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Phylogenetic diversity only weakly mitigates climate-change-driven biodiversity loss in insect communities

Zongxu Li^{1,2} | Benjamin Linard^{3,4}  | Alfried P. Vogler^{5,6}  | Douglas W. Yu^{1,7,8}  | Zhengyang Wang⁹ 

¹State Key Laboratory of Genetic Resources and Evolution and Yunnan Key Laboratory of Biodiversity and Ecological Security of Gaoligong Mountain, Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming, China

²Kunming College of Life Science, University of Chinese Academy of Sciences, Kunming, Yunnan, China

³LIRMM, University of Montpellier, CNRS, Montpellier, France

⁴SPYGEN, Le Bourget-du-Lac, France

⁵Department of Life Sciences, Natural History Museum, London, UK

⁶Department of Life Sciences, Imperial College London, Ascot, UK

⁷Center for Excellence in Animal Evolution and Genetics, Chinese Academy of Sciences, Kunming, China

⁸School of Biological Sciences, University of East Anglia, Norwich, UK

⁹Department of Organismic and Evolutionary Biology and Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA

Correspondence

Douglas W. Yu, State Key Laboratory of Genetic Resources and Evolution and Yunnan Key Laboratory of Biodiversity and Ecological Security of Gaoligong Mountain, Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming, China.
Email: dougwyu@mac.com

Zhengyang Wang, Department of Organismic and Evolutionary Biology and Museum of Comparative Zoology, Harvard University, 26 Oxford Street, Cambridge, MA 02138, USA.
Email: zhengyangw@hotmail.com

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Abstract

To help address the underrepresentation of arthropods and Asian biodiversity from climate-change assessments, we carried out year-long, weekly sampling campaigns with Malaise traps at different elevations and latitudes in Gaoligongshan National Park in southwestern China. From these 623 samples, we barcoded 10,524 beetles and compared scenarios of climate-change-induced biodiversity loss, by designating seasonal, elevational, and latitudinal subsets of beetles as communities that plausibly could go extinct as a group, which we call “loss sets”. The availability of a published mitochondrial-genome-based phylogeny of the Coleoptera allowed us to compare the loss of species diversity with and without accounting for phylogenetic relatedness. We hypothesised that phylogenetic relatedness would mitigate extinction, since the extinction of any loss set would result in the disappearance of all its species but only part of its evolutionary history, which is still extant in the remaining loss sets. We found different patterns of community clustering by season and latitude, depending on whether phylogenetic information was incorporated. However, accounting for phylogeny only slightly mitigated the amount of biodiversity loss under climate change scenarios, against our expectations: there is no phylogenetic “escape clause” for biodiversity conservation. We achieve the same results whether phylogenetic information was derived from the mitogenome phylogeny or from a de novo barcode-gene tree. We encourage interested researchers to use this data set to study lineage-specific community assembly patterns in conjunction with life-history traits and environmental covariates.

KEYWORDS

barcodes, beetles, coleoptera, Gaoligongshan, Hengduan Mountains, operational taxonomic unit, phylogenetic diversity, phylogenetic placement

1 | INTRODUCTION

Insect populations appear to be declining worldwide (Abrego et al., 2021; Cardoso et al., 2020; Vaidyanathan, 2021). Our particular interest here is to gauge the threat posed by climate change to arthropod communities. Their responses to changing climate are underrepresented in vulnerability assessments (Pacifi et al., 2015), and the requisite long-term time-series data of their community composition needed for such assessment are especially lacking in Asia (Sánchez-Bayo & Wyckhuys, 2019; Srivathsan et al., 2022). To start addressing this underrepresentation, we conducted year-long, weekly sampling campaigns with Malaise traps at different elevations and latitudes in Gaoligongshan (Chinese for Mt. Gaoligong, 高黎贡山) National Park in Yunnan province in southwestern China, part of the Hengduan Mountains biodiversity hotspot (Myers et al., 2000).

Gaoligongshan runs nearly 500 km north to south between 28°30'N and 24°40'N, paralleling the China-Myanmar border (Figure 1) and varying in elevation from 523 m above sea level to a snow cap at 5128 m. Its vegetation types range from mixed coniferous-broadleaf forest in the north to subtropical forest in the south (Li & Li, 2020; Liu et al., 2021). The region's rugged topography has generated high species richness in plants (Xing & Ree, 2017), vertebrates (Dumbacher et al., 2011; Yang et al., 2019), and arthropods (Liu et al., 2020; Yi et al., 2021). At 28,000 km² (7% of the area of Yunnan), Gaoligongshan contains at least 57.5% of birds, 61% of mammals, and 23% of ant species ever reported in Yunnan.

We barcoded beetles (Phylum: Arthropoda, Order: Coleoptera) from our Malaise trap samples to estimate the extent of biodiversity loss if seasonal, elevational, or latitudinal subsets of them are to be extirpated by a changing climate. We designate these subsets of beetles communities that plausibly could go extinct as a group as "loss sets". (1) Latitudinal loss set: northern biota might be more at risk in response to global warming because these species tend to be replaced by poleward-moving tropical organisms ("tropicalisation", see Osland et al., 2021), while the southern biota might be more at risk if, for instance, heatwaves and forest fires become frequent (Neeraja et al., 2021; Ward et al., 2020). (2) Elevational loss set: mountainous species could migrate upslope in response to warming (Elsen & Tingley, 2015) while high-elevation endemics could go extinct (Wilson et al., 2007). (3) Seasonal loss set: either summer or winter specialists might be more at risk, depending on the effects of climate change on species physiologies and the phenologies of host plants (Abrego et al., 2021; Ding & Gao, 2020; Schuldt et al., 2020).

These latitudinal, elevational and seasonal loss sets map directly to the three predominant patterns predicted for vegetation responses to future climate change in the Hengduan Mountains: (1) a northern shift of plant distributions (He, Burgess, Gao, et al., 2019; He, Burgess, Yang, et al., 2019; Liang et al., 2018; Peng et al., 2022);

(2) an upward shift in both treeline and alpine species (He et al., 2020; Liang et al., 2018; Tian et al., 2022); (3) and a 4–5°C increase of mean annual temperature by 2070, under the pessimistic high-emission scenario (RCP 8.5). To put this increase in context, the current temperature difference between mean summer and winter temperatures is around 13°C at Gaoligongshan (calculated from WorldClim CMIP5, 2.5 min resolution, Fick & Hijmans, 2017). Combining these effects, Liang et al. (2018) modelled the distribution shift of 151 representative plants in the Hengduan Mountains (under RCP 8.5) and predicted that by 2050, their distributions would on average shift 1° north and 400 m upward. Since insect and plant distributions are correlated (reviewed in Zhang et al., 2016), we posit that it is reasonable for the same projected changes in climate to result in similar range shifts (and concomitant contractions and extinctions) in insects.

Our loss set approach complements existing approaches to species climate-vulnerability assessment such as correlation analysis (Araújo & Peterson, 2012), mechanistic modelling (Jenouvrier et al., 2009), and indicator scoring (Thomas et al., 2011) in that these methods are trying to predict plausible loss sets, whereas we are measuring the amount of biodiversity contained in plausible loss sets.

What makes this more than a species-counting exercise is that we have taken into account shared evolutionary history between species (Cavender-Bares et al., 2009; Davies, 2021; Webb et al., 2002). For instance, two loss sets might have no species in common but still share considerable evolutionary history if their members are closely related. The extinction of one loss set would result in the disappearance of all its species but only part of its evolutionary history, which is still extant in the remaining loss sets. We therefore hypothesise that while certain climate change scenarios (e.g., a 5°C rise in mean winter temperature causing the extinction of winter-adapted beetles, or replacement of northern species by those dispersed from the south) will drive biodiversity loss by reducing species richness in one or more ecological communities, shared phylogenetic history might mitigate that loss via the preservation of evolutionary history in other communities.

However, a test of the above hypothesis requires (1) a phylogeny that encompasses the focal taxon (here, Coleoptera) and (2) each sampled individual in each community to be genotyped and placed on the phylogeny (Ahrendsen et al., 2016; Jin et al., 2021; Kembel et al., 2011). For this reason, we individually DNA-barcoded the 10,524 beetles we collected, using a combination of Sanger sequencing and multiplexed individual barcoding (Creedy et al., 2020; Ratnasingham, 2019), and placed the barcodes on a published mitochondrial-genome-based phylogeny of the Coleoptera (Linard et al., 2018). Such "phylogenetic placement" (Barbera et al., 2018) on a robust phylogeny has previously been shown to improve inference in community ecological studies (Janssen et al., 2018).

While the placement-based approach offers a robust phylogenetic position for each barcode, broad-taxon-coverage phylogenies

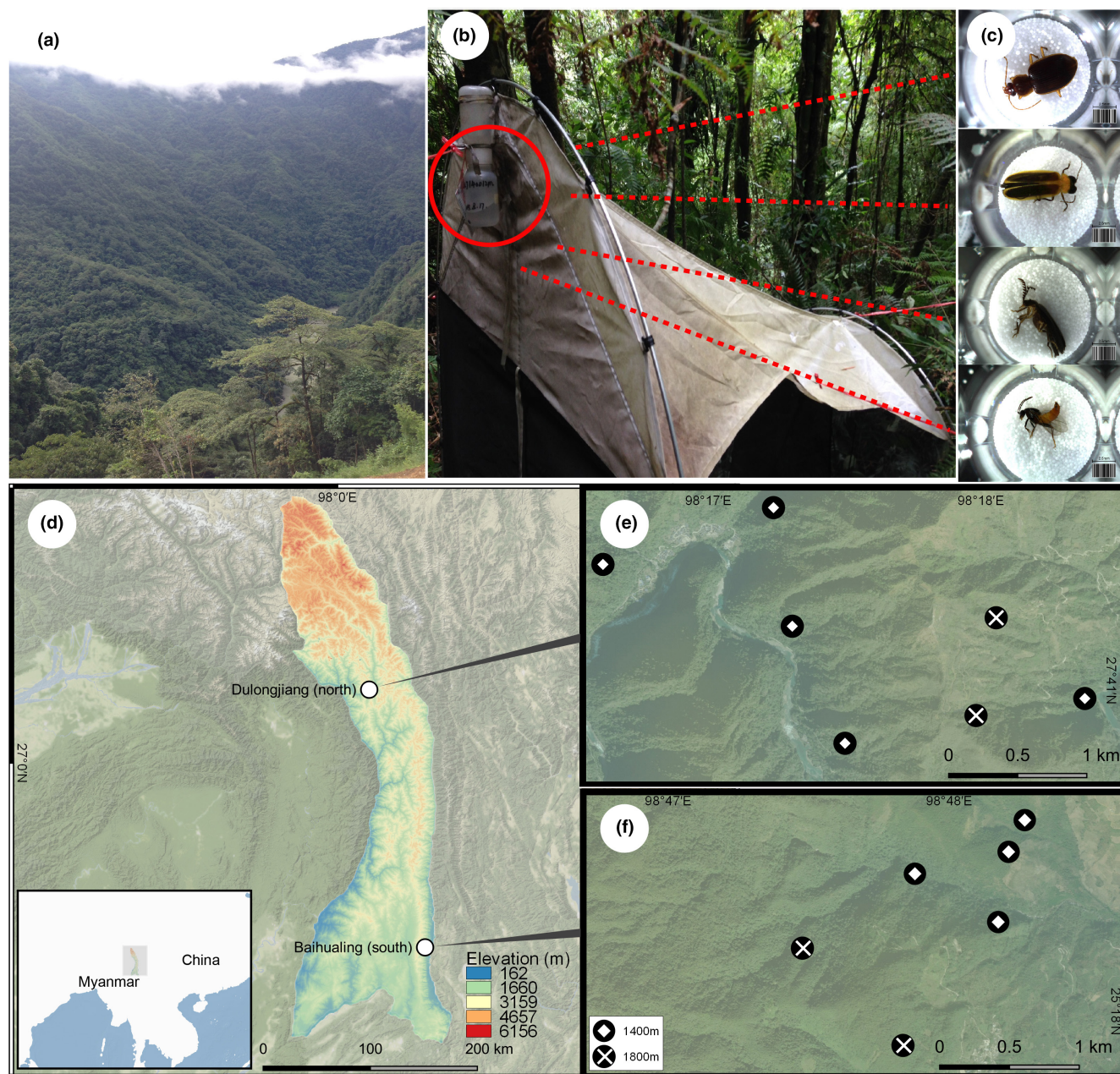


FIGURE 1 Study area and sampling scheme. (a) Gaoligongshan (photo taken at northern site, around 1800m, summer 2015. Photo credit: ZL). (b) One of 13 Malaise traps set up in our study, at northern site, 1800m, in August 2015. The collection bottle (circled in red) was changed once per week. Photo credit: ZL. (c) Exemplars of beetles collected in Malaise trap bottles, from top to bottom: Samples from family Carabidae, Lampyridae, Ptilodactylidae and Staphylinidae. (d) The range of Gaoligongshan, and our northern (Dulongjiang) and southern (Baihualing) site. (e–f) Topographical maps of northern and southern sites, with their Malaise traps set up at 1400 and 1800m.

that include the locus used for barcoding are not available for most taxa (which is why our study is limited to the beetles, despite them being a minority catch in Malaise traps, which more effectively sample Diptera, Lepidoptera, and Hymenoptera). We thus also asked whether we could achieve similar results with a gene-tree approach, that is, a single-gene phylogeny constructed using only the DNA barcodes, following the routine use of single-gene phylogenies in microbiome community analysis (Lozupone & Knight, 2005). In other words, we asked whether phylogenetically informed ecological conclusions are dependent upon the choice of a robust reference phylogeny versus an ad hoc barcode gene tree.

We compare these phylogeny-informed results to the nonphylogenetically-informed method of treating every species independently, which we call the operational taxonomic unit (OTU) analysis because we clustered the 10,524 barcodes into a smaller number of self-similar sequence clusters (i.e. OTUs), which approximate species (Blaxter et al., 2005; Floyd et al., 2002).

Here, we report that (1) communities clustered differently by season and latitude, dependent on whether phylogenetic information was accounted for, and that (2) compared with the nonphylogenetically informed OTU analysis, accounting for phylogeny only slightly mitigated the amount of biodiversity lost when loss sets

were removed from the data set, contrary to our expectation described above. In broader terms, phylogenetic diversity is highly correlated with species count and only weakly mitigates potential climate-driven biodiversity loss in Gaoligongshan beetle communities. We also report that (3) conveniently for the study of taxa without a well-resolved phylogeny, we achieved the same results whether we conducted placement on a multilocus reference phylogeny or used a single-gene phylogeny.

2 | MATERIALS AND METHODS

Our workflow is summarized in Figure 2.

2.1 | Beetle sampling

We set up Malaise traps to sample flying arthropods in the north (Dulongjiang, 独龙江, 27.68°N, 98.28°E) and south (Baihualing, 百花岭, 25.31°N, 98.80°E) of Gaoligongshan. The two sites are 268 km apart (Figure 1d). The northern site has a higher diversity of seed plants (2816 vs. 1549 species in the south) and higher, more uniform precipitation: monthly average precipitation is 156.14 mm in the north (SD = 81.5) and 148.1 mm in the south (SD = 90.0). The northern site is also cooler than is the south: mean monthly temperature is 13.7°C in the north (SD = 5.6) and 16.1°C in the south (SD = 4.6). This information is visualized in Figure S1, plotted from 0.5 degrees meteorological data from the China Meteorological Data Service Center (<http://data.cma.cn/site/index.html>). Under a pessimistic

climate-change scenario (RCP 8.5), by 2070, the mean annual temperatures of the northern and southern sites will increase by 4.1°C and 4.4°C, respectively, and the mean temperatures of the coldest quarter will increase by 4.4°C and 4.2°C, respectively (WorldClim CMIP5, 2.5 min resolution, Fick & Hijmans, 2017).

From June 2014 to May 2015, we set up six Malaise traps in a site in the south (four at 1400 m, two at 1800 m); from August 2015 to August 2016, we set up seven Malaise traps in a site in the north (five at 1400 m, two at 1800 m) (Figure 1e,f). The extra trap at 1400 m in the north was inadvertently set up near a local *Amomum tsaoko* (Zingiberaceae) plantation, which we did not abandon. We used 95% ethanol as killing and preserving agent. Local farmers assisted by changing sampling bottles weekly and storing bottles in -18°C freezers that were given to them as compensation. We then periodically transferred stored bottles to a -80°C freezer at Kunming Institute of Zoology (KIZ), China. At KIZ we replaced the collecting ethanol with 99.9% ethanol and hand-picked the beetles from the weekly sampling bottles into individual Thermo Scientific matrix 2D storage tubes, each with a unique 2D barcode.

2.2 | DNA extraction and metabarcoding

We extracted DNA from each southern-site beetle following the glass fibre plate DNA extraction protocol of the Canadian Centre for DNA Barcoding (<https://ccdb.ca/resources/>), except for using a nondestructive protocol for tissue lysis (Tin et al., 2014). For the north-site beetles, we extracted DNA from a single leg of each larger individual (>2 mm length) using the Tiangen kit (Tiangen Biotech),

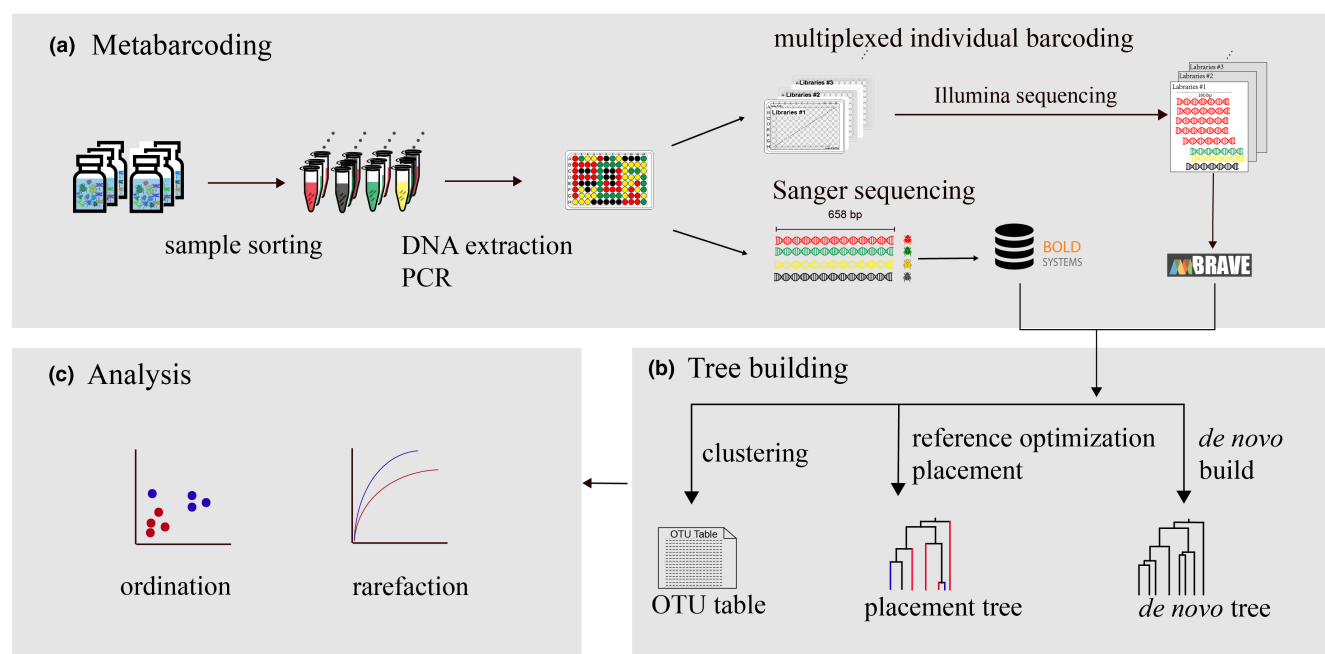


FIGURE 2 Study design. (a) Each beetle was barcoded with Sanger sequencing (658 or 313 bp) or high-throughput, multiplexed individual barcoding (180 bp). (b) Barcodes were used to construct an OTU table, a placement tree, and a maximum likelihood, de novo gene tree. (c) We conducted two sets of ecological analysis, using different barcode-derived inputs generated in the previous step.

and from whole bodies of the smaller individuals (≤ 2 mm) using the Qiagen kit (Qiagen).

For all beetles, we first attempted to amplify the full DNA barcode (658 bp, COI-5P) using the LCO1490/HCO2198 primer pair (Vrijenhoek, 1994). PCR was carried out in a 15 μ l reactions consisting of 10.625 μ l ddH₂O, 1.5 μ l 10 \times buffer, 1.2 μ l dNTP, 0.075 μ l TaKaRa Taq, 0.3 μ l of each primer (10 μ M), 1 μ l of DNA. PCR reactions were carried out under the following conditions: initial denaturation at 94°C for 1 min, followed by five cycles of (94°C for 1 min, 45°C for 1 min, 72°C for 1 min), 30 cycles of (94°C for 1 min, 51°C for 1 min, 72°C for 1 min) and a final extension of 72°C for 5 min. For each extraction, we resolved 2 μ l of PCR product by electrophoresis on a 2% agarose gel. Successful amplicons were Sanger-sequenced. For beetles that failed to generate a full-length amplicon with the above-mentioned protocol, we repeated the PCR procedure with the mCOLintF/jgHCO2198 primer pair (313 bp, a subset of COI, Leray et al., 2013), with same reaction and PCR cycles.

If samples failed these two amplification attempts, they were amplified with the CFMRb primer pair (180 bp, a subset of COI, Jusino et al., 2019), which was then sequenced using a multiplexed individual barcoding protocol (Creedy et al., 2020). For every 96 samples that we planned to pool into a single library, we used 96 twin-tagged primer pairs to identify samples and eliminate tag-jump errors (Schnell et al., 2015; Yang et al., 2021). PCR was carried out in a 15 μ l reaction which was the same as the previous approach. For failed PCR runs, a second round of PCR was carried out in 15 μ l reactions consisted of 5.9 μ l ddH₂O, 7.5 μ l KAPA HiFi HotStart ReadyMix (2 \times), 0.3 μ l of each primer (10 μ M), and 1 μ l of DNA. PCR products were pooled and gel-purified by using a Qiagen QIAquick PCR purification kit. In total, 3120 beetles were pooled into 35 libraries (96 beetles per library). The PCR products were sent to Novogene for library construction and 150 bp paired end sequencing on an Illumina NovaSeq 6000.

2.3 | Bioinformatics

2.3.1 | Read processing and OTU table

Read processing

Sanger-sequenced barcodes (i.e., those amplified from LCO1490/HCO2198 or mCOLintF/jgHCO2198 primer pairs) were assembled in GENEIOUS version 10.2.6. For reads of multiplexed individual bar-coded samples (i.e., those amplified with the CFMRb primer pair), we used ADAPTERREMOVAL version 2.2.2 (Schubert et al., 2016) to trim Illumina adapters and SICKLE version 1.33 (Joshi & Fass, 2011) to remove reads with average Phred score < 20 . Reads were then demultiplexed using DTD (Double Tag Demultiplexer, <https://github.com/yoann-dufresne/DoubleTagDemultiplexer>) and dereplicated on MBRAVE (<http://mbrave.net>, Ratnasingham, 2019). We translated dereplicated sequences to codons using GOTRANSEQ (<https://github.com/feliixx/gotranseq>) and chose the most abundant read without a stop codon as the sample barcode.

Community assignment

Our smallest unit of analysis was two Malaise-trap bottles from consecutive weeks pooled together (hereafter referred to as a “sample”). Each barcode was assigned a set of three environmental covariates: (1) elevation (1400 or 1800 m); (2) latitude (north or south); and (3) season (spring, summer, autumn, winter). Samples from June, July, and August are summer; September, October, November are autumn; December, January, and February are winter; March, April, May are spring. To assign samples to month, we used the month in which the starting date of each biweekly sample fell. Samples were also assigned a week number.

OTU table construction

To quantify biodiversity loss using a count-based approach for bar-coded samples, we used SUMACLUST 1.0.31 (Mercier et al., 2013) to group barcodes into 97%-similarity operational taxonomic units (OTUs). If an OTU contained a barcode from a sample, it is deemed to be present in that community. We refer to the resulting sample \times OTU matrix as an “OTU table”. The cell values of the OTU table are the counts of barcodes (beetles) belonging to that row's sample and that column's OTU.

2.3.2 | Phylogenetic placement

Maximum likelihood (ML) tree for phylogenetic placement

To quantify biodiversity loss using a phylogenetic-placement approach, we needed a robust reference tree. The most comprehensive beetle reference phylogeny to date has 10 partitions in its 19-loci alignment (Linard et al., 2018), but multiple partitions (i.e., multiple sets of model parameters for the ML tree) are not supported in phylogenetic placement programs such as EPA-NG (Barbera et al., 2018). We thus needed to “downsize” the existing alignment of Linard et al. (2018) to a single partition and obtain a single set of parameters for its ML tree. We did this by trimming the alignment of Linard et al. (2018) down to a subset that contained only COI, cytb, 16s, and 12s regions (all three barcodes in our study are nested within COI, and all four loci are widely used in metabarcoding studies). The resulting alignment, along with the original tree from Linard et al. (2018), were used to re-optimize model parameters and to reinfer the best beetle ML tree (“--evaluate” command in RAXML-NG-MPI version 0.9.0, Kozlov et al., 2019). We used KTREEDIST version 1.0 (Soria-Carrasco et al., 2007) and TREECMP version 2.0-b76 (Goluch et al., 2020) to check if the new ML tree was significantly different from that of Linard et al. (2018). The new best ML tree (and its set of model parameters) were used for phylogenetic placement.

Phylogenetic placement

We placed every unique barcode onto the ML tree using EPA-NG version 0.3.5 (Barbera et al., 2018). Each barcode (called “queries” in EPA-NG) could be placed on multiple edges of the tree with different likelihoods. We evaluated the certainty of each barcode's placement by looking at (1) the expected distance among all its placement locations (“--edpl” command in GAPP version 0.5.0, Czech

& Stamatakis, 2019) and (2) the likelihood weight ratios of all of its placements ("--lwr" command in GAPP). To extract a "placement tree", we represented each barcode as a pendant edge on its most likely placement position ("--graft --fully resolve" command in GAPP).

2.3.3 | De novo tree construction

To investigate whether the result of biodiversity assessment is dependent on the availability of a robust reference phylogeny (Section 2.3.2), we also built a maximum-likelihood de novo gene tree from our (unique) barcode sequences only. We used MODELINDER (Kalyaanamoorthy et al., 2017) to estimate the best partition scheme, and searched for most likely tree in IQ-TREE version 1.6.12 (Nguyen et al., 2015), with 1000 iterations for ultrafast bootstrap approximation (Minh et al., 2013). We refer to this best gene tree as our de novo tree. This procedure mimics the single-gene tree approach widely used in microbiome community analysis (Lozupone & Knight, 2005). We compared the topology between de novo tree and our placement tree using KTRIEDIST version 1.0 (Soria-Carrasco et al., 2007) and TREECMP version 2.0-b76 (Goluch et al., 2020).

2.4 | Statistical analysis

Unless otherwise noted, statistical analyses were performed in R version 3.6.3 (R Core Team, 2020). We conducted two sets of analyses across all samples (Figure 2c): (1) we performed ordination analysis in the form of nonmetric multidimensional scaling (NMDS, Kruskal, 1964) to visualize the compositional similarity across all samples; (2) we performed rarefaction analysis to compare how much biodiversity is lost when removing sets of ecological communities (see Section 2.4.2 below).

We carried out these analyses on the three outputs obtained above (Figure 2b): (1) the OTU table (see Section 2.3.1), (2) the placement tree (see Section 2.3.2), and (3) the de novo tree (see Section 2.3.3).

2.4.1 | Ordination with nonmetric multidimensional scaling

With the OTU table, we calculated both Jaccard and Bray-Curtis dissimilarity among samples (Bray & Curtis, 1957; Jaccard, 1912, implemented as "(distance = 'jaccard')" or "(distance = 'bray')" option in "--metaMDS" command in VEGAN version 2.5-6, Oksanen et al., 2019). In contrast, phylogenetically informed samples are represented as sets of tips on the placement tree and de novo trees. We generated dissimilarity matrices by measuring both weighted and unweighted UniFrac distances between samples (Lozupone et al., 2011, implemented in "--UniFrac" command, "weighted = FALSE" or "weighted = TRUE" options in PHYLOSEQ version 1.30.0, McMurdie & Holmes, 2013). Since tree tips in our analysis are unique barcodes, unweighted UniFrac only accounted

for unique barcode presence/absence, while weighted UniFrac also accounted for the abundance of each unique barcode in each sample. We visualized these dissimilarity matrices with nonmetric multidimensional scaling (NMDS, Kruskal, 1964, implemented with the "--metaMDS" command in VEGAN), with each point being a sample, scored for season (summer vs. winter), latitude (north vs. south), and elevation (1400m vs. 1800m).

2.4.2 | Comparing diversity loss scenarios

We define a loss set as the subset of all samples that share the same season, latitude, or elevation, these being subsets that could plausibly be lost as a group due to future climate warming. To avoid confusion, when we refer to a "summer loss set scenario" for example, we mean the whole data set minus all summer samples. We have six loss set scenarios: (12) loss of all summer or of all winter samples; (3-4) loss of all northern or of all southern samples; and (5-6) loss of all 1400m or of all 1800m samples.

With the OTU table, we estimated the effect on total diversity of each loss set scenario by extrapolating abundance-based species richness with INEXT.3D version 0.0.1 (Chao et al., 2021, "diversity = TD" option in "--iNEXT3D" command). With the phylogenetically informed data sets, samples are tips on the placement and de novo trees, and we also used INEXT.3D to extrapolate abundance-based Faith's phylogenetic diversity (Faith, 1992) ("diversity = PD" option in "--iNEXT3D" command).

3 | RESULTS

3.1 | Sampling and barcoding

We hand-pulled 12,195 beetles (3935 from the north and 8251 from the south) out of 632 weekly Malaise trap bottles (a 93% bottle retrieval rate, while 44 bottles in the northern site were lost due to trap loss and transportation difficulties from December to March). See Table S1 for site and OTU information for each beetle.

Our Sanger-based and multiplexed individual barcoding attempt obtained 10,524 barcodes, 7057 of which are unique. Of all the barcodes, 7842 were full-length (658 bp) COI barcodes, 265 were mCOLintF/jgHCO2198 barcodes of 313 bp in length, and 2417 were CFMRb barcodes 180 bp in length. Of the 1671 unbarcoded samples, nine were discarded due to missing sample information, and 1662 (910 south + 752 north) were discarded due to PCR failures or not being Coleoptera. Full-length barcodes, along with individual photographs and site information, are available on BOLD (see Data Availability statement); the mCOLintF/jgHCO2198 barcodes are included in Supporting Information; and the CFMRb barcodes (and quality control summary) are available on MBRACE (see Data Availability statement). The spatiotemporal and taxonomic distribution of all barcodes are visualized in Figure 3, Figures S2 and S3 and tallied in Table S2.

3.2 | OTU clustering

A total of 10,258 out of 10,524 barcodes were clustered by 97% similarity into 2822 OTUs. We omitted all 265 of our 313 bp mICOI-intF/jgHCO2198 barcodes because while they overlapped with full length barcodes, they did not overlap with CFRMb sequences (all three types of barcodes could not be clustered together to generate representative OTU sequences).

Table S1 contains the OTU assignment of each barcode, while Table S3 presents the OTU table. In summary, the north contains 1277 OTUs, and (with some overlap) the south contains 1597 OTUs. The summer contains 1796 OTUs, and the winter contains 205 OTUs. The 1400m elevation contains 2110 OTUs, and the 1800m elevation contains 1101 OTUs.

3.3 | Phylogenetic placement

Our reoptimized, single-partition ML tree contained four loci, 3091 alignment sites and 13,995 species tips (see [Supporting Information](#) for the new ML tree and model parameters). The new ML tree had a similar genetic distance scale (K factor = 1.08 in *KTREE*DIS; K factor of 1 indicates identical distance scale) to the original 10-partition tree. The Robinson-Foulds clustering value ($RC = 0$, measured in *TREECMP*) indicated identical topology between the new and original trees.

All barcodes were placed onto the new ML tree (see [Supporting Information](#) for our placement tree). The most likely placement position of 27.63% of the barcodes have higher than 0.96 likelihood weight ratio (LWR), indicating high certainty of placement (Figure S4A). A total of 43% of the barcodes have <0.44 LWR for their most likely placement, but 93.85% of those placements have an

expected distance between placement locations <0.13 (Figure S4B). Since our ML tree has an average branch length of 0.087, a value of 0.13 means that multiple likely placements of the same sequence are on average within two branch lengths of each other.

3.4 | De novo tree

See [Supporting Information](#) for the de novo tree and its model parameters. Our de novo tree and placement tree are different in mean branch lengths (K factor = 0.56, see Soria-Carrasco et al., 2007 for interpretation of K factor) and topology ($RC = 6895$ for a total of 14,112 edges, see Robinson & Foulds, 1981 for interpretation of the RC value).

3.5 | Ordination

We removed 11 samples that contained fewer than 20 OTUs for our ordination analysis. Nonmetric multidimensional scaling (NMDS) of the OTU table data set resulted in samples clustering by latitude (north vs. south) on the first axis and then by season (winter vs. summer) on the second axis (Figure 4a, Figure S5A). In contrast, when phylogenetic diversity was taken into consideration, communities clustered by season on the first axis and then by latitude on the second axis (Figure 4b,c for unweighted UniFrac, Figure S5B,C for weighted UniFrac). Compared with OTU-derived ordinations, phylogenetically informed ordinations showed considerably more overlap between northern and southern samples, indicating phylogenetic relatedness between the two latitudes. We found no signal of clustering by elevation (Figure S6A).

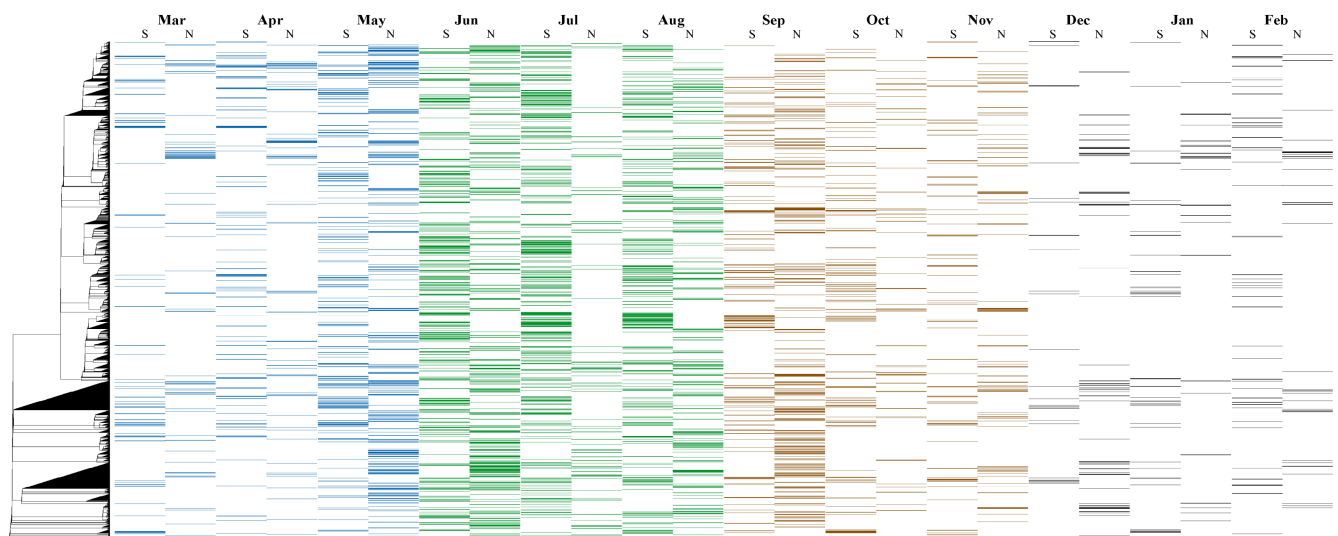


FIGURE 3 Unique barcodes generated from northern and southern sites at 1400m, across the year. See Figure S2 for samples collected at 1800m. The placement tree is positioned to the left, and the coloured bars show the most likely placement position of each month's barcodes on the tree. Columns for "N" and "S" indicate northern and southern samples, while the different colours for barcodes indicate assigned seasons (blue for Spring, green for Summer, brown for Autumn, black for Winter).

3.6 | Species diversity and loss set scenarios

With the OTU table, the seasonal loss set scenarios result in little (summer) or no (winter) reduction of extrapolated species richness (Figure 5a) and diversity (Figure S7), whereas the latitude and elevation loss set scenarios do cause declines in extrapolated species-richness (Figure 5a). We then ask whether taking into account phylogenetic relatedness mitigates these declines. That is, upon the extinction of a loss set (e.g., North), is much of the phylogenetic history retained in the remaining part of the reserve (e.g., South)? Contrary to our expectations, the outcomes are nearly the same (Figure 5b,c), with at most a small mitigation of diversity loss when phylogenetic relatedness is taken into account (Figure 5d).

4 | DISCUSSION

We generated a data set of 10,524 barcoded, photographed beetles from year-long, weekly sampling using 623 Malaise trap bottles across both elevational and latitudinal gradients of Gaoligongshan (Figures 3 and 4). While further projects will build upon this data set to explore coleopteran lineage-specific community assembly in conjunction with their functional traits and environmental covariates (see Section 4.3 below), this work reports a broad-stroke visualization and analysis of community change over space and time. We asked how much species diversity would decline upon the removal of subsets of total beetle diversity (subsets grouped by season, latitude, or elevation) that could plausibly be lost together due to climate heating, and we asked whether the answer to this question would change depending on whether phylogenetic relatedness was taken into account (Figure 5). Our main message is that there is no phylogenetic “escape clause” for biodiversity conservation. Below, we discuss our ordination and rarefaction results, and hypothesise why taking phylogeny into account does not materially mitigate species loss.

4.1 | Count-based vs. phylogenetically informed matrices

The effect of incorporating phylogenetic information into community analysis is visible when comparing ordination results calculated from discrete OTUs versus UniFrac distances (Figure 4a vs. Figure 4b,c). When analysed as unrelated OTUs, the samples first cluster by latitude (north vs. south) and then by season (winter vs. summer) (Figure 4a). This is not surprising: out of 2822 OTUs, only 52 were shared between the north and south samples; slightly more than that, 59 OTUs were shared between winter and summer samples. In contrast, when phylogenetic information was accounted for, we observed the opposite pattern: samples first separated by season and then by latitude (Figure 4b,c). Change in the predominant axis of variation from latitudinal to seasonal difference after incorporating phylogenetic information suggests that northern and southern beetles communities share more evolutionary history than

do winter and southern beetles, which is hidden from the OTU data set. Although yet to be examined in beetles, this pattern of lineage diversification along mountain valleys is a major theme of speciation in the Hengduan Mountains found in plants (Xing & Ree, 2017), vertebrates (Wan et al., 2021) and other insects (Wang & Pierce, 2022). Specifically, winter (and some summer) samples from the north and south overlapped (Figure 4b,c, grey circles, grey dots, and green dots), reflecting shared evolutionary history among winter beetles across Gaoligongshan. We found no observable elevational clustering in our data set (Figure S6A), probably in large part because the elevational difference is only 400m. Studies on plants, insects and birds in the same region show large differences when communities are further apart in elevation (He et al., 2022; Liu et al., 2018; Sreekar et al., 2018).

However, although the ordinations revealed an effect of shared evolutionary history on sample similarities, we did not see this effect when undertaking the loss set scenarios (Figure 5). Our expectation was that with the OTU table, where species are treated as discrete entities, extrapolated species richness would decline in line with the number of species in a loss set, but with the de novo and placement trees, where phylogenetic relatedness is taken into account, extrapolated phylogenetic diversity would decline by relatively less upon removal of the same loss set. For example, removal of the species-rich summer loss set from the OTU data set should cause a large decline in extrapolated species richness, while removal of the summer loss set from the de novo- and placement-tree data sets should cause less decline because some of the evolutionary history of the summer species would remain in other seasonal samples.

However, we did not observe convincing evidence for phylogenetic mitigation: for example, the spacings between the “all samples” and the “summer loss set” rarefaction curves are similar in size across Figure 5a–c. We observed, at most, small effect sizes in the 1400m, South, and North loss set scenarios (Figure 5d).

Alternatively, one could argue that intersections of loss sets (e.g., “winter” + “south” + “1800m”) are more realistic biodiversity loss scenarios representing species coexisting in space and time. Any given community will be confronted by both rising mean habitat temperature and contracting high elevation habitat under future climate change. However, phylogenetic mitigation of such intersection loss sets is likely also to be minimal. For instance, the “winter-south-1800m” set contains only nine OTUs, which constitute 0.32% of all OTUs and 0.20% or 0.38% of phylogenetic diversity, on the de novo and placement trees, respectively.

The effective absence of phylogenetic mitigation recovers the theoretical expectation that PD is a generalized form of richness index (Chao et al., 2010). Studies have found high correlation between PD and species richness (Davies & Buckley, 2011; Dias et al., 2020; Safi et al., 2011). In other words, in our data set, we can use OTU or number of barcodes as a proxy number to rank loss sets by phylogenetic diversity (Table S2). This is also shown via inspection of Figure 3, in which the columns with the highest number of barcodes (coloured bars) are in summer, 1400m, and the south, which are the loss sets causing the largest declines in PD when removed (Figure 5c).

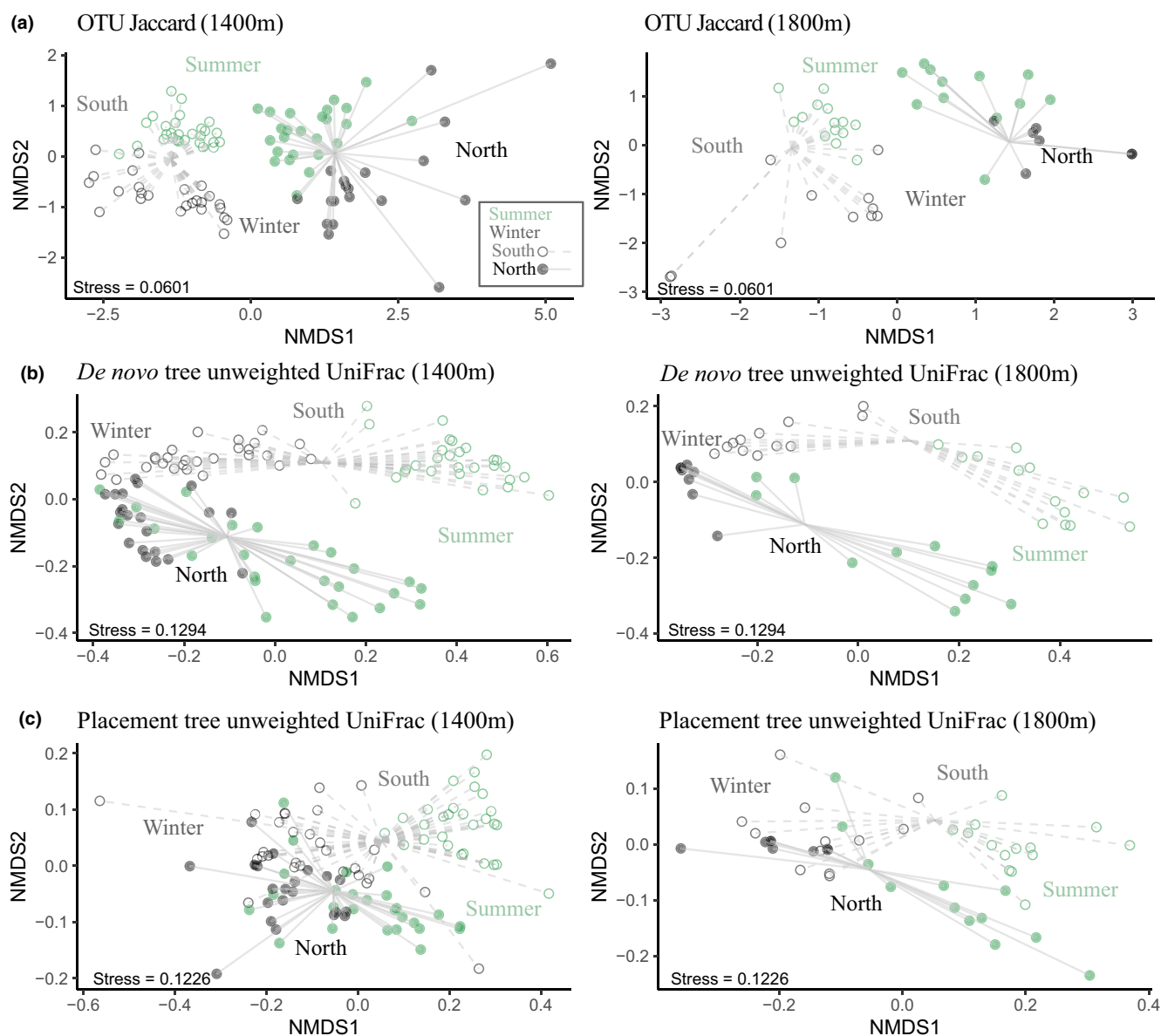


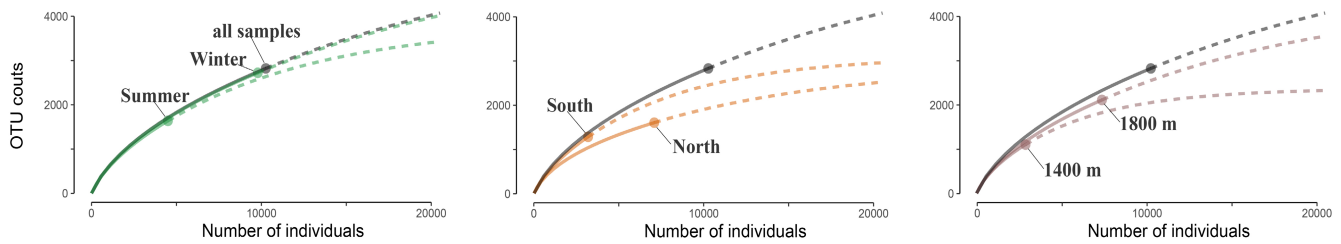
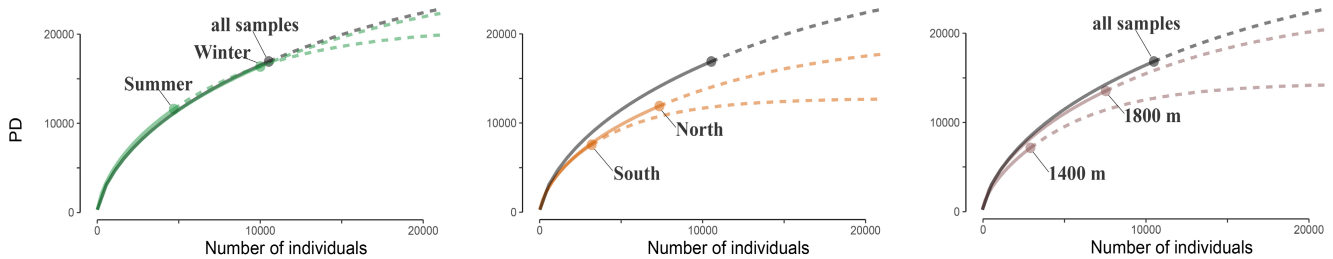
FIGURE 4 Nonmetric multidimensional scaling (NMDS) ordination for biweekly samples in winter and summer. See Figure S6B,C for ordination including all four seasons. Ordinations highlighting elevational differences are shown in Figure S6A. (a) NMDS plot based on Jaccard distances between samples in the OTU table, shown separately for 1400m (left) and 1800m (right). For both elevations, samples first separate by latitude (north vs. south on NMDS axis 1), then by season (summer vs. winter on NMDS axis 2). (b) NMDS plot based on unweighted UniFrac distances on the de novo tree among samples, shown separately for those at 1400m (left) and 1800m (right). (c) NMDS plot based on unweighted UniFrac distances on the placement tree among samples, shown separately for those at 1400m (left) and 1800m (right). For both b and c, samples first separate by season and then by latitude. Moreover, the winter (and some summer) samples from the north and south overlap.

4.2 | Placement and de novo trees

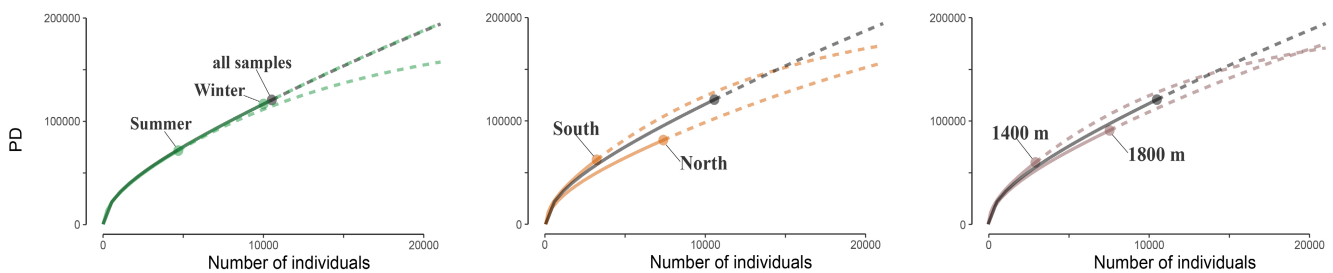
We carried out our analyses on beetles because this insect order had available a broad-coverage phylogeny, even though our trap bottles also contain many lepidopteran, hymenopteran and dipteran samples yet to be (meta)barcoded. With these taxa, future phylogenetic trees could be assembled de novo from barcodes, which is why we have tested whether lack of a multilocus phylogeny prevents correct inference. Despite differences in tree topologies, we did not observe

major differences between de novo-tree-derived and placement-tree-derived loss set scenarios (Figure 5). Both their PD values were highly correlated with OTU counts. These results suggest that barcode-gene trees can indeed be used to test for the effect of phylogenetic relatedness on community structure and assembly, although this conclusion requires further testing in different taxa. We also note that although both approaches generate similar ordination plots (Figure 4b,c), there is a greater degree of clustering of the high-elevation, winter samples in the ordination based on the placement tree.

(a) species richness

(b) phylogenetic diversity: *de novo* tree

(c) phylogenetic diversity: placement tree



(d) proportions of diversity remaining

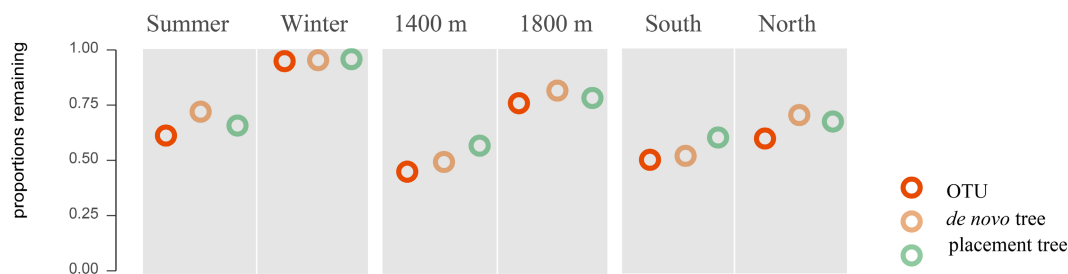


FIGURE 5 Rarefaction results comparing loss set scenarios. (a–c) Rarefaction results comparing the species richness (a), *de novo* tree-based Faith's PD (b), and placement tree-based Faith's PD (c) among all samples and their seasonal (first column), latitudinal (second column), elevational (third column) loss sets. Solid lines are rarefactions and dashed lines are their extrapolations. The labels on the figure indicate sets that are subtracted from all samples. (d) Proportions of species richness or PD remaining after subtraction of each loss set. For instance, in the Summer box, all three ways of measuring diversity estimate a loss of about 40% when the summer samples are removed.

4.3 | Future directions

While we report broad-stroke pattern of community diversity change across space and time in our data set, we have not examined intraspecific and interspecific variations in response to climate change across taxa, such as thermal plasticity, micro-habitat and dispersal ability (Forrest, 2016). We invite interested

researchers to utilize this data set and take further investigations in two directions. First, in this study we have not touched on the evolutionary assembly process at the sample (i.e., community) level, and their environmental covariates. At the sample level, metrics that reveal historical and climatic patterns of community assembly (while accounting for effect of species richness) include the standardized effect size of PD (Webb et al., 2008), as well as

net relatedness index (NRI) and nearest taxon index (NTI) (Webb et al., 2002). We are interested in whether the community assembly process itself (e.g., a phylogenetically clustered vs. dispersed set of species in a community) has environmental or temporal drivers. Second, we encourage researchers with taxonomic expertise to explore our data set by pairing ecological and phylogenetic covariates with trait information on, for instance, feeding habit (e.g., xylophagous vs. herbivorous vs. insectivorous) and microhabitat preference (e.g., leaf vs. bark dwelling)—while keeping in mind that Malaise traps are less likely than other methods to sample ground-dwelling beetles (Musthafa et al., 2022). It is possible that major lineages of beetles (e.g., Cerambycidae, Carabidae, Curculionidae) show convergent patterns of community assembly in response to environmental and temporal covariates; certain taxa might respond to climate change as a functional group (despite being analysed in different spatiotemporal subsets in this study); it is also possible that functional subsets of the beetles (or indeed the other arthropod taxa captured by the Malaise traps) could exhibit the phylogenetic mitigation that we hypothesised would exist for the whole-beetle data set analysed here. We also note that climate change could drive the divergence of phenologies between insects and their food plants (known as phenological mismatch or trophic asynchrony, Renner & Zohner, 2018), which is another potential driver of community-level diversity loss (Visser & Gienapp, 2019) that could be examined using our data set in combination with local plant phenology data set (Peng et al., 2022).

AUTHOR CONTRIBUTIONS

Douglas W. Yu conceived the study. Benjamin Linard and Alfried P. Vogler generated the beetles reference phylogeny data. Zongxu Li, Douglas W. Yu and Zhengyang Wang gathered field data, conducted experiments and analysis. Zongxu Li, Douglas W. Yu and Zhengyang Wang prepared the manuscript, with input from Benjamin Linard and Alfried P. Vogler.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All barcodes can be downloaded from NCBI by their accession number (see Table S1). Barcode information and OTU table are presented in the Supporting Information.

ORCID

Benjamin Linard  <https://orcid.org/0000-0002-5555-898X>

Alfried P. Vogler  <https://orcid.org/0000-0002-2462-3718>

Douglas W. Yu  <https://orcid.org/0000-0001-8551-5609>

Zhengyang Wang  <https://orcid.org/0000-0003-3244-1954>

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