1 **Geometrid moth assemblages reflect high conservation value of <mark>naturally</mark>**

2 **<mark>regenerated se</mark>condary forests in temperate China**

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Abstract

The widespread destruction of mature forests in China has led to massive ecological degradation, counteracted in recent decades by substantial efforts to promote forest plantations and protect secondary forest ecosystems. The value of the resulting forests for biodiversity conservation is widely unknown, particularly in relation to highly diverse invertebrate taxa that fulfil important ecosystem services. We aimed to address this knowledge gap, establishing the conservation value of secondary forests on Dongling Mountain, North China based on the diversity of geometrid moths – a species-rich family of nocturnal pollinators that also influences plant assemblages through caterpillar herbivory. Results showed that secondary forests harboured similar geometrid moth assemblage species richness and phylogenetic diversity but distinct species composition to assemblages in one of China's last remaining mature temperate forests in the Changbaishan Nature Reserve. Species overlap between these sites was about 30%, and species did not form separate phylogenetic clusters according to site. Species assemblages at Dongling Mountain were strongly differentiated according to forest type; a pattern not found at Changbaishan. Our results indicate that protected naturally regenerated secondary forests in northern China provide suitable habitats for species-rich and genetically diverse geometrid moth assemblages, highlighting the potential importance of these forests for conservation and ecosystem function provision across the wider landscape.

Keywords

Phylogenetic diversity; Lepidoptera; mature forest; Donglingshan; Changbaishan

1. Introduction

Widespread deforestation across China has led to dramatic biodiversity losses since

the 1950s. These triggered severe population declines and local extinctions in more

than 200 plant species, and in over half of the country's large mammals (see Zhang *et*

al., 2000). In response to the widespread ecological degradation associated with this

deforestation, the Chinese government established a variety of ecological protection

programmes such as Nature Forest Protection Programme, Nature Reserve

Development Programme and Desertification Reduction Programme. These

programmes were aimed at both the protection of the last remaining mature forests

and regenerating secondary forests, and at triggering re- and afforestation activities on

a globally unprecedented scale (Wang *et al.*, 2007; Chinese State Forestry Bureau,

2011). These activities were chiefly focussed on erosion control, lacking clear

objectives for biodiversity conservation and for the provision of associated ecosystem

services (Cao *et al.*, 2010; Ma *et al.*, 2013; Ran *et al.*, 2013). It is generally assumed

that the recent net increasing in China's forest cover has had little positive impact on

biodiversity in forest ecosystems (Lü *et al.*, 2011), but very little evidence has been

gathered about the actual conservation value of China's secondary and plantation

forests.

Mature forests are crucial for global biodiversity conservation, as they harbour a

unique and often highly specialized fauna and flora (Gibson *et al.*, 2011; Ruiz-Benito

1   *et al.*, 2012; Adams and Fiedler, 2015). At the same time, the potential of both

2   plantation and secondary forests to contribute towards ecosystem service provision

3   and conservation of diverse species assemblages is being increasingly recognized

4   (Brockerhoff *et al.*, 2008; Chazdon *et al.*, 2009; Bremer and Farley, 2010; Martin and

5   Blackburn, 2014; Zou *et al.*, 2015). Comparative assessment of biological

6   assemblages between mature and secondary forests can help to establish the relative

7   importance of the latter for biodiversity conservation and ecosystem functioning

8   across wider scale landscapes. Assessment in number of species for target taxa can

9   give us a direct view of biodiversity value, whereas the assessment of species

10   composition changes can indicate the sensitivity of these target taxa to the change of

11   environmental conditions and can provide information of historical factors (Condit *et*

12   *al.*, 2002; McKnight *et al.*, 2007).

13   Species-rich taxa that fulfill important roles in forest ecosystems are logical target

14   taxa for assessments of biodiversity conservation for mature and secondary forests.

15   Geometrid moths (Lepidoptera: Geometridae) represent one such taxonomic group.

16   With more than 35,000 described species (McLeod *et al.*, 2009), geometrids are one

17   of the most diverse monophyletic insect families. They provide a number of key

18   ecosystem services, as an important pollinator group that can also contribute towards

19   weed control, since caterpillar herbivory influences the composition and competitive

20   balance in the vegetation (Scoble, 1999; Palmer *et al.*, 2007; Grenis *et al.*, 2015;

21   Macgregor *et al.*, 2015). In turn, their diversity and abundance in forest ecosystems

22   makes them an important food source for predatory species like birds or spiders.

1   Changes in forest geometrid diversity and assemblage structure can be expected to

2   directly impact the ecosystem functioning of forest ecosystems at multiple trophic

3   levels, with wide implications for ecosystem service provisions.

4   From an evolutionary perspective, phylogenetic analysis of species assemblages

5   allows us to have an insights view in terms of evolutionary pathways and ecological

6   traits. For example, species losses from species-poor, phylogenetically highly distinct

7   clades are considered more detrimental than losses from species-rich, closely related

8   clades (Mace *et al.*, 2003; Mouquet *et al.*, 2012). Phylogenetic diversity therefore

9   reflects evolutionary information and can be used as a proxy for functional diversity

10   (Winter *et al.*, 2013). DNA barcoding-based phylogenetic analysis is increasingly

11   promoted as a complementary approach to more traditional species richness and

12   composition-focussed measures of conservation value (Lahaye *et al.*, 2008; Smith and

13   Fisher, 2009; Liu *et al.*, 2015). DNA barcoding method has been applied for

14   geometrid moths in quite a few studies (Hausmann *et al.*, 2011; Sihvonen *et al.*, 2011;

15   Strutzenberger *et al.*, 2011; Brehm *et al.*, 2013; Brehm *et al.*, 2016; Zou *et al.*, 2016).

16   In this study, we compare and contrast the species richness, species composition and

17   phylogenetic diversity of geometrid assemblages in two forest regions of northern

18   China that experience similar climatic conditions. The first, on Dongling Mountain

19   (DLM), comprises a mosaic of naturally regenerated secondary forests and forest

20   plantations. The second region is located in the Changbaishan Nature Reserve (CNR)

21   at a distance of 1100km from DLM. This reserve contains one of the largest

1   remaining mature forests in temperate China. Due to historical clearance of the forest

2   cover at DLM, forest specialist species are assumed to have been widely replaced by

3   generalists in the regenerating secondary forests (Warren-Thomas *et al.*, 2014). We

4   hypothesised that this would lead to a depleted, homogenous geometrid moth

5   assemblage in these secondary forests when compared to assemblages at CNR. In

6   addition, we also hypothesised that the widely undisturbed forest cover at the CNR

7   would support more phylogenetically distinct moth assemblages and hence has a

8   higher phylogenetic diversity, as a wider variety of historically consistently available

9   niches in these forests should have allowed them to preserve assemblages containing

10 more moth species with unique ecological traits. In combination, CNR was therefore

11 assumed to have a higher conservation value, both in terms of species richness,

12 species composition and phylogenetic diversity, compared to the secondary forests at

13 DLM that have established following the near-complete clearance of forest vegetation

14 at this region. In order to achieve the above goals, we compared DLM and CNR in (1)

15 number of genera rarefied to minimum sample size for a plot, which can be used as a

16 proxy of diversity (Brehm *et al.*, 2013), (2) Chao1 expected species richness, (3)

17 Shannon diversity, (4) extrapolated expected species richness, (5) species turnover

18 pattern, (6) phylogenetic diversity rarefied to minimum shared number of species and

19 (7) nearest-taxon index (NTI).

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21 **2. Methods**

2.1 Study areas and insect sampling

Our study was conducted in two geographically distinct, forested regions in northern China (Fig. 1). The first study region, Dongling Mountain (DLM; 39º58' N, 115º26' E), is located on the boundary between Beijing and Hebei Provinces in China. Originally covered by oak (*Quercus wutaishanica* Mayr, 1906) - dominated forests, the region was completely deforested before the 1950s. Large areas were subsequently recolonised by a mosaic of oak-dominated, birch (*Betula platyphylla* Sukaczev, 1911 and *B. dahurica* Pall, 1776) -dominated and mixed-broadleaved forests. We established 12 sampling plots at altitudes between 1100m and 1400m in this region, with four plots each located in the three aforementioned secondary forest types. The second study region is located within the Changbaishan Nature Reserve (CNR; 41°41' – 42°51' N, 127°43' –128°16' E) in Jilin Province near the boundary to North Korea. CNR harbours one of the largest remaining mature temperate forest ecosystems in northern China. At CNR, we established 11 sampling plots at elevations between 700m and 1100m within a mixed coniferous and broadleaved forest zone. While plots at CNR were located at lower elevations than DLM plots, their location further north means that both forest ecosystems experience very similar climatic conditions (Zou *et al.*, 2015). The annual mean temperature at 1100 m in DLM was 4.8°C, while the average annual precipitation reached 612 mm (Sang, 2004). In comparison, the average annual temperature recorded at 712m in CNR was 3.4°C, with an average annual precipitation of 654 mm (Sang and Bai, 2009).

1   Geometrid moths were sampled using automatic light traps, similar in design to Heath

2   light traps (Heath, 1965). These traps comprised a 12V, 20W mercury UV light tube

3   of 60cm length surrounded by three clear plastic vanes, mounted on top of the

4   sampling box. Sampling was carried out at each plot once a month between 19:30 and

5   22:30 hrs (the activity peak of geometrid moths). Although some late-night-active

6   species may have been missed by closing the traps at 22:30, this should have a limited

7   influence on our comparative results among sites, as trap closure times were

8   consistent at all sampling localities at the same time. No sampling was conducted five

9   days before and after the full moon to minimize the effects of a strong moonlight on

10   moth activity (Yela and Holyoak, 1997). One trap was deployed in each sampling plot.

11   Sampling was conducted from June to August 2011 at DLM, and in July and August

12   2011 and June 2012 at CNR. Three sampling nights were completed in each plot,

13   giving a total of 36 sampling nights at DLM and 33 sampling nights at CNR.

14   **2.2 Data analysis**

15   All geometrid specimens were initially sorted to morpho-species. A single leg of each

16   individual was used for amplifying DNA barcode region of the mitochondrial

17   Cytochrome Oxidase Subunit 1 (COI) 5's region. Specimens were further

18   differentiated into molecular operational taxonomic units (MOTUs) based on the

19   Kimura 2-parameter (K2P) distance (Kimura, 1980) with a 2% sequence divergence

20   threshold (Hausmann *et al.*, 2011). In many cases, this allowed us to confirm or

21   allocate species names from the Barcode of Life Data System (BOLD) (Ratnasingham

and Hebert, 2007). MOTU information for three easily identifiable species was excluded from barcoding, with their barcode information subsequently obtained from BOLD. We were unable to obtain phylogenetic data for one species, *Horisme radicaria* de La Harpe, 1855, which was represented by a single individual in our samples. A final 182 MOTUs species were identified (a detailed information of specimen and barcoding data are publicly accessible in BOLD under XXX). These 182 sequences were used for the calculating the maximum likelihood of phylogenetic tree based on K2P distance.

Rarefied number of genera for each sampling plot was calculated based on the minim sampling size of 29 individuals. The expected species richness of the two study regions was estimated based on the MOTUs using the Chao 1 richness estimator (Chao, 1984) and rarefaction–extrapolation methods (Colwell *et al.*, 2012). We calculated the species richness for an extrapolated sample size of 4000 individuals. This figure represents four times the smallest sample size we recorded (DLM, pooled across all plots). In addition, the Shannon (exponential) diversity index for each sampling plots was calculated (Jost, 2006). Species turnover patterns within each forest region were analysed based on a Euclidean distance matrix for individual sampling plots. This matrix was visualized using Non-metric Multidimensional Scaling (NMDS) ordination plots.

Species' phylogenetic diversity (PD) was calculated as the sum of the overall phylogenetic branch length for all species recorded at any one plot, based on Faith's

1   index (Faith, 1992). As total phylogenetic branch length increased linearly with the

2   increase in recorded species (Pearson correlation, r=0.99, p<0.001), a rarefied PD was

3   used to compare the standardized difference in phylogenetic diversity between plots.

4   This rarefaction was based on the smallest species number recorded at any sampling

5   plot (n=16 species). NTI values were opposite values of standardized effect size of

6   mean nearest taxon distances (Webb *et al.*, 2002), which were calculated based on the

7   null model across all taxa included in distance matrix. Calculation had 1000 runs of

8   randomization.

9   All calculations and statistics were conducted in R (R Core Team, 2014), using the

10   packages "vegan" (Oksanen *et al.*, 2012) to calculate Chao1, Shannon diversity,

11   rarefied number of genera and species turnover pattern, "iNEXT" (Chao *et al.*, 2014;

12   Hsieh *et al.*, 2014) to calculate extrapolated species richness, "ape" (Paradis *et al.*,

13   2004) to calculate K2P distance, "phangorn" (Schliep, 2011) to calculate the

14   maximum likelihood phylogenetic tree and "Picante" (Kembel *et al.*, 2010) to

15   calculate PD and NTI.

16   **3. Results**

17   A total of 3932 individuals representing 183 species (182 MOTUs and one without

18   phylogenetic information) were sampled at the 23 plots. Of these, 1,017 specimens

19   were collected at DLM and 2915 at CNR (see full species list in the Appendix). A

20   similar number of species was recorded in the two regions: 107 species on DLM

21   versus 113 species at the CNR. Species dominance between two areas in terms of the

1   number of common (i.e. accounting for $\geq$0.5% of the total regional sample) and rare

2   species (<0.5% of the total sample) were extremely similar: 38 (33.6% in number of

3   observed species) and 40 (37.4%) common species for CNR and DLN, and 75 (66.4%)

4   and 67 (62.6%) rare species encountered at the two regions (Fig. 2). DLM and CNR

5   shared 37 species in total, leaving 70 and 76 unique species, respectively at the two

6   regions. Of the 37 species occurring in both regions, only six were commonly

7   observed at both DLM and CNR, while 13 species were rare in both regions (Fig. 2).

8   A total of 178 species were identified to genus level that belonged to 106 genera, of

9   which DLM had 73 genera and CNR had 77 genera. Rarefying to minimum sample

10   size of all plots (m=29), DLM had an average of 16.3 (SE of 0.7) genera that was

11   higher than CNR (mean and SE of 13.5$\pm$0.4, ANOVA, *P*=0.003).

12   Values for Chao 1 indicated that there was no significant difference in the estimated

13   species richness between DLM (124$\pm$8.1 species with 95% CI) and CNR (121$\pm$4.8

14   species with 95% CI), while also indicating a high sampling completeness for both

15   regions (86.3% for DLM and 93.4% for CNR). In addition, no significant difference

16   was observed for the Shannon diversity index (mean and SE for DLM=21.1$\pm$1.9;

17   CNR=19.9$\pm$1.4; ANOVA, *P*=0.62). These numbers were also closely aligned with the

18   extrapolated species richness for the sample size of 4000 individuals, predicting 122

19   ($\pm$14.2, 95% CI) species at DLM and 117 ($\pm$7.6, 95% CI) at CNR forest plots, with

20   differences again not significant (Fig. 3).

21   NMDS ordination plots confirmed distinct differences in assemblage composition

between DLM and CNR (Fig. 4). Assemblage composition was much more

heterogeneous among plots within the DLM region than at CNR. Substantial

differentiation was observed at DLM both within forest types (i.e. among plots) and

between birch forests and the other two forest types (Fig. 4).

Phylogenetic lineages did not cluster separately between the two regions (Fig. 5). The

rarefied phylogenetic branch length based on the lowest recorded species number

(n=16) at DLM (mean and SE of 0.925 ± 0.011) and CNR (mean and SE of $0.919 \pm$

0.008) was again not significantly different between the two regions (ANOVA,

P=0.70). NTI value for DLM (mean and SE of 1.05 ± 0.29) and CNR (mean and SE

of 0.68 ± 0.36) were again no difference (ANOVA, P=0.43).

4. Discussion

Our study has following findings: (1) the naturally generated secondary forest (DLM)

harboured similar species richness and phylogenetic diversity with one of China's last

remaining mature temperate forests (CNR); (2) these two forest types had distinctive

species compositions; (3) species assemblages at DLM were strongly differentiated

according to forest type, but not at CNR; (4) species from these two forest types did

not form separate phylogenetic clusters

4.1 Species richness and composition

The species richness recorded in our study (107 species from 1017 individuals at

DLM and 113 species from 2915 individuals at CNR) is very similar to other

inventories of geometrid moths in temperate regions across China, with 75 species

(1000 individuals) recorded at Ziwu mountain in Gansu province (Jiang and Zhang,

2001), 110 species (14,692 individuals) from a wide mix of agricultural and forest

habitats between Beijing and the Bashang plateau located in Hebei province between

our two study areas (Axmacher *et al.*, 2011), and with 97 species (2,092 individuals)

previously reported from Changbai Mountain (Liu *et al.*, 2007). Our findings are also

well aligned to the species richness recorded in other temperate regions across the

world, with 103 species (1,992 individuals) sampled in the northern Swiss Alps (Beck

et al., 2010) and 123 species (13,324 individuals) in Central Queensland (Mackey,

2006). A substantially higher species richness of 308 species was recorded in forests

of the Jirisan National Park in South Korea by Choi and An (2013). This substantially

higher richness may be strongly attributable to the much larger sampling effort used

in that study spanning 7 years' long-term monitoring encompassing a total of 244 trap

nights that yielded a very substantial sample size of 11,030 individuals.

The similarity in species richness between secondary and mature forest regions

contradicts our first hypothesis, and is a first indication of the similar value relating to

geometrid moth diversity and the provision of associated ecosystem services of these

forests. A very similar species richness in secondary and mature forests has previously

been observed in studies covering a wide range of different taxa, for example large

tropical mammals (Barlow *et al.*, 2007), as well as temperate ant (Maeto and Sato,

2004) and click beetle (Ohsawa, 2004) assemblages. It also corresponds with the

diversity in the undergrowth vegetation in our study area that again showed very

The similarity despite the very different histories of the two forest regions could be linked to a number of different phenomena. The destruction of primary forests in the DLM region before the 1950s and the resulting current cover of DLM in secondary forests suggests that generalist species may contribute a large proportion of the observed species richness. This could be argued to limit the conservation value of these assemblages with view of commonly rare specialist species, although habitat generalists may provide important ecosystem functions as pollinators across the landscape more effectively than strict forest specialists (Aizen *et al.*, 2002). Nonetheless, the observed heterogeneity of DLM geometrid assemblages at the local scale and the partial differentiation of communities according to forest type suggests that generalists do not dominate these assemblages, and that there is habitat specificity among the geometrid species at DLM. Generalist-dominated communities would be expected to show a much more homogeneous distribution across both site individual plots, and different forest types. It therefore appears that forest specialists do not only form important components of forest moth assemblages at the landscape scale, but are differentiated at smaller scales according to differing microclimatic conditions and plant species compositions in the three forest types included in our DLM investigations, with similar patterns also observed in carabid beetles at our study area (Warren-Thomas *et al.*, 2014).

Moth diversity in secondary forests could also be related to the Intermediate

1   Disturbance Hypothesis (Grime, 1973; Connell, 1978), with secondary forests

2   representing a recovering, previously heavily disturbed environment. Secondary

3   forest habitats have had several decades to recover and to be colonized by a wide

4   range of species from surrounding remnant forest or bushland pockets. Habitat

5   mosaics during intermediate succession stage from forest regeneration can increase

6   available niches and result in higher specie diversity than forest at either early or late

7   succession stage (Li *et al.*, 2004; Hilt and Fiedler, 2005). This theory would predict a

8   lower diversity at the stable and mature forest sites in CNR, which was true in terms

9   of rarefied number of genera, but not for number of species. Investigations into

10   diversity patterns of geometrid moths along altitudinal gradients have commonly

11   confirmed the paramount importance of climatic factors on species richness (Brehm *et*

12   *al.*, 2003; Axmacher *et al.*, 2004; Beck and Chey, 2008; Axmacher *et al.*, 2009; Beck

13   and Kitching, 2009). Although sampling plots in CNR located slightly higher latitude

14   than DLM, the lower altitude compensates the latitudinal difference in terms of

15   climatic difference, and hence resulted in similar climatic conditions for our two study

16   sites. The similarity in diversity levels between our two study sites could be explained

17   by similarities in climatic conditions at the two forest ecosystems.

18   One strong difference in diversity patterns between the two forests relates to the

19   heterogeneity of assemblages among plots. In contrast to the clearly

20   differentiated forest types occurring at DLM, habitat heterogeneity at CNR is

21   encountered at much smaller spatial scales. The mixed conifer and broadleaf

22   forest at CNR contains highly variable, spatially finely grained mixtures of tree,

shrub and undergrowth species, and forest age-classes. This in turn supports the

presence of a relatively homogenous, but highly species-rich moth assemblage

throughout this forest, with any habitat-specific differentiation occurring below

the spatial resolution generated by our light traps. The main differentiation

among plots observed at CNR in the ordination analysis is associated with a shift

in elevation, and associated shifts in tree species dominance. The three highest

plots that harboured a slightly different moth assemblage to the remaining plots

on Changbai Mountain were also strongly dominated by Korean Pine (*Pinus*

koraiensis Siebold & Zucc, 1842). Since many geometrid moth species show a

palaearctic distribution patterns, ~30% overlap in species between study regions

appears to be low (Xue and Zhu, 1999; Han and Xue, 2011). It was furthermore

surprising that species shared between the two regions were mainly species that were

rare at both sites, while the composition of the group of dominant species differed

distinctly between the two regions. It can be speculated that the rare shared species

are host plant specialists, relying on plant species that occur in low abundances in

both areas. Only six of the shared moth species were common at both sites; these

included host-plant generalists such as *Angerona prunaria* Linnaeus, 1758

(Ennominae), a highly polyphagous species feeding on members of the Betulaceae,

Ericaceae, Ranunculaceae, Pinaceae, Caprifoliaceae, Fagaceae, Ericaceae and

Rosaceae (Robinson *et al.*, 2010). It could be assumed that these common shared

species have survived the devastation of forests at DLM somewhere within the wider

region, quickly colonising the emerging secondary forest ecosystems. In addition, the

distinctive difference in dominant species between DLM and CNR may refer to the

distinctiveness in some key biotic factor such as different species composition in

vascular plants (Zou *et al.*, 2015) – since two regions have similar climatic factors –

which may indicate two regions have different stress in biodiversity conservation.

4.2 Phylogenetic signals

The similar inter-regional phylogenetic diversity of DLM and CNR mirrored the

species richness patterns in two regions. This is in coherence with earlier studies that

had demonstrated the comparability of these two regions in terms of diversity and

associated ecosystem functions and traits (Cadotte *et al.*, 2008; Mouquet *et al.*, 2012).

Positive NTI values indicate a slightly phylogenetic clustering trend (Webb *et al.,*

2002) for both regions.

It must be noted that our phylogenetic tree is a COI tree that has some some

phylogenetic signal, but not a phylogeny. As our tree is far from perfect in comparison

with phylogeny of geometrids by e.g. Sihvonen *et al.* (2011). For example, species

from subfamily Geometrinae showed scattered clade and nested within Ennominae

and Sterrhinae, whereas Geometrinae formed a distinctive clade in Sihvonen *et al.*

(2011)'s study. In addition, our tree showed that one Larentiinae species (genus

Docirava) was also nested within Ennominae, two *Eilicrinia* spp. were nested within

Lomographa spp., and *Anticypella diffusaria* Leech, 1897 was in *Hypomecis* spp.

These unexpected nesting trends may result from unrepresentative information of the

tree for true phylogenetic signals. The tree also showed that some species were far

away from the same genus, such as *Eustroma aerosa* Butler, 1878, *Hypomecis* sp2 and *Cabera* sp2. These might due to misidentification or again the unrepresentative phylogenetic information of the tree. Furthermore, the tree showed a few paraphyletic cases from different genera, for example, *Hemistola tenuilinea* Alpheraky, 1897 and *Comostola subtiliaria* Bremer, 1864, *Abraxas grossulariata* Linnaeus, 1758 and *Ourapteryx similaria* Matsumura, 1910, *Phthonandria emaria* Bremer, 1864 and *Angerona prunaria* Linnaeus, 1758, and *Horisme tersata* Denis & Schiffermüller, 1775 and Eupithecia spp. Paraphyletic case *H. tenuilinea* and *C. subtiliaria* might be true as certain species from *Hemistola* was reported that transferred to *Comostola* (Han and Xue, 2009). These two genera were also phylogenetic close in Sihvonen *et al.* (2011)'s tree. As some of *Horisme* spp. were reported close to *Eupithecia* spp. (Mironov and Galsworthy, 2012), paraphyletic case of these two genera might also be true. The rest paraphyletic cases might result from lacking phylogenetic signals between two genera or unrepresentative for phylogenetic information of the tree.

4.3 Biodiversity conservation

Decades of severe ecological degradation across the country have resulted in the near-complete disappearance of China's mature temperate forests, with strong implications for populations of large vertebrate and many forest plant species. Despite the lack of respective data, forest insect assemblages are highly likely to have been heavily impacted by these forest losses. Our investigations suggest that this assumption needs to be treated carefully. It must be noted that the secondary forests

1 we investigated here have chiefly originated from natural regeneration, resulting in a

2 high structural and plant-species diversity (Zou *et al.*, 2015), while substantial

3 proportions of reforested sites across China are covered in tree monocultures, in some

4 cases using non-native species ecologically poorly suited to respective plantation

5 localities (Cao *et al.*, 2010; Cao, 2011). Given the high diversity in both, insect and

6 plant assemblages at DLM, we strongly suggest natural forest regeneration processes,

7 potentially accompanied by the planting of locally native tree species, as a method

8 that should be much more widely used in the ongoing re-establishment of forests

9 across large parts of China. The protection of these naturally generated forest is

10 valuable for biodiversity conservation for localities where no mature forest has been

11 remnant. Such an approach could have far-reaching positive implications for

12 biodiversity conservation, and the future provision of ecosystem services, across

13 China's restored forested landscapes.

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Figures

Fig. 1. Map of the study areas (DLM: Dongling Mountain; CNR: Changbaishan Nature Reserve)

Fig. 2. Number of common (representing $\geqslant$ 0.5% of the overall sample) and rare (<0.5%) species, differentiated into unique and shared species for Dongling Mountain (DLM) and Changbaishan Nature Reserve (CNR)

Fig. 3. Rarefaction and extrapolation curves for geometrid moths on Dongling Mountain (DLM) and in the Changbaishan Nature Reserve (CNR), shaded areas represent 95% confidence intervals from bootstrap calculations.

Fig. 4. Nonmetric Multidimensional Scaling (NMDS, stress=0.12) plot based on Euclidean dissimilarities between individual sampling plots for Dongling Mountain (DLM) and Changbaishan Nature Reserve (CNR)

Fig. 5. Maximum likelihood analysis of neighbourhood-joining trees (COI 5' data, based on Kimura 2-parameter distance) of geometrid moths; different text colours refer to species from different regions, where grey refers to species recorded uniquely from Dongling Mountain, cyan refers to species uniquely sampled from Changbaishan Nature Reserve and black refer to species sampled from both regions; different colours of the edge line refer to species from different subfamilies.
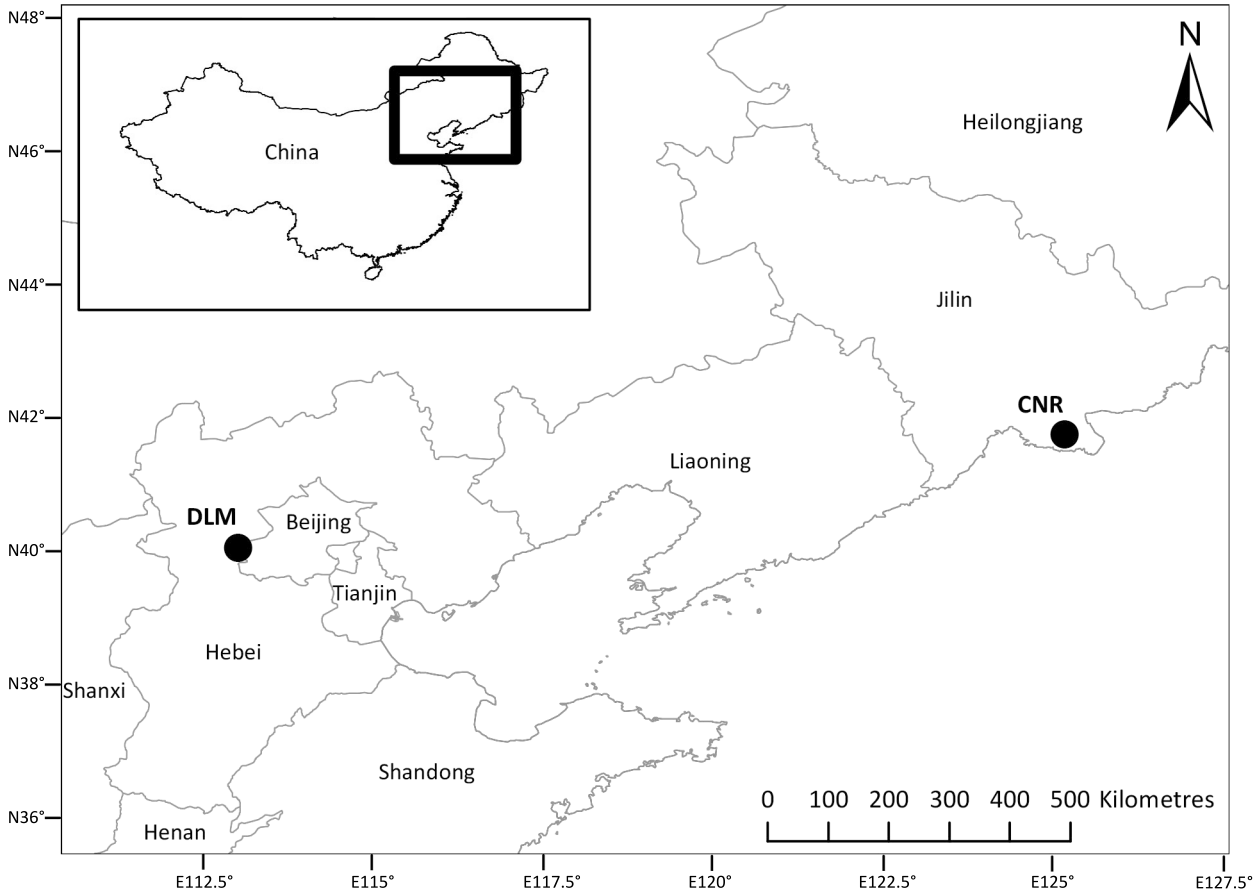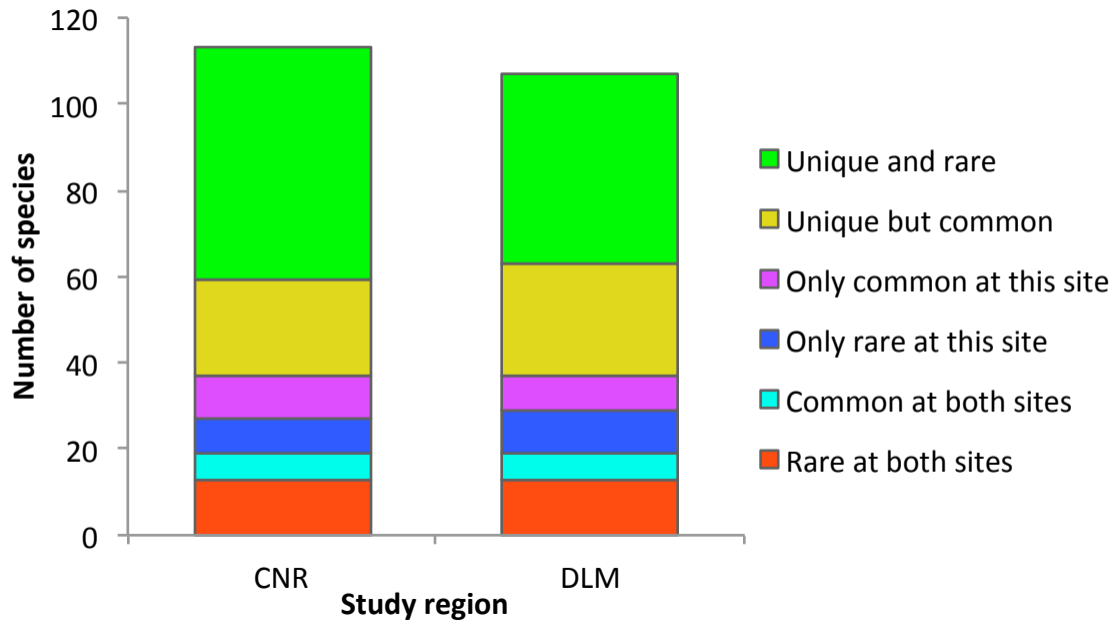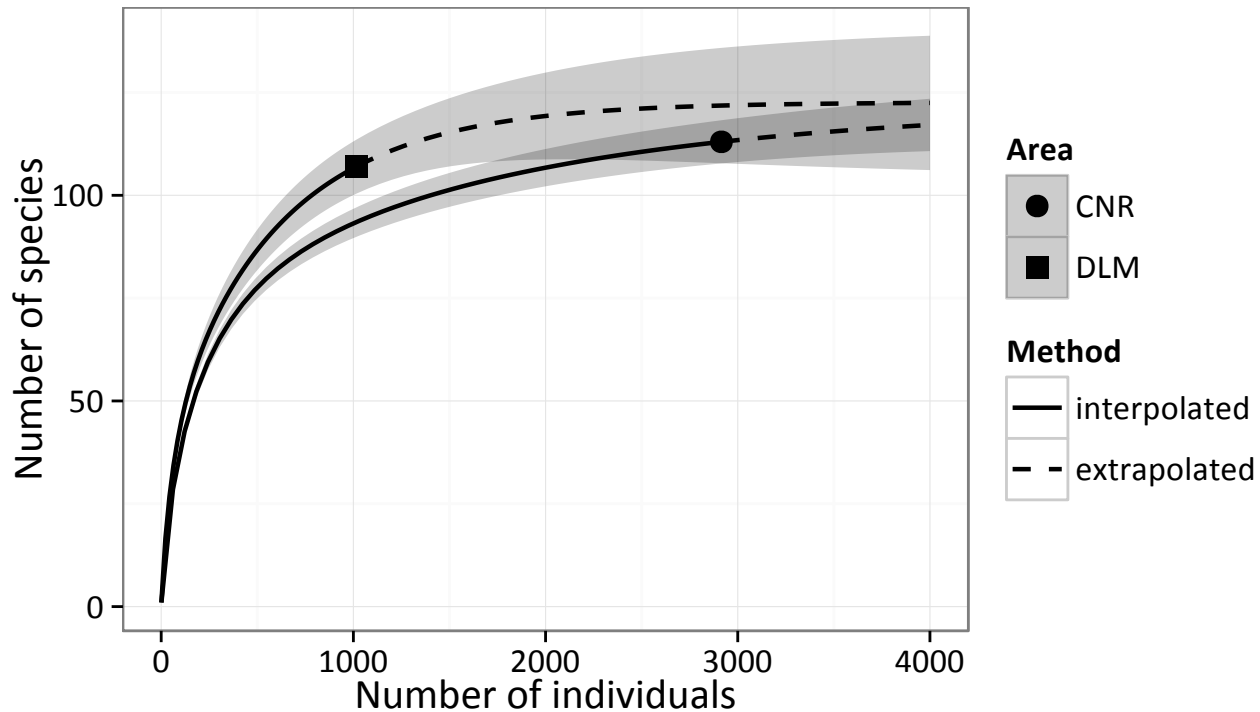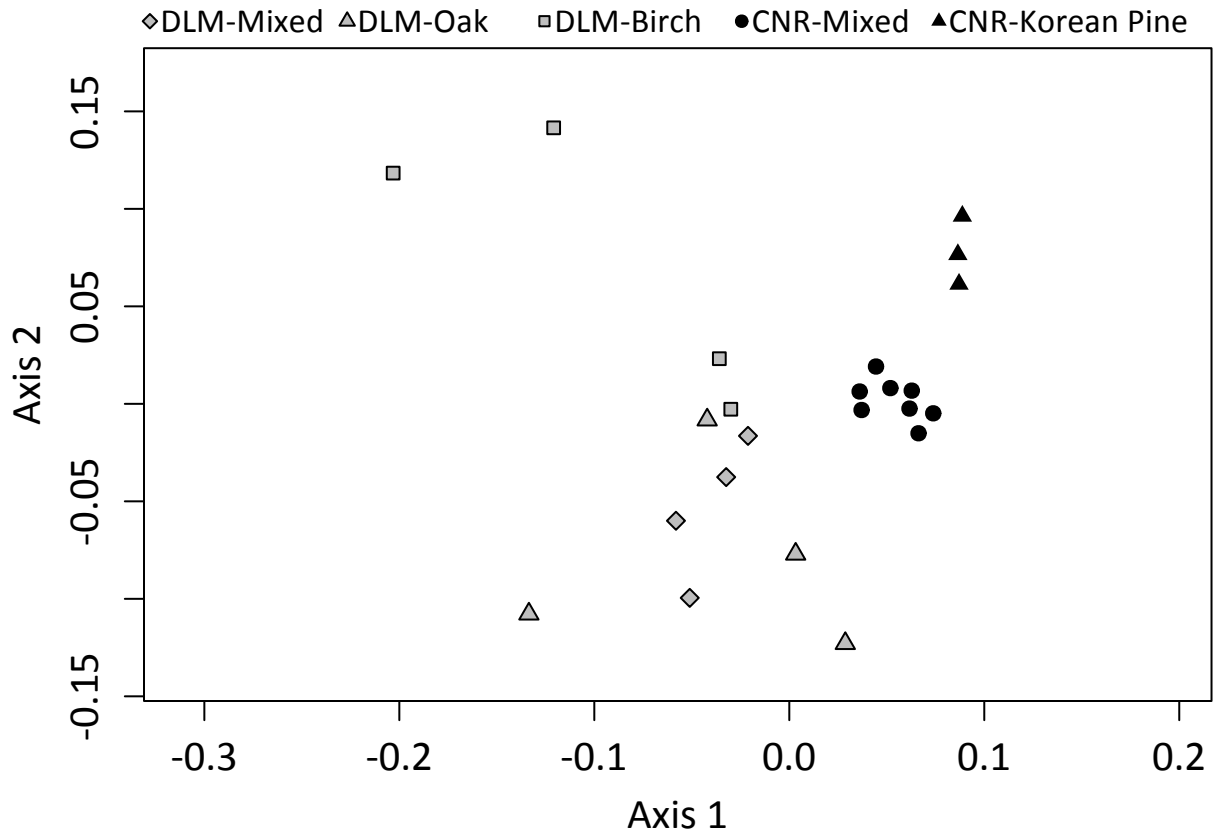
Appendix

Geometridae species list and their abundance in different forest types in Dongling Mountain (DLM) and Changbaishan Nature Reserve (CNR)

Subfamily	Species	DLM Mixed	DLM Oak	DLM Birch	CNR Mixed	CNR Korean Pine
Ennominae	*Abraxas grossulariata* Linnaeus, 1758	0	0	29	8	3
Ennominae	*Abraxas latifasciata* Warren, 1894	0	0	12	0	0
Ennominae	*Abraxas sylvata* Scopoli, 1763	0	0	0	595	21
Ennominae	*Alcis* cf. *medialbifera* Inoue, 1972	0	0	0	0	30
Ennominae	*Alcis picata* Butler, 1881	2	2	16	12	14
Ennominae	*Amraica superans* Butler, 1878	0	0	0	2	0
Ennominae	*Angerona prunaria* Linnaeus, 1758	8	2	7	40	7
Ennominae	*Anticypella diffusaria* Leech, 1897	0	1	1	15	0
Ennominae	*Aporhoptrina semiorbiculata* Christoph, 1881	0	0	0	1	0
Ennominae	*Arichanna melanaria* Linnaeus, 1758	0	1	45	0	11
Ennominae	*Biston betularia* Linnaeus, 1758	0	0	0	1	8
Ennominae	*Cabera exanthemata* Scopoli, 1763	2	0	1	15	1
Ennominae	*Cabera griseolimbata* Oberthür, 1879	2	8	5	49	3
Ennominae	*Cabera pusaria* Linnaeus, 1758	0	0	2	0	0
Ennominae	*Cabera* sp. 1	2	0	2	0	0
Ennominae	*Cabera* sp. 2	11	5	6	0	0
Ennominae	*Cabera* sp. 3	0	0	0	27	0
Ennominae	*Carige cruciplaga* Walker, 1861	0	0	0	9	0
Ennominae	*Cepphis advenaria* Hübner, 1790	0	0	0	3	0
Ennominae	*Cleora insolita* Butler, 1878	0	0	13	11	0
Ennominae	*Ctenognophos grandinaria* Motschulsky, 1860	1	0	0	0	0
Ennominae	*Ctenognophos* sp.	11	23	32	0	0
Ennominae	*Cusiala stipitaria* Oberthür, 1880	0	0	0	1	0
Ennominae	*Deileptenia mandshuriaria* Bremer, 1864	0	0	0	17	0
Ennominae	*Deileptenia ribeata* Clerck, 1759	0	0	0	88	5
Ennominae	*Deileptenia* sp.	0	3	0	0	0
Ennominae	*Diaprepesilla flavomarginaria* Bremer 1864	0	1	0	0	0
Ennominae	*Ectropidia exprimata* Walker, 1861	3	2	6	0	0
Ennominae	*Ectropis crepuscularia* Denis & Schiffermüller, 1775	0	0	0	6	0
Ennominae	*Ectropis excellens* Butler, 1884	0	0	0	10	0
Ennominae	*Eilicrinia parvula* Wehrli, 1940	0	1	0	0	0

Ennominae	*Eilicrinia wehrlii* Djakonov, 1933	0	0	0	2	0
Ennominae	*Endropiodes abjecta* Butler, 1879	12	2	11	241	0
Ennominae	*Endropiodes indictinaria* Bremer, 1864	0	0	0	0	1
Ennominae	Ennominae sp.	0	0	3	0	10
Ennominae	*Epholca arenosa* Butler, 1878	0	0	0	24	0
Ennominae	*Epholca auratilis* Prout 1934	17	12	17	0	0
Ennominae	*Euchristophia cumulata* Christoph, 1880	0	0	0	6	4
Ennominae	*Exangerona prattiaria* Leech, 1891	32	3	6	44	0
Ennominae	*Garaeus mirandus* Butler, 1881	0	0	0	2	0
Ennominae	*Gnophos serratilinea* Sterneck, 1928	5	4	4	0	0
Ennominae	*Heterarmia conjunctaria* Leech, 1897	19	6	27	0	0
Ennominae	*Heterarmia* sp.	0	0	0	18	5
Ennominae	*Heterolocha laminaria* Herrich-Schäffer, 1852	1	0	0	24	0
Ennominae	*Hirasa* sp.	1	1	0	0	0
Ennominae	*Hypomecis punctinalis* Scopoli, 1763	0	0	1	235	6
Ennominae	*Hypomecis roboraria* Denis & Schiffermüller, 1775	0	0	0	125	47
Ennominae	*Hypomecis* sp. 1	0	0	0	12	0
Ennominae	*Hypomecis* sp. 2	1	0	2	3	0
Ennominae	*Hypomecis* sp. 3	0	0	0	1	0
Ennominae	*Hypomecis* sp. 4	0	0	0	15	0
Ennominae	*Jankowskia fuscaria* Leech, 1891	0	0	0	28	0
Ennominae	*Lomaspilis marginata* Linnaeus, 1758	0	0	2	3	0
Ennominae	*Lomographa bimaculata* Fabricius, 1775	0	0	0	99	0
Ennominae	*Lomographa* cf. *lungtanensis* Wehrli, 1939	3	7	2	0	0
Ennominae	*Lomographa* cf. *simplicior* Butler, 1881	0	0	0	6	0
Ennominae	*Lomographa simplicior* Butler, 1881	1	1	0	0	0
Ennominae	*Lomographa subspersata* Wehrli, 1939	0	0	0	7	0
Ennominae	*Lomographa temerata* Denis & Schiffermüller, 1775	0	0	0	16	0
Ennominae	*Macaria* cf. *signaria* Hübner, 1809	0	0	0	1	0
Ennominae	*Macaria notata* Linnaeus, 1758	0	0	3	0	0
Ennominae	*Macaria wauaria* Linnaeus, 1758	0	0	1	2	0
Ennominae	*Medasina* sp.	3	3	6	0	0
Ennominae	*Megaspilates mundataria* Stoll, 1782	0	1	0	0	0
Ennominae	*Menophra senilis* Butler, 1878	0	0	0	4	0
Ennominae	*Mesastrape fulguraria* Walker, 1860	0	0	0	19	1

Ennominae	*Micronidia* sp.	10	4	6	0	0
Ennominae	*Odontopera bidentata* Clerck, 1759	1	0	0	15	0
Ennominae	*Ophthalmitis albosignaria* Bremer & Grey, 1853	1	0	0	11	0
Ennominae	*Ophthalmitis cordularia* Swinhoe, 1893	1	0	2	0	0
Ennominae	*Ophthalmitis irrorataria* Bremer & Grey, 1853	0	0	0	3	0
Ennominae	*Ourapteryx similaria* Matsumura, 1910	4	4	10	0	4
Ennominae	*Paradarisa* cf. *consonaria* Hübner, 1799	9	4	4	0	0
Ennominae	*Paradarisa consonaria* Hübner, 1799	0	0	0	12	0
Ennominae	*Paraleptomiza bilinearia* Leech, 1897	9	3	0	0	0
Ennominae	*Parectropis* cf. *similaria* Hufnagel, 1767	0	0	0	99	0
Ennominae	*Phanerothyris sinearia* Guenée, 1857	96	18	2	0	0
Ennominae	*Phthonandria emaria* Bremer, 1864	9	3	18	0	0
Ennominae	*Phthonosema tendinosaria* Bremer, 1864	0	0	0	1	0
Ennominae	*Plagodis dolabraria* Linnaeus, 1767	1	13	18	14	0
Ennominae	*Plagodis pulveraria* Linnaeus, 1758	3	2	0	46	0
Ennominae	*Psyra boarmiata* Graeser, 1892	0	0	0	53	3
Ennominae	*Psyra* sp.	0	0	2	0	0
Ennominae	*Scardamia aurantiacaria* Bremer, 1864	0	0	0	1	0
Ennominae	*Scionomia anomala* Butler, 1881	0	0	0	10	0
Ennominae	*Selenia sordidaria* Leech, 1897	4	0	2	0	0
Ennominae	*Selenia* sp.	0	0	0	0	2
Ennominae	*Spilopera debilis* Butler, 1878	0	0	0	15	3
Ennominae	*Stegania cararia* Hubner, 1790	1	0	0	0	0
Ennominae	*Taeniophila unio* Oberthür, 1880	0	0	0	11	0
Ennominae	*Xerodes rufescentaria* Motschoulsky, 1861	0	0	0	1	0
Geometrinae	*Agathia carissima* Butler, 1878	0	1	0	4	0
Geometrinae	*Aracima muscosa* Butler, 1878	0	0	0	1	0
Geometrinae	*Chlorissa* cf. *gelida* Butler, 1889	0	0	1	0	0
Geometrinae	*Chlorissa* sp.	0	0	0	7	0
Geometrinae	*Comibaena cassidara* Guenée, 1857	1	0	0	0	0
Geometrinae	*Comibaena hypolampes* Prout,1918	0	0	0	0	4
Geometrinae	*Comibaena nigromacularia* Leech,1897	5	0	0	0	0
Geometrinae	*Comibaena tancrei* Graeser, 1889	0	0	0	0	2
Geometrinae	*Comostola subtiliaria* Bremer, 1864	0	0	0	3	1

Geometrinae	*Geometra dieckmanni* Graeser, 1889	0	0	0	0	1
Geometrinae	*Geometra glaucaria* Ménétriès, 1859	13	2	4	58	2
Geometrinae	*Geometra rana* Oberthür, 1916	0	1	0	17	14
Geometrinae	*Geometra valida* Felder, 1875	2	5	0	0	0
Geometrinae	*Hemistola parallelaria* Leech,1897	1	0	1	0	0
Geometrinae	*Hemistola tenuilinea* Alpheraky, 1897	1	0	0	0	0
Geometrinae	*Hemithea aestivaria* Hübner, 1789	1	1	0	2	0
Geometrinae	*Iotaphora admirabilis* Oberthür, 1883	2	7	1	2	0
Geometrinae	*Maxates sinuolata* Inoue, 1989	0	1	0	0	0
Geometrinae	*Thalera chlorosaria* Graeser, 1890	0	0	1	0	0
Geometrinae	*Thetidia chlorophyllaria* Hedemann 1879	1	1	0	0	0
Larentiinae	*Asthena* sp.	2	4	8	0	0
Larentiinae	*Brabira artemidora* Oberthür, 1884	0	0	0	0	2
Larentiinae	*Callabraxas fabiolaria* Oberthür, 1884	0	2	0	0	0
Larentiinae	*Chartographa ludovicaria* Oberthür, 1880	1	2	0	0	0
Larentiinae	*Chloroclystis v-ata* Haworth, 1809	0	2	0	0	0
Larentiinae	*Docirava* sp.	2	0	0	3	0
Larentiinae	*Dysstroma cinereata* Moore, 1867	0	0	0	2	2
Larentiinae	*Dysstroma latefasciata* Blöcker, 1908	0	0	0	1	0
Larentiinae	*Ecliptopera silaceata* Denis & Schiffermüller, 1775	0	1	0	42	25
Larentiinae	*Electrophaes corylata* Thunberg, 1792	3	0	1	3	0
Larentiinae	*Epirrhoe supergressa* Butler, 1879	4	4	3	14	0
Larentiinae	*Eucosmabraxas placida* Butler, 1878	1	2	0	0	0
Larentiinae	*Eulithis convergenata* Bremer, 1864	1	1	2	4	1
Larentiinae	*Eulithis ledereri* Bremer, 1864	0	0	1	2	0
Larentiinae	*Eulithis prunata* Linnaeus, 1758	0	0	0	15	0
Larentiinae	*Eulithis pyropata* Hubner, 1809	0	0	0	11	0
Larentiinae	*Euphyia cineraria* Butler, 1878	0	0	0	9	1
Larentiinae	*Eupithecia gigantea* Staudinger, 1897	0	0	0	3	0
Larentiinae	*Eupithecia lariciata* Freyer, 1841	0	0	0	15	2
Larentiinae	*Eupithecia* sp. 1	2	1	0	0	0
Larentiinae	*Eupithecia* sp. 2	1	2	0	0	0
Larentiinae	*Eupithecia* sp. 3	0	1	0	0	0
Larentiinae	*Eupithecia* sp. 4	0	0	0	12	1
Larentiinae	*Eupithecia* sp. 5	0	0	0	2	0
Larentiinae	*Eustroma aerosa* Butler, 1878	1	2	0	33	13
Larentiinae	*Eustroma melancholica* Butler, 1878	0	0	0	3	7
Larentiinae	*Eustroma reticulata* Denis & Schiffermüller, 1775	0	0	0	4	3
Larentiinae	*Gandaritis fixseni* Bremer, 1864	0	0	0	14	13

Larentiinae	*Gandaritis flavomacularia* Leech, 1897	1	0	0	0	0
Larentiinae	*Glaucorhoe unduliferaria* Motschulsky, 1861	0	0	0	17	1
Larentiinae	*Horisme brevifasciaria* Leech, 1897	7	10	2	0	0
Larentiinae	*Horisme radicaria* de La Harpe, 1855	0	1	0	0	0
Larentiinae	*Horisme tersata* Denis & Schiffermüller, 1775	4	1	6	0	0
Larentiinae	*Hydrelia flammeolaria* Hufnagel, 1767	0	0	2	7	3
Larentiinae	*Hydrelia parvulata* Staudinger, 1897	2	1	0	1	0
Larentiinae	*Hydrelia shioyana* Matsumura, 1927	1	4	3	0	0
Larentiinae	*Hydrelia sylvata* Denis & Schiffermüller, 1775	0	0	0	2	0
Larentiinae	*Hysterura declinans* Staudinger, 1897	0	0	0	11	3
Larentiinae	*Laciniodes denigrata abiens Prout, 1938*	0	0	1	0	0
Larentiinae	Larentiinae sp. 1	1	7	0	0	0
Larentiinae	Larentiinae sp. 2	0	2	0	0	0
Larentiinae	Larentiinae sp. 3	0	0	0	5	0
Larentiinae	*Lobophora halterata* Hufnagel, 1767	0	1	2	0	0
Larentiinae	*Melanthia procellata* Denis & Schiffermüller, 1775	1	1	0	0	0
Larentiinae	*Paraplaneta conturbata Prout, 1938*	1	1	0	0	0
Larentiinae	*Pasiphila chloerata* Mabille, 1870	1	0	0	0	0
Larentiinae	*Pelurga taczanowskiaria* Oberthür, 1880	0	0	0	1	0
Larentiinae	*Perizoma saxea* Wileman, 1911	0	0	0	16	22
Larentiinae	*Philereme vashti* Butler, 1878	0	0	0	1	1
Larentiinae	*Plemyria rubiginata* Denis & Schiffermüller, 1775	0	0	0	5	0
Larentiinae	*Triphosa dubitata* Linnaeus, 1758	0	0	0	5	7
Larentiinae	*Venusia cambrica* Curtis, 1839	0	0	0	3	2
Larentiinae	*Venusia* cf. *punctiuncula* Prout, 1938	1	0	1	0	0
Larentiinae	*Venusia laria* Oberthür, 1893	1	1	2	0	0
Larentiinae	*Xanthorhoe* cf. *hortensiaria* Graeser, 1889	0	0	0	20	0
Larentiinae	*Xanthorhoe fluctuata* Linnaeus, 1758	0	0	0	0	1
Larentiinae	*Xanthorhoe quadrifasiata* Clerck, 1759	0	2	4	0	0
Larentiinae	*Xanthorhoe rectantemediana* Wehrli, 1927	0	0	0	6	0
Larentiinae	*Xenortholitha propinguata* Kollar, 1844	2	0	0	48	2

Orthostixinae	*Naxa seriaria* Motschulsky, 1866	0	0	0	11	0
Sterrhinae	*Cyclophora albipunctata* Hufnagel, 1767	2	0	7	1	0
Sterrhinae	*Idaea* cf *aversata* Linnaeus, 1758	6	5	9	0	0
Sterrhinae	*Idaea* sp. 1	1	4	0	0	0
Sterrhinae	*Idaea* sp. 2	0	1	1	0	0
Sterrhinae	*Idaea* sp. 3	8	5	0	0	0
Sterrhinae	*Idaea straminata* Borkhausen, 1794	1	2	0	0	0
Sterrhinae	*Scopula floslactata* Haworth, 1809	2	1	7	0	0
Sterrhinae	*Scopula* sp. 1	4	2	2	0	0
Sterrhinae	*Scopula* sp. 2	0	1	0	0	0
Sterrhinae	*Scopula subpunctaria* Herrich-Schäffer, 1847	0	0	2	0	0
Sterrhinae	Sterrhinae sp.	2	0	1	0	0
Sterrhinae	*Timandra apicirosea* Prout, 1935	0	0	0	4	1