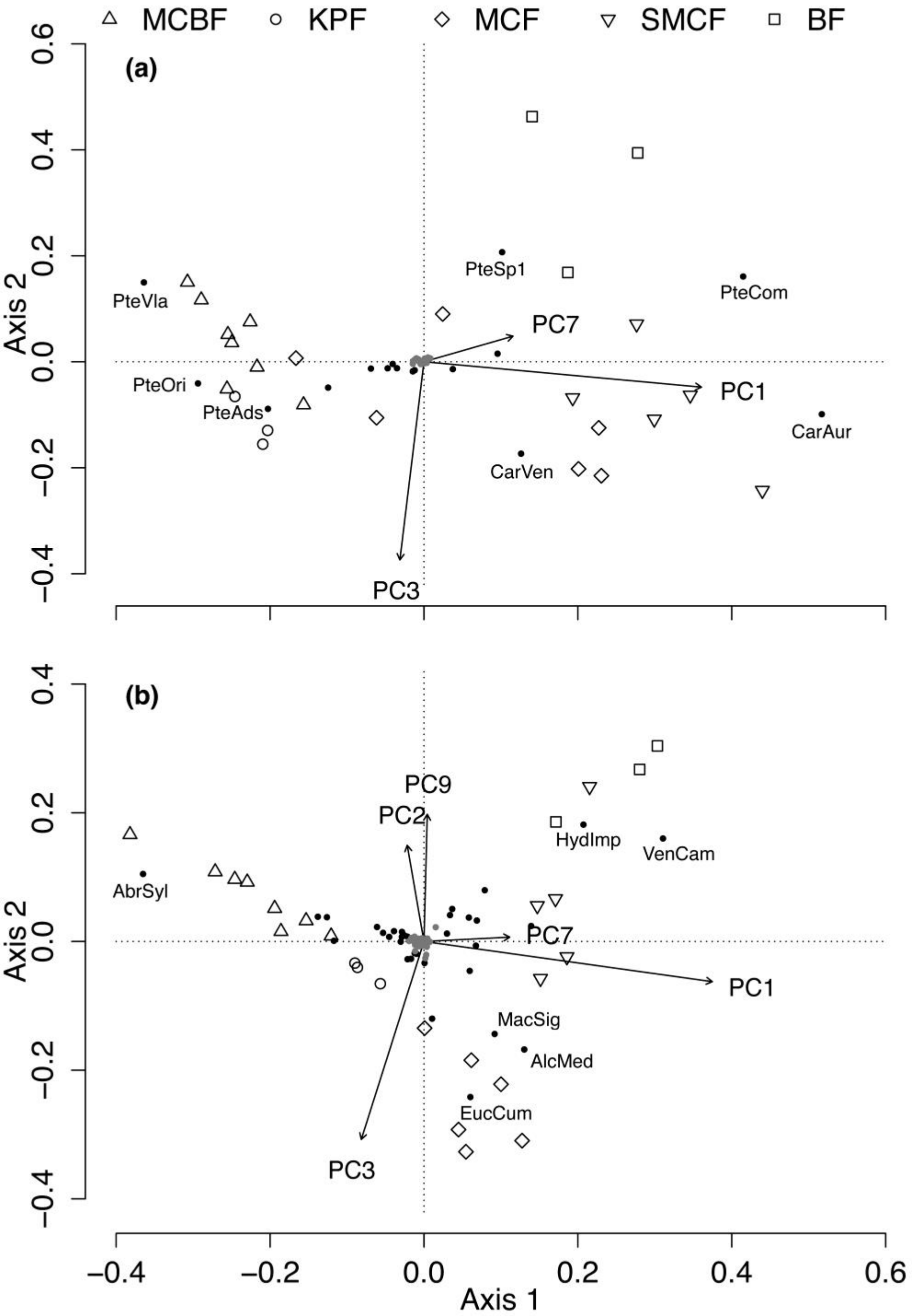
Taxa	**Sample size in CNESS**	**Altitudinal difference**	**Plant Jaccard difference**
Carabid beetles	*m*=1	0．41	0．20
	m=47	0．46	0．22
Geometrid moths	*m*=1	0．54	0．22
	m=87	0．33	0．33

Figures

Fig. 1 Redundancy analysis ordination plots showing the relationship between species community compositions of (a) carabid beetles and (b) geometrid moths and principal components (PCs); black solid dots represent common species (>0.5% of the total number of individuals caught) and grey solid dots represent rare species (<0.5% of the total number of individuals). (△ : mixed coniferous and broad-leaved forest; ○: Korean Pine forest; ◇: mixed coniferous forest; ▽ : sub-alpine mixed coniferous forest; □ : birch forest; abbreviations of species names can be found in Appendix S3 and Appendix S4)

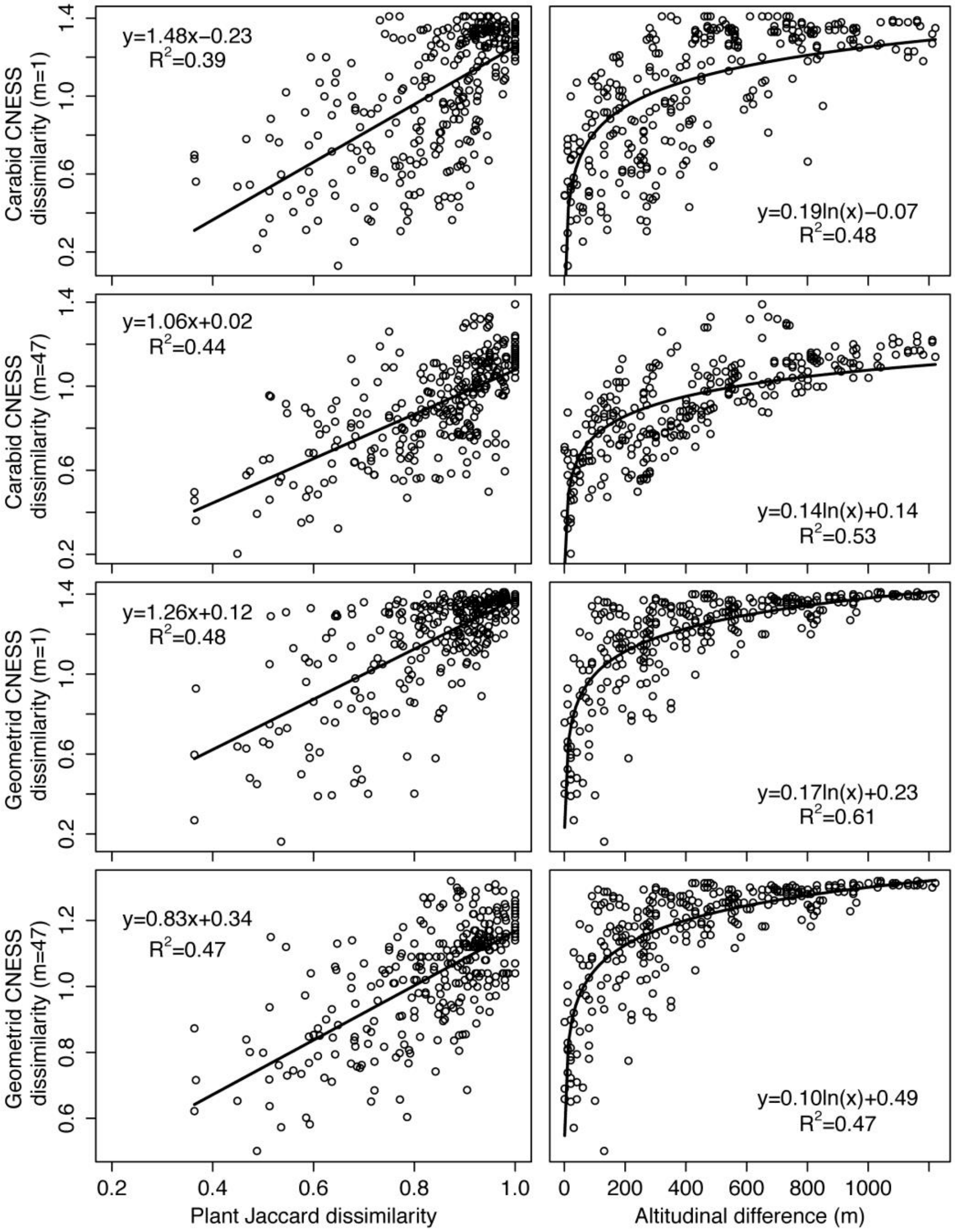
Fig. 2 Scatter plots reflecting pairwise between-plots dissimilarity patterns for the relationships between insect and plant assemblages and between insect assemblages and altitudinal difference, including regression equations and coefficients ($P<0.001$ in all cases); the dissimilarity matrix for plants was calculated based on the Jaccard index using presence-absence data, while the dissimilarity matrix for insects were calculated as The Chord-Normalized Expected Species Shared (CNESS) index.

Figure 1



△ MCBF
○ KPF
◇ MCF
▽ SMCF
□ BF
(a)
(b)
Axis 1
Axis 2
-0.4
-0.2
0.0
0.2
0.4
0.6
PteSp1
PteCom
PteVla
PC7
PC1
PteOri
PteAds
CarAur
CarVen
PC3
PC9
PC2
HydImp
VenCam
AbrSyl
MacSig
AlcMed
EucCum

Figure 2


y=1.48x−0.23
R^2=0.39
y=0.19ln(x)−0.07
R^2=0.48
Carabid CNESS dissimilarity (m=1)
y=1.06x+0.02
R^2=0.44
y=0.14ln(x)+0.14
R^2=0.53
Carabid CNESS dissimilarity (m=47)
y=1.26x+0.12
R^2=0.48
y=0.17ln(x)+0.23
R^2=0.61
Geometrid CNESS dissimilarity (m=1)
y=0.83x+0.34
R^2=0.47
y=0.10ln(x)+0.49
R^2=0.47
Geometrid CNESS dissimilarity (m=47)
0.2
0.6
1.0
1.4
0.6
0.8
1.0
1.2
0.2
0.4
0.6
0.8
1.0
0
200
400
600
800
1000
Plant Jaccard dissimilarity
Altitudinal difference (m)