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Title: The ecological impact of pest-induced tree dieback on insect biodiversity in Yunnan pine plantations, China

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ABSTRACT

China has recently announced a reform of forestry policy, with a major goal being to transform from plantation to heterogeneous forests, which have higher resistance to pests and disease and house more biodiversity. One driver of reform is increased intensity and frequency of pest-induced tree-dieback events. To inform management, we ask what effects these events have on insect biodiversity in *Pinus yunnanensis* monocultures in Yunnan province, the province with one of the highest proportions of forest cover in China. We sampled aerial insect (mostly insect) biodiversity along gradients of *Pinus yunnanensis* dieback severity using Malaise traps and used metabarcoding to characterise the insect community. We used MS-GDM ('multi-site generalized dissimilarity modelling of zeta diversity'), zeta-decline analysis, and iNEXT ('Interpolation and extrapolation for species diversity') to assess community change as functions of forest-structure covariates. Metabarcoding of Malaise-trapped insects reveals that bark-beetle induced forest dieback does not result in detectable differences in species diversity but does result in compositional change, with the biggest turnover occurring between 0%-infested-0%-open-canopy forests and 20%-infested-20%-open-canopy forests. Zeta-decline analysis found that the insect community in low-infestation forests is characterized by a stochastic assembly, while in high-infestation forests, the community structure is consistent with niche assembly. Our results thus suggest that bark-beetle dieback mimics natural forest-gap dynamics, consistent with the interpretation of bark beetles as a keystone species in European conifer forests, where it has been proposed that forest heterogeneity can be created efficiently by allowing natural disturbances, including bark-beetle outbreaks, to proceed naturally, without being mitigated by deadwood removal and dense replanting. In Yunnan's situation, and given predicted increases in bark-beetle dieback severity and frequency, this strategy should probably be supplemented with anthropogenic treatments, such as deadwood enhancement and planting of multiple tree species, to accelerate the succession of plantations into heterogeneous forests.

KEYWORDS: DNA metabarcoding, biodiversity, climate change, bark beetle outbreak, zeta diversity, *Pinus yunnan*ensis

1. INTRODUCTION

The largest reforestation programmes in the world are China's Natural Forest Protection Program (NFPP) and Grain for Green Program (GFGP), which were implemented after widespread flooding in 1998 (Liu et al., 2008; Vina et al., 2016; Xu et al., 2006; Yin et al., 2009). The NFPP protects native forests in the upstream watersheds of the Yangtze and Yellow rivers (Liu et al., 2008; Ren et al., 2015), and the GFGP controls soil erosion by paying farmers to plant trees on sloping land that had been used for food production (Delang & Yuan, 2015; Liu et al., 2008; Ma et al., 2017; Xu et al., 2006; Zhai et al., 2014). The GFGP reforested 9.06 million ha of cropland between 1999 and 2014, and not surprisingly, the GFGP has primarily established low-diversity tree plantations ('plantations' hereafter), rather than restoring native forest (Hua et al., 2018, 2016; Zhai et al., 2014).

Studies have previously shown that these plantations support lower levels of bird, bee, and general insect diversity than do native forests in the same locations (Hua et al., 2016; Wang et al., 2019). These findings complement those of Cao et al. (2019), who recently calculated that plantations in China return a lower net value of ecosystem services relative to native forests, even after counting income from timber sales. Plantations require a high initial outlay for tree planting, some non-native tree species like *Eucalyptus* require more water input than do native tree species, and more management effort is required to protect plantations from pest attack (Brockerhoff et al., 2013). In contrast, income from timber sales is low. Thus, to better protect and restore terrestrial biodiversity, studies have recommended that reforestation policy in China should prioritize the conservation and restoration of native forest over plantations (Hua et al., 2016; Wang et al., 2019).

These initial results in China are consistent with those from a larger body of research on forest biodiversity and ecosystem functioning in Central Europe, where professional silviculture has long promoted plantations, which have now grown to be dominated by dense tree stands with few canopy gaps and low volumes of deadwood (Doerfler et al., 2018; Thorn et al., 2018, 2019). Such forests support a low diversity of plants and animals, especially of saproxylic species (Thorn et al., 2018, 2019) and are more vulnerable to large-scale bark-beetle

(Curculionidae, Scolytinae) outbreaks because the forests are even-aged and thus grow to provide an extensive and continuous cover of the large trees that are ideal hosts for bark beetles (Seidl et al., 2016).

Bark-beetle outbreaks are now a primary killer of coniferous forest in central Europe (Thorn et al., 2019), as well as North America (Robertson et al., 2009) and China (Gan, 2015; He & Zhang, 2004). Moreover, climate change is increasing the frequency of bark-beetle outbreaks (Carroll et al., 2004; Esper et al., 2007; Sambaraju et al., 2012; Seidl et al., 2017). For instance, more frequent and severe droughts and high temperatures impede pines from producing enough toxic resin to disable attacking beetles (Erbilgin et al., 2017; Kichas et al., 2020; Raffa & Berryman, 1983), and consequently, bark-beetle populations can more easily grow to outbreak levels (Cullingham et al., 2011).

Bark-beetle outbreaks leave many standing dead trees, leading to an overall increase in deadwood amount and stand structural heterogenity (Swanson et al., 2011). Forest managers often carry out salvage logging by removing infected trees in order to stop the expansion of the beetles (Stadelmann et al., 2013) and to recover the economic value of wood (Lindenmayer et al., 2008). The removal of infected trees has a negative impact not only on bark beetles but also on other species associated with dead wood (Thorn et al., 2018) but can have positive effects by on species that are normally associated with open areas (Rost & Clavero, 2012).

Our study region of Yunnan province, southwestern China, has one of the highest proportions of forest cover in China (Ren et al., 2015; SFA, 2016), and *Pinus yunnanensis* plantations account for 28.2% of this forest cover (YNFA, 2018), 80% of which is monoculture (Cai et al., 2006). Most of the *Pinus yunnanensis* forest has grown up on land where primary evergreen broadleaved forests had been destroyed (Deng et al., 2014). The provincial forestry bureau carries out salvage logging by cutting and removing ‘snags’ (upright dead trees) to control local outbreaks of three species of pine shoot beetles of genus *Tomicus* (Coleoptera: Curculionidae: Scolytinae) (Gan, 2015; Kirkendall et al., 2008; Lu & Zhang, 2000; Lu et al., 2014; Wang et al., 2015). In addition, locals remove logs for firewood, leading to very low volumes of dead wood in *Pinus yunanesis* plantations, despite massive shoot beetle outbreaks

affecting over 200,000 ha of pine plantations in Yunnan (Ji et al., 2007; Lieutier et al., 2003). This combination in Yunnan of GFGP-financed plantation dominance, *Tomicus* outbreaks, and salvage logging results in conifer forests similar to those in Central Europe: structurally simple, even-aged tree cover that, despite cut-and-removal of infested trees, remains vulnerable to bark-beetle outbreaks (Cai et al., 2006) and supports low levels of native biodiversity compared to native forest.

However, China announced its intention to implement a new forest restoration plan in 2019 (Xinhua News Agency, 2019), with a major policy goal being to transform plantations into heterogeneous forests that have higher resistance to pests and disease.

In this study, we used Malaise traps to sample aerial insect biodiversity (dominated by Diptera and Hymenoptera) along gradients of *Pinus yunnanensis* dieback severity. The initial goal of our study was to study the ecological impact of bark-beetle-induced dieback on flying insect diversity. In particular, we were interested in whether patterns of forest insect diversity in Yunnan plantations are similar to those in Central Europe, where impacts of tree-dieback on habitat structure and salvage logging have been extensively studied (Doerfler et al., 2018; Hilmers et al., 2018; Müller et al., 2010; Seibold et al., 2016a, 2016b, 2018; Thorn et al., 2018). If similar, then this increases our confidence in applying lessons learned there to Yunnan and neighboring provinces (e.g. the efficacy of deadwood enrichment as a means of promoting saproxylic taxa; Doerfler et al., 2018; Seibold et al., 2016a, 2016b). Secondly, given China's recent forest-policy reform announcement, our results serve as a baseline survey of aerial insect biodiversity in Yunnan's *Pinus yunnanensis* plantations, to allow comparison with future forests in which, we presume, China will promote, or at least allow, the accumulation of greater structural and age heterogeneity and more deadwood.

We characterized the Malaise-trap samples using DNA metabarcoding, which combines DNA barcoding with high-throughput DNA sequencing to generate large sample X species tables that can be used to test the effects of candidate environmental variables on biodiversity. We did not specifically collect saproxylic taxa because the current cut-and-remove policy means that there are no *Pinus yunnanensis* forests in Yunnan with high volumes of deadwood

to act as a contrast. Metabarcoding has been tested against morphologically identified samples and been shown to be a reliable and efficient method of characterizing the species compositions of bulk samples of insects and invertebrates generally (Aylagas et al., 2018; Cordier et al., 2017; Edwards et al., 2014; Ji et al., 2013; Lejzerowicz et al., 2015; Pawlowski et al., 2016; Wang et al., 2019; Yu et al., 2012). Accessible explanations of metabarcoding are available in Bush et al. (2017), Ji et al. (2013), Piper et al. (2019), Yang et al. (2020), and Zinger et al. (2019).

2. METHODS

2.1. Field sampling and environmental variables

Following the distribution of *Pinus yunnanensi*s in Yunnan province, southwest China, we sampled in five counties across the elevational range of optimal growth (1800–3000 m, Table 1) (Deng et al., 2013). In each county, we sampled in six *P. yunnanensi*s-dominated forest stands of at least 1 Ha extent along a gradient of bark-beetle-induced dieback severity: two sites each in low, medium, and high severity (Figure 1) (sampling locations and elevations in Table S1). Severity was judged by local forestry officials, who are charged with responding to bark-beetle outbreaks, using a method defined in 2006 by the then-State Administration of Forestry (now National Forestry and Grassland Administration) (SFA 2006). All sampling plots are reported to have been attacked the first time in the 1980s (Zhao & Långström, 2012). Our goal with this initial blocking was only to maximize coverage of the local gradient of dieback severity.

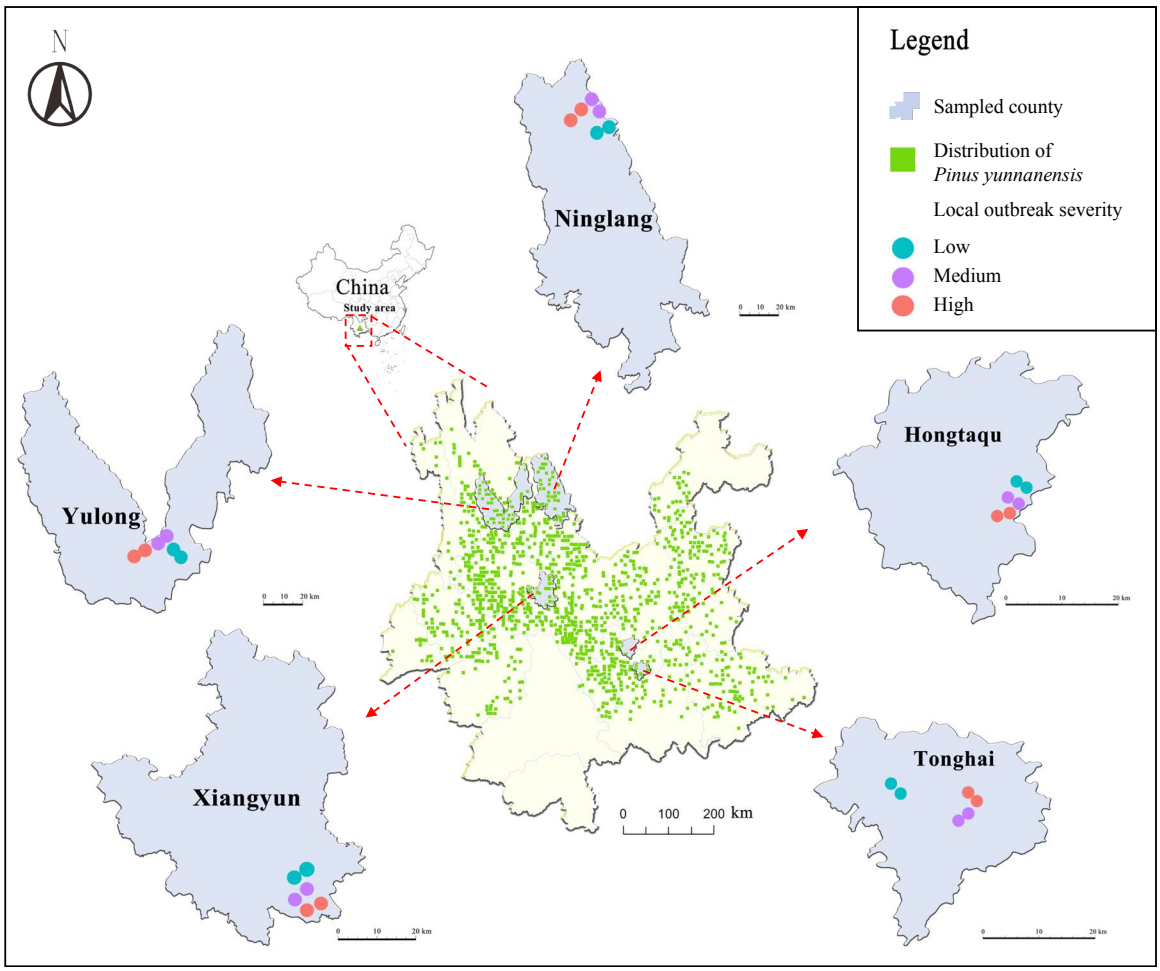


Figure 1. Map of study area, Yunnan province, southwest China. Blue insets are the five sampled counties. Green squares indicate *Pinus yunnanensis* forest distribution. Coloured circles indicate sampling sites, stratified by severity of bark-beetle outbreak, as judged subjectively by local forestry officials.

We set out and retrieved Malaise traps during 4-14 July 2016, placing two traps 10 m apart in each forest site (pairs were pooled at DNA extraction before downstream processing) for a total of 60 samples (5 counties X 6 sites/county X 2 traps/site). We used absolute ethanol as the killing and preserving agent, and the traps were left out for seven days each. For efficiency, we set out all traps in one county and then moved the next day to another county. Retrieval followed the same schedule, and we replaced the ethanol in each trap with fresh ethanol for transport at ambient temperature to our laboratory, where samples were stored at -80 ºC until DNA extraction. In addition, in each of the 30 sampling sites, we centered a 30 X 30 m quadrat over the Malaise traps and measured six environmental covariates: elevation, mean tree height, diameter at breast height (DBH), percentage canopy openness, mean

infestation rate (the percentage of trees with one or more bark beetle emergence holes on all four cardinal sides), and stump number (details in Table 1).

Table 1. Environmental covariates and definitions

Environmental covariates	Definitions	Range(of means)
Elevation	Recorded by GPS at the plot center.	1757-3052 m
Height	Mean height of 40 trees in the quadrat, where the trees are the first 10 trees north, south, east, and west of the quadrat centre.	4.61-13.00 m
DBH	Mean diameter at breast height of 40 trees in the quadrat, using the same trees used for the height measurement.	7.9-23.6 cm
Canopy openness	Mean proportion of sky visible in the quadrat, measured by spherical densiometer (Paletto & Tosi, 2009). Measurements were taken at quadrat centre and each corner, and averaged.	0.01-0.68
Infestation rate	The percentage of trees that are infested. Trees with one or more bark beetle emergence holes on the north, south, east, and west sides of their trunks were scored as infected, using the same trees used for the height measurement.	0-0.79
Stumps	The total number of tree stumps in the quadrat.	0-22

2.2. DNA extraction and PCRs

Before DNA extraction, the storage ethanol was decanted, and the sample was air-dried on single-use filter papers. To reduce PCR dominance by large-biomass individuals (Elbrecht et al., 2017), we used two legs from all individuals larger than a housefly and whole bodies of everything smaller. Tissue was digested using a modified non-destructive protocol from Gilbert et al. (2007) and Nielsen et al. (2019) in one 50-ml falcon tube per sample, followed by DNA extraction with the DNEasy Blood & Tissue Kit (Qiagen GmbH, Germany). After extraction, we pooled the DNA from the paired Malaise traps, leaving us with 30 samples, one per site.

We used *mlCOIintF–Fol-degen-rev* primers (Leray et al., 2013; Yu et al., 2012), which amplify a 313-bp fragment of the COI barcode, and we followed the DAMe metabarcoding protocol (Alberdi et al., 2018; Bohmann et al., 2018; Zepeda-Mendoza et al., 2016), which is a co-designed wet-lab and bioinformatic pipeline that combines qPCR-optimized PCR conditions, multiple, independent PCR replicates per sample, twin-tagging, and negative and positive controls to (i) remove sequence-to-sample misassignment due to tag-jumping (Schnell et al., 2015), (ii) reduce sequence dropout and taxonomic bias in amplification, and (iii) reduce erroneous sequences. Twin-tagging means that the same tag is used on both the forward and reverse primers in a reaction (F1-R1, F2-R2,…), and multiple, independent PCR replicates per sample means that a different twin tag is used for each of the six PCRs per sample, which lets them be distinguished in bioinformatic processing. The DAMe logic is that tag-jump events can be filtered out by removing reads carrying non-twinned tags (e.g. F1-F2, F3-F5) and that nearly all erroneous sequences (indels, substitutions, chimeras) can be filtered out by removing sequences that appear in only one (or a low number of) PCR replicate(s) at a low copy number, while true sequences are more likely to appear in multiple PCRs at higher copy numbers. Extensive testing with a recently updated version of DAMe (now called Begum) using mock samples finds that erroneous sequences can be nearly eliminated at the cost of only a small rise in drop-outs, and a detailed explanation of the protocol can be found there (Yang et al., 2020).

We used qPCR on a subset of samples to optimize PCR annealing temperature, cycle number, and initial DNA template concentration, as recommended by Murray et al. (2015) and Bohmann et al. (2018). Afterwards, for each sample, we ran 6 independent PCRs with 6 different twin-tags, under the following qPCR-optimised conditions: initial denaturation 95 ℃ for 5 min, followed by 27 cycles of 95 ℃ for 10s, 45.5 ℃ for 45s, 72 ℃ for 1 min, and finishing at 72 ℃ for 10 mins. All PCRs were performed in 20 µl reactions containing 0.6 U Ex Taq HS DNA polymerase, 1 × Ex Taq Buffer (Mg^{2+} plus), 0.2 mM dNTP Mixture (TaKaRa, Biotechnology Co. Ltd, Dalian, China), 0.4 µM of each primer, 1 µl DMSO, 0.1 µg/µl BSA (Bovine Serum Albumin Solution, TaKaRa Biotechnology Co. Ltd, Dalian, China), and 2 µl genomic DNA. We visualized the PCR products on 2% agarose gels. The PCR plate also

included three extraction blanks and a row of PCR blanks. Finally, we included a positive control containing seven insect species from France. The 30 samples were combined into six, approximately equimolar pools for bead purification (Agencourt AMPure XP kit, Beckman Coulter, Inc., USA) and subsequent library preparation using the NEXTflex Rapid DNA-Seq Kit for Illumina (Bioo Scientific Corp., Austin, USA). The six libraries were sequenced on the Illumina MiSeq platform (300PE) at the Southwest Biodiversity Institute Regional Instrument Center in Kunming.

2.3. Bioinformatic processing

Raw MiSeq data were first trimmed for remnant Illumina adapters with *AdapterRemoval* 2.2.0 (Schubert et al., 2016), followed by Schirmer et al.'s (2015) recommended pipeline: we trimmed low-quality ends using *sickle* 1.33 (Joshi & Fass, 2011), denoised reads using the *BayesHammer* module in *SPAdes* 3.10.1 (Nikolenko et al., 2013), and merged read pairs using *PandaSeq* 2.11 (Masella et al., 2012). In all cases, we used default parameters.

Sequence were demultiplexed to sample and filtered for tag-jumps using a modified version of DAMe that ignores heterogeneity spacers in the primers (github.com/shyamsg/DAMe, accessed 10 October 2020). We then filtered out putatively erroneous sequences by keeping only those that appeared in >2 of the 6 PCRs per sample, at a minimum copy number of 30 per PCR, which is the stringency level that minimized false negatives and maximized true positives in the positive control. We further filtered by removing sequences ≤300 bp length and using the *de novo* chimera search function in *vsearch* 2.4.3 (Rognes et al., 2016). After filtering, sequences were clustered into 97% similarity Operational Taxonomic Units (OTUs) using *SUMACLUST* 1.0.20 (Mercier et al., 2013), from which we created a Sample X OTU table, and we used the *R* package 'lulu' 0.1.0 (Frøslev et al., 2017) with default parameters to combine likely 'parent' and 'child' OTUs that had failed to cluster. Finally, we assigned taxonomies to the remaining OTUs with the RDP Classifier function (Wang et al., 2007) on the Midori metazoan mitochondrial gene website (Leray et al., 2018). OTUs assigned to Arthropoda with <80% probability were removed. No OTUs remained in

the extraction-blank and PCR negative controls, and the positive control and samples shared no OTUs. We also tried assigning taxonomies on BOLD (Ratnasingham & Hebert, 2007), but only a few OTUs received hits, due to a lack of samples from this region.

2.4. Statistical analyses

All statistical analyses were carried out in R 3.6.3. Read numbers per OTU per sample were transformed to presence/absence (1/0). We first used the 'boral' 1.6.1 R package (Hui, 2016) to cluster sites by community composition. Boral is a Bayesian, model-based ordination method that allows the selection of an appropriate error distribution. We used a binomial error distribution and no row effect to fit the model since we were using presence/absence data. For the same reason, we used 'mvabund' 3.12.3 (Wang et al., 2012) to test for the effects of environmental covariates on community composition.

Because the boral ordination showed that the dominant driver of change in community composition is geographic distance, which is not surprising given the large spatial extent of our sampling (Figure 1), we followed up with Multi-Site Generalized Dissimilarity Modelling (MS-GDM), using the 'zetadiv' 1.2.0 package (Latombe et al., 2017). Classical GDMs try to identify the dominant drivers of change in community composition by using a combination of pairwise (i.e. between-two-sites) differences in geographic distance and in environmental-covariate values to explain pairwise differences in community composition (Ferrier et al., 2007). However, pairwise differences in composition (e.g. 1-Jaccard) are dominated by the contributions of the many species that are present in just two samples (i.e. rare species), resulting in GDMs that more heavily weight the variables that explain turnover in rare species, such as geographic distance.

To identify the environmental variables that are more important for explaining the distributions of widespread species (i.e. those present in multiple samples), Latombe et al. (2017) combined GDMs with the concept of zeta diversity (Hui & McGeoch, 2014) to create MS-GDMs. Zeta diversity is a generalization of pairwise beta diversity and is the mean number of species shared by *i* number of sites, where *i* is known as the zeta order. Zeta diversity order 4, for instance, is the mean number of species shared by 4 sites (in a dataset of 100 sites, there

are ~3.9 million combinations of 4 sites). Zeta diversities can be converted to multi-site equivalents of the pairwise Jaccard dissimilarity and used as response variables in an MS-GDM (Latombe et al., 2017, 2019), with the six environmental covariates as candidate predictors (Table 1), rescaled between 0 and 1. We also used zeta diversity to ask if the insect communities in low- and high-infestation forests show evidence for different assembly mechanisms, by using the 'zetadiv' package to calculate zeta diversity decline and species retention rates for low- and for high-infestation forests. Finally, we partitioned variation in zeta diversity into environmental, distance, indistinguishable, and unexplained components.

To compare alpha diversity across infestation levels (Species richness, Shannon and Simpson diversities), we used the sample-based rarefaction-extrapolation approach in the 'iNEXT' 2.0.12 package (Hsieh et al., 2016). Significant differences in estimated alpha diversity were judged by non-overlapping confidence intervals, which is considered slightly conservative (MacGregor-Fors & Payton, 2013). In case we had oversplit some biological species into multiple OTUs, leading to artefactual differences in species richness, we also carried out a phylogenetic-diversity (PD) analysis because a single species split into multiple OTUs should cluster on a phylogenetic tree and thus contribute less to PD than two OTUs from two different biological species. Our protocol followed that of Wang et al. (2019), in which we aligned the OTU sequences, built a maximum-likelihood (ML) phylogenetic tree (details in S2), and estimated PD with the 'iNextPD' 0.3.2 package (Hsieh & Chao, 2017). We omitted two OTUs because they produced long branches.

3. RESULTS

3.1. Bioinformatic processing and taxonomic composition

The six libraries yielded 11,128,217 paired-end reads. After removing a very large number of tag-jumped, paired-end reads (7,526,449), followed by DAMe filtering (retaining 1,217,449 sequences in ≥2 of the 6 PCRs per sample at ≥ 30 copies per PCR), and removal of chimeras and OTUs not assigned to Arthropoda, we ended up with 1,107,100 reads, clustered into 880 97% OTUs, for downstream analysis. Mean reads per OTU was 1,258 (Range = 66–54,775; SD = 2930), and mean reads per sample was 36,903 (n = 30; range 3,881–72,575; SD =

17,396). These 880 OTUs were assigned to 35.8% Diptera, 21.7% Lepidoptera, 19.1% Hymenoptera, 9.7% Coleoptera, 7% Hemiptera, and 6.7% other orders.

Read depth varied across samples (Figure S3A), and we found a positive correlation between read depth and species richness (Pearson, $p<0.001$). Thus, to test the robustness of our results, we removed eight samples that had < 25,000 reads, which removed the positive correlation (Pearson, $p = 0.68$, Figure S3B), reran the analyses below (3.2-3.5) and, as we report below and in Supplementary Information (S4, S6, S9, S10), found essentially the same results. We report the full-dataset results in Main Text.

3.2. Boral ordination

Boral ordination (Figure 2) clustered the 30 sites by the five counties in which we sampled (Figure 1) and arranged the clusters by elevation (latent variable 1) and tree-infestation rate (latent variable 2). Mvabund analysis confirmed the same effects (Table 2) and found no evidence for an interaction effect. Boral results without low-read-depth samples in Figure S4.

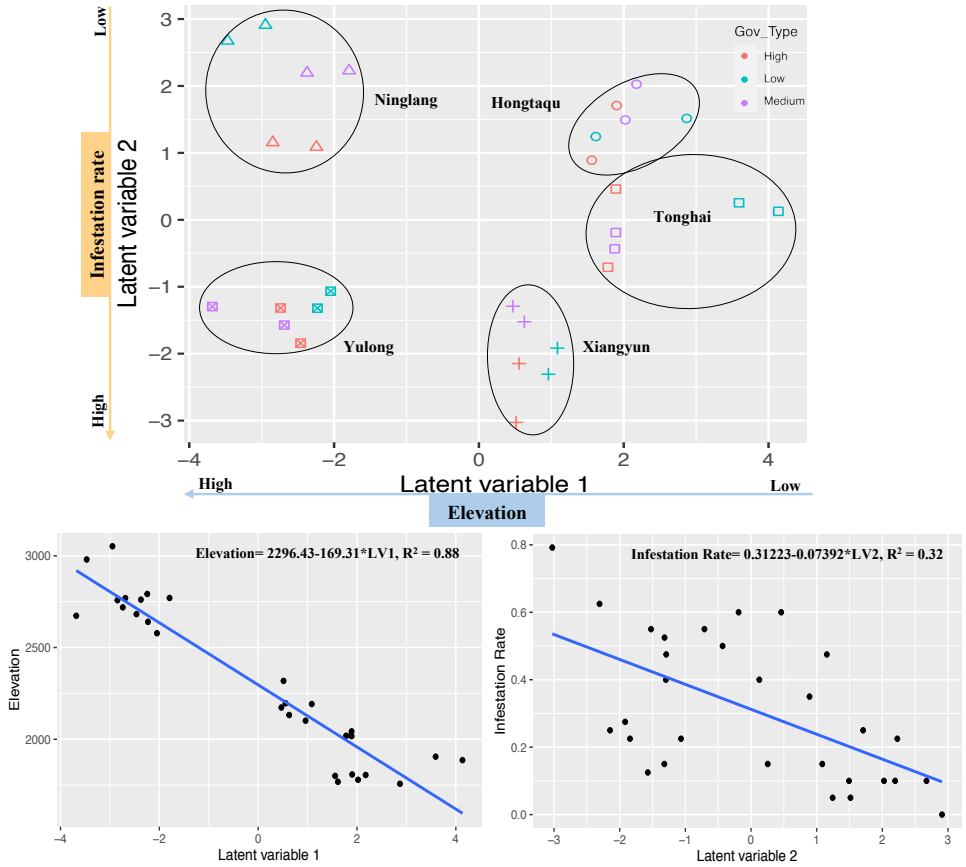


Figure 2. 'Boral' ordination of beta diversity by disturbance type. Color codes for outbreak severity as in Figure 1. Symbols (and surrounding ovals) indicate the five counties, and points represent samples. Latent variable 1 predicts elevation (2296.43-169.31*LV1, R^2 = 88.0%, df = 28, p = 4.42e-15), and latent variable 2 predicts tree-infestation rate (0.31-0.07*LV2, R^2 = 31.5%, df = 28, p = 0.0007). Boral residuals in Figure S5.

Table 2. Mvabund analysis. Testing for the effects of Elevation, Infestation rate, and their interaction on community composition.

	Res.Df	Df.diff	Score	Pr(>score)
Intercept	29			
Elevation	28	1	100.1	0.001
Infestation rate	27	1	136.8	0.044
Elevation:Infestation rate	26	1	131.1	0.935

3.3. Multi-Site Generalized Dissimilarity Modelling

We carried out MS-GDM to identify the main drivers of change in community composition after controlling for geographical distance. Initially, we ran the model with five environmental covariates from Table 1 (omitting elevation), plus geographic distances between sites, because geographic distance and elevation are correlated. At zeta order 2 (equivalent to the Jaccard index, which is pairwise and thus dominated by rare species), distance is the dominant driver of compositional turnover, followed by the local environmental variables canopy openness and DBH (Figure 3A, Order2). Distance is largely linear in its effects, meaning that changes in community composition occur along the full range of distance, as rare species turnover from site to site and county to county. In contrast, for canopy openness, most compositional turnover occurs in the first 20% of its range, in the transition from closed to partially open-canopy forest, and for DBH, most change occurs in the last 20% of its range, in the transition to sites with the largest trees. MS-GDM with low-read-depth samples removed in Figure S6.

By definition, as zeta order rises, common species increasingly dominate the analysis, and starting at zeta order 4 (Figure 3A, Order4), the distance variable starts to be less important than the local variables of infestation rate and canopy openness, which both exert their effects primarily in the first ~20% of their ranges. That is, most of the compositional change occurs in the transition from 0%-infested-0%-open-canopy forests to 20%-infested-20%-open-canopy forests. At higher zeta orders, distance explains even less of the change in composition, except at very large distances, since common species are by definition more widespread.

We then re-ran the MS-GDM with elevation included, which returned similar results: as zeta order increases, the five environmental covariates other than elevation (Table 1) explain an increasingly larger proportion of total variation, while distance and elevation become less important (Figure S7).

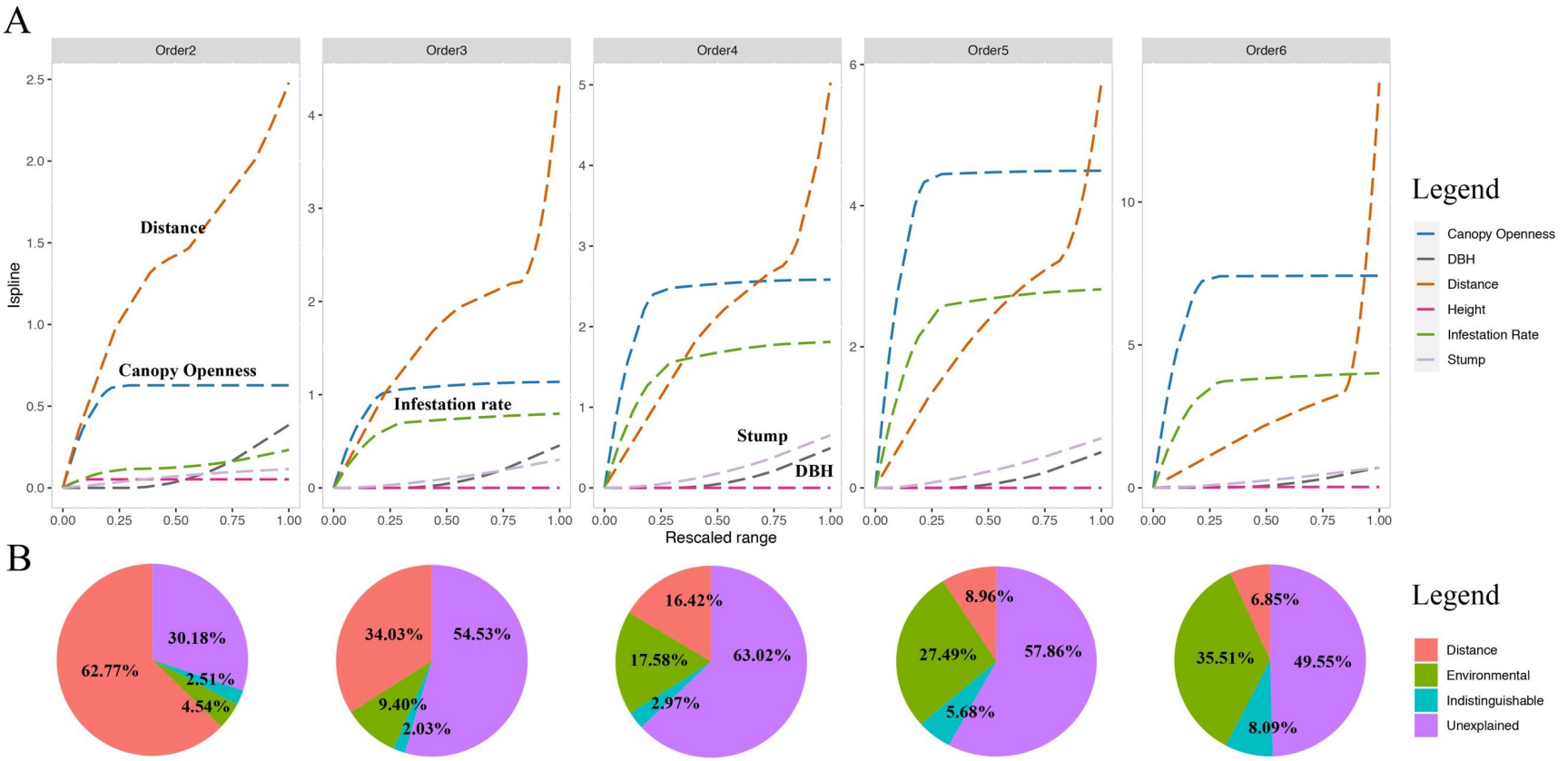


Figure 3. Multi Site Generalised Dissimilarity Modelling (MS-GDM) analysis. A. Contributions of five environmental covariates and distance to explaining zeta diversity and B. and variation partitioning. Environmental covariates were rescaled between 0 and 1. The vertical axes indicate the relative contributions of each environmental variable, at each zeta order. Geographic distance is most important at low zeta orders, which are dominated by rare species, and as zeta order increases (increasing the importance of common species), canopy openness and then infestation rate become increasingly more important, with most of the compositional change occurring in the first 20% of change in those two covariates. Overall when zeta order >4, environmental covariates explain more compositional change than distance.

3.4. Zeta diversity decline and retention ratios

Another application of zeta diversity is to infer the relative roles of niche partitioning and stochastic assembly in community assembly (McGeoch et al., 2019). Zeta diversity declines as zeta order increases, since fewer and fewer species are shared amongst more and more sites. Steeper rates of decline indicate greater numbers of rarer species over more common species. Here, we asked how infestation affects community assembly over the infestation-rate gradient. To simplify the comparison, we divided the sites roughly evenly into 'low' (≤ 0.25, n = 14) and 'high' (>0.25, n = 16) infestation-rate categories (Figures 4, S8), and test the goodness of zeta-diversity decline functional forms using the Akaike information criterion (AIC).

In the low-infestation forests, zeta-diversity decline is both steeper and better fit by an exponential function (points are equally spaced with increasing zeta order) than by a power-law (points get closer with increasing order) function ($-7.54_{AIC\_exp} < 10.67_{AIC\_pl}$) (Figure 4A). This is consistent with low-infestation forests being characterized by a stochastic assembly process. In the extreme form, there is no niche partitioning; all the species have equal probability of occurring at any given site despite environmental variation across sites, and across-species variation in occupancy and turnover arises only stochastically, due to, for instance, random dispersal governing establishment (Hui & McGeoch 2014; McGeoch et al. 2019). Consistent with this, the zeta-ratio analysis shows fewer common species and generally low retention of species when a new site is sampled (McGeoch et al. 2019, Figure 4B).

In contrast, in the high-infestation forests, zeta-diversity decline is relatively shallower and better fit by power-law function ($8.52_{AIC\_exp} > 0.80_{AIC\_pl}$) (Figure 4A), which obtains when the probability that a species occurs in a newly sampled site increases with that species' overall occupancy, which in turn is consistent with community assembly being driven by niche differentiation. Each OTU has a species-specific probability of occurring at a site due to environmental conditions at that site (Hui & McGeoch 2014, McGeoch et al. 2019). The zeta-ratio analysis shows that species in the high-infestation forests generally have higher occupancy, even beyond order 6 (Figure 4B), which is the number of sites per county (Figure 2) and which thus shows that high-infestation forests share species across large geographic

distances, apparently because of shared environmental conditions (Figure 3A). (See Figure S9 for the same analysis with low-read-depth samples removed).

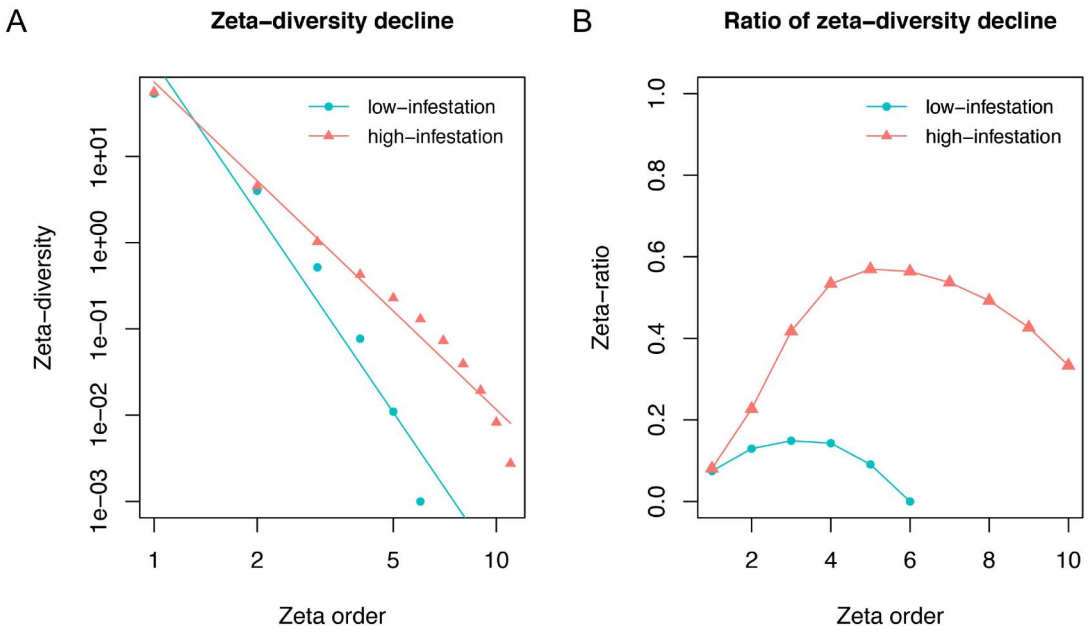
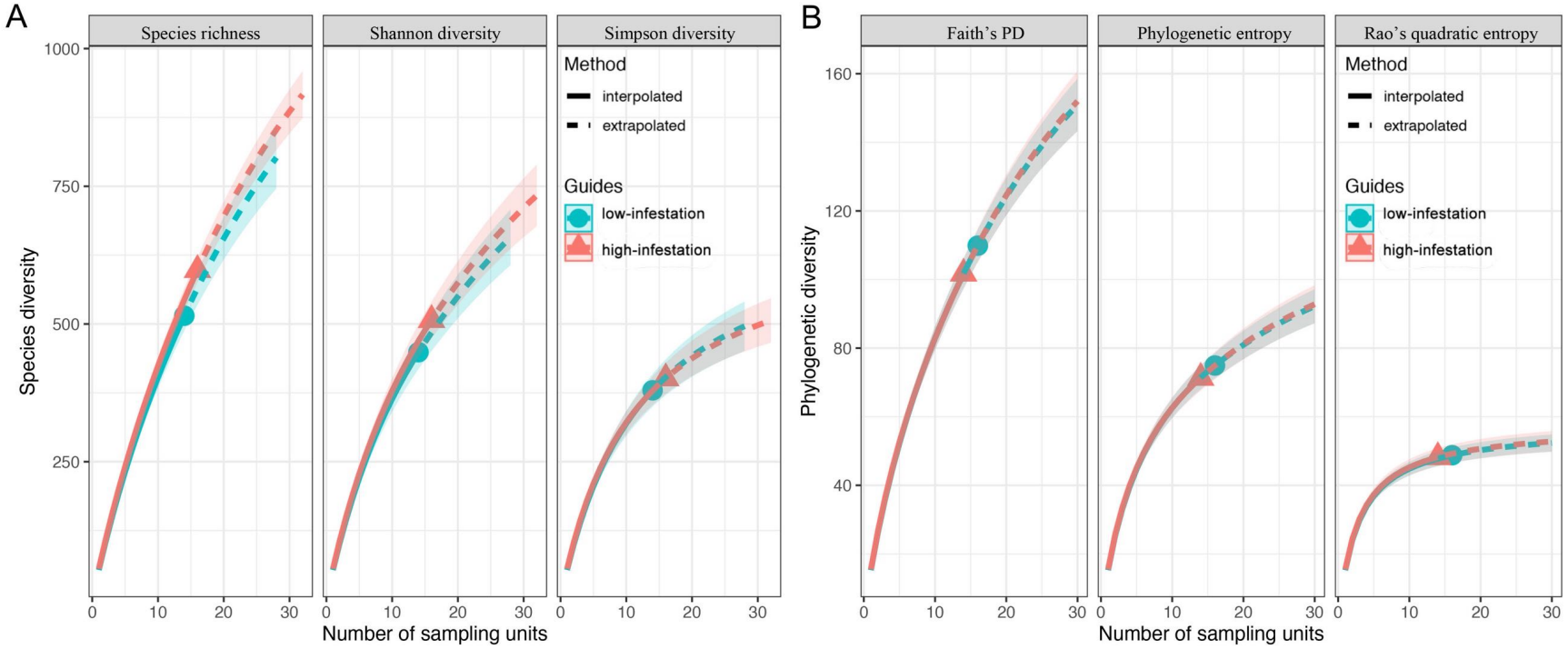


Figure 4. Community assembly mechanism. A. Comparison of zeta diversity decline and B. retention rate between low- and high-infestation forests. Zeta orders 1 to 11 are shown, as zeta diversity equals zero for orders >11. High-infestation sites A. are characterized by a power-law decline and B. share more common species, consistent with a niche-differentiated community. Low-infestation sites A. are characterized by an exponential zeta-diversity decline and B. share fewer common species, consistent with a stochastic community-assembly process.

3.5. Alpha diversity

The iNEXT and iNextPD analyses found no evidence for a difference in species or phylogenetic diversity between low- and high-infestation forests (Figure 5, iNEXT analyses with low-read-depth samples removed in Figure S10).



386 **Figure 5.** Alpha diversity analysis by A. iNEXT and B. iNextPD. Sample-size-based rarefaction (solid lines) and extrapolation (dashed
387 lines) sampling curves for three measures of A. species diversity and B. phylogenetic diversity in low-infestation and high-infestation forests.
388 Shaded areas represent 95% confidence intervals. Symbols indicate sample size per forest type. Overlapping confidence intervals indicate no
389 evidence for difference between forest types.

390

4. DISCUSSION

Metabarcoding of Malaise-trapped insects reveals that bark-beetle induced forest dieback does not result in detectable differences in species richness or phylogenetic diversity (Figure 5) but does result in compositional change (Figures 2, 3). For rarer species, MS-GDM and boral ordination explain this turnover with distance and elevation (Figures 2, 3), which are correlated in our sampling design (Figure 1). For more common species, local-forest environmental variables explain relatively more of the compositional differences, with the biggest compositional change occurring between 0%-infested-0%-open-canopy forests and 20%-infested-20%-open-canopy forests (Figures 3, S7). Bark-beetle dieback thus appears to affect the larger insect community (at least the portion that can be sampled by Malaise traps) by mimicking the transition between closed-canopy forest and structurally heterogeneous forest. That said, at higher zeta orders, just over half of compositional variation across sites remains unexplained (Figure 3).

The zeta-decline analysis found that low-infestation sites showed evidence of stochastic assembly, while high-infestation forest sites showed evidence of niche partitioning as the dominant community assembly mechanism (Figure 4). This suggests that the species which colonize the higher-infestation-rate (and higher-energy-availability) sites are adapted to these conditions. This result is also consistent with the conclusion that bark-beetle dieback mimics natural forest-gap dynamics.

Interestingly, Müller et al. (2010) have also reported that saproxylic beetle composition changes nonlinearly with canopy openness (measured as LiDAR penetration), with rapid compositional change occurring from closed canopy up to 23% penetration (11-49% 95% CI), after which composition changes slowly. Our results are thus remarkably similar (Figure 3, S7), despite differences in geography, dominant tree species, and focal taxa, and we speculate that the driving mechanism is the effect of light availability on understorey vegetation and microclimate. Seibold et al. (2016a) have also reported that canopy openness is a major driver of species assemblage composition of non-saproxylic epigeal arthropods after intensive logging (see also Bishop et al., 2009; Bouget et al., 2013; Franc et al., 2007). Unfortunately,

unlike Müller et al. (2010), we were unable to measure the biodiversity effects of deadwood volume (and thus, the effect of deadwood removal), given that, to our knowledge, there are no *Pinus yunnanensis* sites in Yunnan with high amounts of deadwood to contrast with low-deadwood-volume sites. If possible, there would be value in running deadwood enrichment experiments in Yunnan, in order to test the prediction that saproxylic animal and fungal species will benefit (Doerfler et al., 2018; Seibold et al., 2015, 2018). With that important omission, our results in Yunnan seem consistent with Thorn et al.'s (2020) diagnosis of biodiversity decline in European forests, which they attribute to the loss of tree species diversity and the loss of age and structural heterogeneity, which together provide microhabitats for light-demanding plant and insect species. Species, age, and structural heterogeneity also likely contribute to resilience against large-scale bark-beetle outbreaks (Seidl et al., 2016). On the other hand, Trzcinski & Reid (2008) argue that deadwood removal could be effective at preventing the long-distance spread of bark-beetle outbreaks.

Given China's recent announcement that afforestation and reforestation efforts should now aim to create heterogeneous forests that are higher in biodiversity and more resilient to disease and pests, what is the best way to achieve this? Part of the solution is to allow natural disturbances to create forest structural and age heterogeneity, which in turn will benefit light-demanding plants and animals and also provide deadwood volume for saproxylic taxa (Thorn et al., 2020). These natural disturbances include windstorms, bark-beetle outbreaks, and drought-induced diebacks, as long as dead trees are not subsequently removed and open areas not replanted with plantation trees (Thorn et al., 2020). In particular, bark beetles can be seen as a keystone species (Müller et al., 2008), with their attacks on weak and old trees accelerating the succession of monoculture forests into heterogeneous forests (Cai et al., 2006; Yue et al., 2011). However, extreme climate events are predicted to increase, resulting in a greater rate and severity of natural disturbances (Allen et al., 2010, 2015; Thom et al., 2017; Thom & Seidl, 2016), including an expansion of bark beetles to higher latitudes and elevations (Bentz et al., 2010; Hlásny et al., 2011), which raises the short-term costs of allowing bark beetle outbreaks to proceed unimpeded. Thus, in many areas, anthropogenic treatments could be implemented

to accelerate the succession of plantation forests into heterogeneous forests (Baeten et al., 2019; Felipe-Lucia et al., 2018; Schall et al., 2018; Yue et al., 2011), especially given that *Pinus yunnanensis* covers large areas of poor soil, where tree growth is generally slow and seed sources of other tree species distant.

Methodological considerations. – The combination of metabarcoding and Malaise traps, which preferentially capture species-rich Hymenoptera and Diptera, naturally produces datasets with a large proportion of low-prevalence species. In consequence, we used zeta diversity and MS-GDM to analyse community subsets of increasingly more common species, which showed that local environmental covariates were more important for explaining species distributions at higher orders (Figure 3). Zeta-decline analysis showed that high-infestation and low-infestation sites differed in their community assembly mechanisms (Figure 4). In short, removal of the lowest-prevalence species made clearer the effects of forest structure on community composition. In contrast, we failed to find any differences in alpha diversity across low- and high-infestation forests, even for the measures that clearly reached an asymptote: Simpson diversity, Phylogenetic entropy, and Rao's quadratic entropy (Figure 5). That said, our study is underpowered for comparing alpha diversities, and we draw only a tentative conclusion on this front. Finally, to test robustness, we reran all analyses after removing the eight lowest-read-depth samples, which removed the correlation between read-depth and species richness, and we recovered the same results (S4, S6, S9, S10).

Another aspect of metabarcoding is that it can be applied to samples from locations where taxonomic coverage is poor, such as arthropods from Southwest China. The resulting OTU dataset, identified only to higher taxonomic ranks, can be used to visualise biodiversity patterns. However, with limited taxonomic information, we are unable to carry out functional (trait-based) analyses to try to explain why particular taxa are favoured or disfavoured under different silvicultural regimes (e.g. Cours et al., 2020; Thorn et al., 2018). We also note that our dataset represents only a single time point, while temporal turnover of forest arthropod communities appears to be high (Barsoum et al., 2019). However, we have shown elsewhere (Zhang et al., 2016) that metabarcoding sample sets taken in rainy season and in dry season are equally able

to differentiate forest disturbance gradients, and we have shown in two large studies that Malaise-trapped invertebrates show similar responses to several other methods and taxa in their responses to forest structure and disturbance (Ji et al., 2013, Edwards et al., 2014). Thorn et al. (2018) also found taxonomic congruence in biodiversity response to salvage logging. In the future, one partial way around the lack of taxonomic information for functional inference is to apply joint species distribution modelling to DNA-based time series datasets to infer the relative contributions of environmental covariates and species interactions to changes in species abundances (Abrego et al., 2021).

Conclusion. – Long-term monitoring will be necessary for tracking the biodiversity consequences of conversion from simple to heterogeneous forests and for comparing different anthropogenic treatments. Studies in China, the UK, and Borneo have shown that DNA metabarcoding is an efficient and standardizable tool for measuring how animal biodiversity in forests varies as a function of management and inherent condition (Barsoum et al., 2019; Edwards et al., 2014; Hua et al., 2016; Ji et al., 2013, 2020; Wang et al., 2019; Yang et al., 2014; Yang et al., 2016; Zhang et al., 2016). We also think that there is considerable scope for using remotely sensed measures (multispectral and LiDAR) to efficiently generate environmental covariates for the large-scale mapping and monitoring of pest outbreaks like bark beetles in particular Ji et al. (2007) and Wang et al. (2015) and terrestrial biodiversity in general (Bush et al., 2017).

CRediT authorship contribution statement: D.W.Y., C.LV. designed the study. L.L. and C.LV. designed the environmental covariate measurements. C.Y.Y. and C.W. collected samples and made the environmental covariate measurements. W.C., W.C.Y. and C.Y.Y. performed the molecular experiments. W.C. and X.Y.W. performed the bioinformatic and statistical analyses. D.W.Y., W.C. and Q.Z.W. contributed to the manuscript.

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Declaration of Competing Interest: D.W.Y. is a co-founder of NatureMetrics (www.naturemetrics.co.uk), which provides commercial metabarcoding services.

Data accessibility statement: Sequence data are under GenBank accession number PRJNA668449. Bioinformatic scripts, R scripts are available at https://github.com/CaiWang0503/climtree_China.

REFERENCES

Abrego, N., Roslin, T., Huotari, T., Ji, Y.Q., Schmidt, N.M., Wang, J.X., Yu, D.W., Ovaskainen, O. (in press) Accounting for trophic interactions is necessary for predicting how arctic arthropods respond to climate warming. Ecography.

Alberdi, A., Aizpurua, O., Gilbert, M. T. P., & Bohmann, K. (2018). Scrutinizing key steps for reliable metabarcoding of environmental samples. *Methods in Ecology and Evolution, 9*, 134–147. https://doi.org/10.1111/2041-210X.12849

Allen, C. D., Breshears, D. D., & McDowell, N. G. (2015). On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere*, *6*, 1–55. https://doi.org/10.1890/ES15-00203.1

Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D. D., Hogg, E. H. Ted., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J. H., Allard, G., Running, S. W., Semerci, A., & Cobb, N. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, *259*, 660–684. https://doi.org/10.1016/j.foreco.2009.09.001

Aylagas, E., Borja, Á., Muxika, I., & Rodríguez-Ezpeleta, N. (2018). Adapting metabarcoding-based benthic biomonitoring into routine marine ecological status assessment networks. *Ecological Indicators*, *95*, 194–202. https://doi.org/10.1016/j.ecolind.2018.07.044

Baeten, L., Bruelheide, H., van der Plas, F., Kambach, S., Ratcliffe, S., Jucker, T., Allan, E., Ampoorter, E., Barbaro, L., Bastias, C. C., Bauhus, J., Benavides, R., Bonal, D., Bouriaud, O., Bussotti, F., Carnol, M., Castagneyrol, B., Charbonnier,

Y., Chećko, E., … Scherer-Lorenzen, M. (2019). Identifying the tree species compositions that maximize ecosystem functioning in European forests. *Journal of Applied Ecology*, *56*, 733–744. https://doi.org/10.1111/1365-2664.13308

Barsoum, N., Bruce, C., Forster, J., Ji, Y. Q., & Yu, D. W. (2019). The devil is in the detail: Metabarcoding of arthropods provides a sensitive measure of biodiversity response to forest stand composition compared with surrogate measures of biodiversity. *Ecological Indicators*, *101*, 313–323. https://doi.org/10.1016/j.ecolind.2019.01.023

Bentz, B. J., Rgnire, J., Fettig, C. J., Hansen, E. M., Hayes, J. L., Hicke, J. A., Kelsey, R. G., Negron, J. F., & Seybold, S. J. (2010). Climate change and bark beetles of the western United States and Canada: Direct and indirect effects. *BioScience*, *60*, 602–613. https://doi.org/10.1525/bio.2010.60.8.6

Bishop, D. L. J., Majka, C. G., Bondrup-Nielsen, S., & Peck, S. B. (2009). Deadwood and saproxylic beetle diversity in naturally disturbed and managed spruce forests in Nova Scotia. *ZooKeys, 22*, 309–340. https://doi.org/10.3897/zookeys.22.144

Bohmann, K., Gopalakrishnan, S., Nielsen, M., Nielsen, L. dos S. B., Jones, G., Streicker, D. G., & Gilbert, M. T. P. (2018). Using DNA metabarcoding for simultaneous inference of common vampire bat diet and population structure. *Molecular Ecology Resources*, *18*, 1050–1063. https://doi.org/10.1111/1755-0998.12891

Bouget, C., Larrieu, L., Nusillard, B., & Parmain, G. (2013). In search of the best local habitat drivers for saproxylic beetle diversity in temperate deciduous forests. *Biodiversity and Conservation, 22*, 2111–2130. https://doi.org/10.1007/s10531-013-0531-3

Brockerhoff, E. G., Jactel, H., Parrotta, J. A., & Ferraz, S. F. B. (2013). Role of eucalypt and other planted forests in biodiversity conservation and the provision of biodiversity-related ecosystem services. *Forest Ecology and Management, 301*, 43–50. https://doi.org/10.1016/j.foreco.2012.09.018

Bush, A., Sollmann, R., Wilting, A., Bohmann, K., Cole, B., Balzter, H., Martius, C., Zlinszky, A., Calvignac-Spencer, S., Cobbold, C. A., Dawson, T. P., Emerson, B. C., Ferrier, S., Gilbert, M. T. P., Herold, M., Jones, L., Leendertz, F. H., Matthews, L., Millington, J. D. A., … Yu, D. W. (2017). Connecting Earth observation to high-throughput biodiversity data. *Nature Ecology & Evolution*, *1*, 0176. https://doi.org/10.1038/s41559-017-0176

Cai, N. H., Li, G. Q., & Lu, Y C. (2006). Discussion on the approaching nature forestry management of *Pinus yunnanensis* pure forest. *Journal of North West Forestry University, 21*: 85-88+120.

Carroll, A.L., Taylor, S.W., Regniere, J., Safranyik, L. (2004). Effects of climate and climate change on the mountain pine beetle. In: Proceedings of the MountainPine Beetle Symposium on Challenges and Solutions, October 30–31, 2003, Kelowna, British Columbia, Canada. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC. *Information Report* BC-X-399, pp. 21–32.

Cao, S., Zhang, J., & Su, W. (2019). Difference in the net value of ecological services between natural and artificial forests in China. *Conservation Biology*, *33*, 1076–1083. https://doi.org/10.1111/cobi.13293

Cordier, T., Esling, P., Lejzerowicz, F., Visco, J., Ouadahi, A., Martins, C., Cedhagen, T., & Pawlowski, J. (2017). Predicting the Ecological Quality Status of Marine Environments from eDNA Metabarcoding Data Using Supervised Machine Learning. Environmental Science and Technology, 51, 9118–9126. https://doi.org/10.1021/acs.est.7b01518

Cours, J., Larrieu, L., Lopez-Vaamonde, C., Müller, J., Parmain, G., Thorn, S., & Bouget, C. (2021). Contrasting responses of habitat conditions and insect biodiversity to pest- or climate-in. Forest Ecology and Management, 482, 118811. https://doi.org/10.1016/j.foreco.2020.118811

Cullingham, C. I., Cooke, J. E. K., Dang, S., Davis, C. S., Cooke, B. J., & Coltman, D. W. (2011). Mountain pine beetle host-range expansion threatens the boreal forest. Molecular Ecology, 20, 2157–2171. https://doi.org/10.1111/j.1365-294X.2011.05086.x

Delang, C. O., & Yuan, Z. (2015). China's grain for green program. *Switzerland: Springer International Publishing.*

Deng, X. Q., Huang, B. L., Wen, Q.Z., Hua, C.L., & Tao, J. (2013). A research on the distribution of *Pinus yunnanensis* forest in Yunnan Province. *Journal of Yunnan University*, *35*: 843-848. https://doi.org/10.7540/j.yun.20130114

Deng, X. Q., Huang, B. L., Wen, Q. Z., Hua, C. L., Tao, J., & Zhang, J. H. (2014). Dynamic of *Pinus yunnanensis* forest resources in Yunnan. *Journal of natural resources*, *29*: 1411-1419. https://doi.org/10.11849/zrzyxb.2014.08.013

Doerfler, I., Gossner, M. M., Müller, J., Seibold, S., & Weisser, W. W. (2018). Deadwood enrichment combining integrative and segregative conservation elements enhances biodiversity of multiple taxa in managed forests. *Biological Conservation, 228*, 70–78. https://doi.org/10.1016/j.biocon.2018.10.013

Edwards, D. P., Magrach, A., Woodcock, P., Ji, Y., Lim, N. T. L., Edwards, F. A., Larsen, T. H., Hsu, W. W., Benedick, S., Khen, C. V., Chung, A. Y. C., Reynolds, G., Fisher, B., Laurance, W. F., Wilcove, D. S., Hamer, K. C., & Yu, D. W. (2014). Selective-logging and oil palm: Multitaxon impacts, biodiversity indicators, and trade-offs for conservation planning. *Ecological Applications*, *24*, 2029–2049. https://doi.org/10.1890/14-0010.1

Elbrecht, V., Peinert, B., & Leese, F. (2017). Sorting things out: Assessing effects of unequal specimen biomass on DNA metabarcoding. *Ecology and Evolution*, *7*, 6918–6926. https://doi.org/10.1002/ece3.3192

Erbilgin, N., Cale, J. A., Lusebrink, I., Najar, A., Klutsch, J. G., Sherwood, P., Bonello, P. E., & Evenden, M. L. (2017). Water-deficit and fungal infection can differentially affect the production of different classes of defense compounds in two host pines of mountain pine beetle. *Tree Physiology*, *37*, 338–350. https://doi.org/10.1093/treephys/tpw105

Esper, J., Büntgen, U., Frank, D. C., Nievergelt, D., & Liebhold, A. (2007). 1200 years of regular outbreaks in alpine insects. *Proceedings of the Royal Society B: Biological Sciences*, *274*, 671–679. https://doi.org/10.1098/rspb.2006.0191

Felipe-Lucia, M. R., Soliveres, S., Penone, C., Manning, P., van der Plas, F., Boch, S., Prati, D., Ammer, C., Schall, P., Gossner, M. M., Bauhus, J., Buscot, F., Blaser, S., Blüthgen, N., de Frutos, A., Ehbrecht, M., Frank, K., Goldmann, K., Hänsel, F., … Allan, E. (2018). Multiple forest attributes underpin the supply of multiple ecosystem services. *Nature Communications*, *9*, 4839. https://doi.org/10.1038/s41467-018-07082-4

599 Ferrier, S., Manion, G., Elith, J., & Richardson, K. (2007). Using generalized dissimilarity modelling to analyse and predict
600 patterns of beta diversity in regional biodiversity assessment. *Diversity and Distributions*, *13*, 252–264.
601 https://doi.org/10.1111/j.1472-4642.2007.00341.x
602 Franc, N., Götmark, F., Økland, B., Nordén, B., & Paltto, H. (2007). Factors and scales potentially important for saproxylic
603 beetles in temperate mixed oak forest. *Biological Conservation, 135*, 86–98. https://doi.org/10.1016/j.biocon.2006.09.021
604 Frøslev, T. G., Kjøller, R., Bruun, H. H., Ejrnæs, R., Brunbjerg, A. K., Pietroni, C., & Hansen, A. J. (2017). Algorithm for
605 post-clustering curation of DNA amplicon data yields reliable biodiversity estimates. *Nature Communications*, *8*, 1188.
606 https://doi.org/10.1038/s41467-017-01312-x
607 Gan, L. R. (2015). A battle for the life of pine forests with bark beetles. *Yunnan forestry*, *36*(5): 31-33.
608 Gilbert, M. T. P., Moore, W., Melchior, L., & Worebey, M. (2007). DNA extraction from dry museum beetles without
609 conferring external morphological damage. *PLoS ONE*, *2*, e272. https://doi.org/10.1371/journal.pone.0000272
610 He, D. M., Zhang, F. Q. (2004). Conservation and control of bark beetles in Yunnan Province. *Forest Inventory and Planning*,
611 *5*, 251-253.
612 Hilmers, T., Friess, N., Bässler, C., Heurich, M., Brandl, R., Pretzsch, H., Seidl, R., & Müller, J. (2018). Biodiversity along
613 temperate forest succession. *Journal of Applied Ecology*, *55*, 2756–2766. https://doi.org/10.1111/1365-2664.13238
614 Hlásny, T., Zajíčková, L., Turčáni, M., Holuša, J., & Sitková, Z. (2011). Geographical variability of spruce bark beetle
615 development under climate change in the Czech Republic. *Journal of Forest Science*, *57*, 242–249.
616 https://doi.org/10.17221/104/2010-jfs
617 Hsieh, T. C., & Chao, A. (2017). Rarefaction and extrapolation: Making fair comparison of abundance-sensitive phylogenetic
618 diversity among multiple assemblages. *Systematic Biology*, *66*, 100–111. https://doi.org/10.1093/sysbio/syw073
619 Hsieh, T. C., Ma, K. H., & Chao, A. (2016). iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill
620 numbers). *Methods in Ecology and Evolution*, *7*, 1451–1456. https://doi.org/10.1111/2041-210X.12613
621 Hua, F., Wang, L., Fisher, B., Zheng, X., Wang, X., Yu, D. W., Tang, Y., Zhu, J., & Wilcove, D. S. (2018). Tree plantations
622 displacing native forests: The nature and drivers of apparent forest recovery on former croplands in Southwestern China
623 from 2000 to 2015. *Biological Conservation*, *222*, 113–124. https://doi.org/10.1016/j.biocon.2018.03.034
624 Hua, F., Wang, X., Zheng, X., Fisher, B., Wang, L., Zhu, J., Tang, Y., Yu, D. W., & Wilcove, D. S. (2016). Opportunities for
625 biodiversity gains under the world's largest reforestation programme. *Nature Communications*, *7*, 1–11.
626 https://doi.org/10.1038/ncomms12717
627 Hui, C., & McGeoch, M. A. (2014). Zeta diversity as a concept and metric that unifies incidence-based biodiversity patterns.
628 *American Naturalist*, *184*, 684–694. https://doi.org/10.1086/678125
629 Hui, F. K. C. (2016). boral – Bayesian Ordination and Regression Analysis of Multivariate Abundance Data in r. *Methods in*
630 *Ecology and Evolution*, *7*, 744–750. https://doi.org/10.1111/2041-210X.12514

631 Ji, M., Xie-qiong, D., Hong-ping, L., Li-shai, L., Hong, X., Xiao-peng, Y., Haoran, L. & Sang-zi, Z. (2007) Preliminary study
632 on remote sensing detection of Yunnan pine forest damaged by *Tomicus piniperda*. *Journal of West China Forestry*
633 *Science, 36*, 87–90.
634 Ji, Y., Ashton, L., Pedley, S. M., Edwards, D. P., Tang, Y., Nakamura, A., Kitching, R., Dolman, P. M., Woodcock, P.,
635 Edwards, F. A., Larsen, T. H., Hsu, W. W., Benedick, S., Hamer, K. C., Wilcove, D. S., Bruce, C., Wang, X., Levi, T.,
636 Lott, M., … Yu, D. W. (2013). Reliable, verifiable and efficient monitoring of biodiversity via metabarcoding. *Ecology*
637 *Letters*, *16*, 1245–1257. https://doi.org/10.1111/ele.12162
638 Ji, Y., Baker, C. C., Li, Y., Popescu, V., Wang, Z., Wang, J., Wang, L., Wu, C., Hua, C., Yang, Z., Yang, C., Xu, C. C., Wen,
639 Q., Pierce, N., & Yu, D. (2020). Large-scale Quantification of Vertebrate Biodiversity in Ailaoshan Nature Reserve from
640 Leech iDNA. *bioRχiv.* https://doi.org/10.1101/2020.02.10.941336
641 Joshi, N. A., & Fass, J. N. (2011). Sickle: A sliding-window, adaptive, quality-based trimming tool for FastQ files (Version
642 1.33) [Software]. Available at https://github.com/najoshi/sickle
643 Kichas, N. E., Hood, S. M., Pederson, G. T., Everett, R. G., & McWethy, D. B. (2020). Whitebark pine (*Pinus albicaulis*)
644 growth and defense in response to mountain pine beetle outbreaks. *Forest Ecology and Management*, *457*, 117736.
645 https://doi.org/10.1016/j.foreco.2019.117736
646 Kirkendall, L., Faccoli, M., & Ye, H. (2008). Description of the Yunnan shoot borer, *Tomicus yunnanensis* Kirkendall &
647 Faccoli sp. n. (Curculionidae, Scolytinae), an unusually aggressive pine shoot beetle from southern China, with a key to
648 the species of *Tomicus*. *Zootaxa*, *1819*, 25–39. https://doi.org/10.5281/zenodo.182961
649 Latombe, G., Hui, C., & McGeoch, M. A. (2017). Multi-site generalised dissimilarity modelling: using zeta diversity to
650 differentiate drivers of turnover in rare and widespread species. *Methods in Ecology and Evolution*, *8*, 431–442.
651 https://doi.org/10.1111/2041-210X.12756
652 Latombe, G., Roura-Pascual, N., & Hui, C. (2019). Similar compositional turnover but distinct insular environmental and
653 geographical drivers of native and exotic ants in two oceans. *Journal of Biogeography*, *46*, 2299–2310.
654 https://doi.org/10.1111/jbi.13671
655 Lejzerowicz, F., Esling, P., Pillet, L., Wilding, T. A., Black, K. D., & Pawlowski, J. (2015). High-throughput sequencing and
656 morphology perform equally well for benthic monitoring of marine ecosystems. *Scientific Reports*, *5*, 13932.
657 https://doi.org/10.1038/srep13932
658 Leray, M., Ho, S. L., Lin, I. J., & Machida, R. J. (2018). MIDORI server: a webserver for taxonomic assignment of unknown
659 metazoan mitochondrial-encoded sequences using a curated database. *Bioinformatics*, *34*, 3753–3754.
660 https://doi.org/10.1093/bioinformatics/bty454
661 Leray, M., Yang, J. Y., Meyer, C. P., Mills, S. C., Agudelo, N., Ranwez, V., Boehm, J. T., & Machida, R. J. (2013). A new
662 versatile primer set targeting a short fragment of the mitochondrial COI region for metabarcoding metazoan diversity:

663 Application for characterizing coral reef fish gut contents. *Frontiers in Zoology*, *10*, 1–14. https://doi.org/10.1186/1742-
664 9994-10-34
665 Lieutier, F., Ye, H., & Yart, A. (2003). Shoot damage by *Tomicus sp.* (Coleoptera: Scolytidae) and effect on *Pinus yunnanensis*
666 resistance to subsequent reproductive attacks in the stem. *Agricultural and Forest Entomology, 5*, 227–233.
667 https://doi.org/10.1046/j.1461-9563.2003.00182.x
668 Lindenmayer, D.B., Burton, P.J., Franklin, J.F., 2008. Salvage logging and its ecological consequences. *Island Press.*
669 Liu, J., Li, S., Ouyang, Z., Tam, C., & Chen, X. (2008). Ecological and socioeconomic effects of China's policies for ecosystem
670 services. *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 9477–9482.
671 https://doi.org/10.1073/pnas.0706436105
672 Lü, J., Hu, S. J., Ma, X. Y., Chen, J. M., Li, Q. Q., & Ye, H. (2014). Origin and expansion of the Yunnan shoot borer, *Tomicus*
673 *Yunnanensis* (Coleoptera: Scolytinae): A mixture of historical natural expansion and contemporary human-mediated
674 relocation. *PLoS ONE, 9*, e111940. https://doi.org/10.1371/journal.pone.0111940
675 Lu, N., & Zhang, X. (2000). Techniques of cleaning *Tomicus piniperda* damaged woods in *Pinus yunnanensis* stand. *Yunnan*
676 *forestry science and technology, 91*, 43-45. https://doi.org/10.16473/j.cnki.xblykx1972.2000.02.011
677 Ma, K., Shen, X., Grumbine, R. E., & Corlett, R. (2017). China's biodiversity conservation research in progress. *Biological*
678 *Conservation*, *210*, 1–2. https://doi.org/10.1016/j.biocon.2017.05.029
679 MacGregor-Fors, I., & Payton, M. E. (2013). Contrasting Diversity Values: Statistical Inferences Based on Overlapping
680 Confidence Intervals. *PLoS ONE*, *8*, 8–11. https://doi.org/10.1371/journal.pone.0056794
681 Masella, A. P., Bartram, A. K., Truszkowski, J. M., Brown, D. G., & Neufeld, J. D. (2012). PANDAseq: Paired-end assembler
682 for illumina sequences. *BMC Bioinformatics*, *13*, 31–37. https://doi.org/10.1186/1471-2105-13-31
683 McGeoch, M. A., Latombe, G., Andrew, N. R., Nakagawa, S., Nipperess, D. A., Roigé, M., Marzinelli, E. M., Campbell, A.
684 H., Vergés, A., Thomas, T., Steinberg, P. D., Selwood, K. E., Henriksen, M. V., & Hui, C. (2019). Measuring continuous
685 compositional change using decline and decay in zeta diversity. *Ecology*, *100*, e02832. https://doi.org/10.1002/ecy.2832
686 Mercier, C., Boyer, F., Bonin, A., & Coissac, E. (2013). SUMATRA and SUMACLUST: fast and exact comparison and
687 clustering of sequences. In Programs and Abstracts of the SeqBio 2013 workshop. Abstract.
688 https://doi.org/10.1109/RCIS.2013.6577673
689 Müller, J., Bußler, H., Goßner, M., Rettelbach, T., & Duelli, P. (2008). The European spruce bark beetle *Ips typographus* in a
690 national park: From pest to keystone species. *Biodiversity and Conservation*, *17*, 2979–3001.
691 https://doi.org/10.1007/s10531-008-9409-1
692 Müller, J., Noss, R. F., Bussler, H., & Brandl, R. (2010). Learning from a " benign neglect strategy" in a national park:
693 Response of saproxylic beetles to dead wood accumulation. *Biological Conservation*, *143*, 2559–2569.
694 https://doi.org/10.1016/j.biocon.2010.06.024

695 Murray, D. C., Coghlan, M. L., & Bunce, M. (2015). From benchtop to desktop: Important considerations when designing
696 amplicon sequencing workflows. *PLoS ONE*, *10*, 1–21. https://doi.org/10.1371/journal.pone.0124671
697 Nielsen, M., Gilbert, M. T. P., Pape, T., & Bohmann, K. (2019). A simplified DNA extraction protocol for unsorted bulk
698 arthropod samples that maintains exoskeletal integrity. *Environmental DNA*, *1*, 144–154. https://doi.org/10.1002/edn3.16
699 Nikolenko, S. I., Korobeynikov, A. I., & Alekseyev, M. A. (2013). BayesHammer: Bayesian clustering for error correction in
700 single-cell sequencing. *BMC Genomics*, *14*, 1–11. https://doi.org/10.1186/1471-2164-14-S1-S7
701 Paletto, A., & Tosi, V. (2009). Forest canopy cover and canopy closure: Comparison of assessment techniques. *European*
702 *Journal of Forest Research, 128*, 265–272. https://doi.org/10.1007/s10342-009-0262-x
703 Pawlowski, J., Esling, P., Lejzerowicz, F., Cordier, T., Visco, J. A., Martins, C. I. M., Kvalvik, A., Staven, K., & Cedhagen,
704 T. (2016). Benthic monitoring of salmon farms in Norway using foraminiferal metabarcoding. *Aquaculture Environment*
705 *Interactions*, *8*, 371–386. https://doi.org/10.3354/AEI00182
706 Piper, A. M., Batovska, J., Cogan, N. O. I., Weiss, J., Cunningham, J. P., Rodoni, B. C., & Blacket, M. J. (2019). Prospects
707 and challenges of implementing DNA metabarcoding for high-throughput insect surveillance. *GigaScience*, *8*, 1–22.
708 https://doi.org/10.1093/gigascience/giz092
709 Raffa, K. F., & Berryman, A. A. (1983). The Role of Host Plant Resistance in the Colonization Behavior and Ecology of Bark
710 Beetles (Coleoptera: Scolytidae). *Ecological Monographs*, *53*, 27–49. https://doi.org/10.2307/1942586
711 Ratnasingham, S., & Hebert, P. D. N. (2007). The Barcode of Life Data System. *Molecular Ecology Notes*, *7*, 355–364.
712 https://doi.org/10.1111/j.1471-8286.2006.01678.x
713 Ren, G., Young, S. S., Wang, L., Wang, W., Long, Y., Wu, R., Li, J., Zhu, J., & Yu, D. W. (2015). Effectiveness of China's
714 National Forest Protection Program and nature reserves. *Conservation Biology*, *29*, 1368–1377.
715 https://doi.org/10.1111/cobi.12561
716 Robertson, C., Farmer, C. J. Q., Nelson, T. A., MacKenzie, I. K., Wulder, M. A., & White, J. C. (2009). Determination of the
717 compositional change (1999-2006) in the pine forests of British Columbia due to mountain pine beetle infestation.
718 *Environmental Monitoring and Assessment*, *158*, 593–608. https://doi.org/10.1007/s10661-008-0607-9
719 Rognes, T., Flouri, T., Nichols, B., Quince, C., & Mahé, F. (2016). VSEARCH: A versatile open source tool for metagenomics.
720 *PeerJ*, *2016*, 1–22. https://doi.org/10.7717/peerj.2584
721 Rost, J., Clavero, M., Brotons, L., & Pons, P. (2012). The effect of postfire salvage logging on bird communities in
722 Mediterranean pine forests: The benefits for declining species. *Journal of Applied Ecology*, 49, 644–651.
723 https://doi.org/10.1111/j.1365-2664.2012.02127.x
724 Sambaraju, K. R., Carroll, A. L., Zhu, J., Stahl, K., Moore, R. D., & Aukema, B. H. (2012). Climate change could alter the
725 distribution of mountain pine beetle outbreaks in western Canada. *Ecography*, *35*, 211–223.
726 https://doi.org/10.1111/j.1600-0587.2011.06847.x

727 Schall, P., Gossner, M. M., Heinrichs, S., Fischer, M., Boch, S., Prati, D., Jung, K., Baumgartner, V., Blaser, S., Böhm, S.,
728 Buscot, F., Daniel, R., Goldmann, K., Kaiser, K., Kahl, T., Lange, M., Müller, J., Overmann, J., Renner, S. C., … Ammer,
729 C. (2018). The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in
730 European beech forests. *Journal of Applied Ecology*, *55*, 267–278. https://doi.org/10.1111/1365-2664.12950
731 Schirmer, M., Ijaz, U. Z., D'Amore, R., Hall, N., Sloan, W. T., & Quince, C. (2015). Insight into biases and sequencing errors
732 for amplicon sequencing with the Illumina MiSeq platform. *Nucleic Acids Research*, *43*, e37.
733 https://doi.org/10.1093/nar/gku1341
734 Schnell, I. B., Bohmann, K., & Gilbert, M. T. P. (2015). Tag jumps illuminated-reducing sequence-to-sample
735 misidentifications in metabarcoding studies. *Molecular Ecology Resources*, *15*, 1289–1303.
736 https://doi.org/10.1111/1755-0998.12402
737 Schubert, M., Lindgreen, S., & Orlando, L. (2016). AdapterRemoval v2: Rapid adapter trimming, identification, and read
738 merging. *BMC Research Notes*, *9*, 1–7. https://doi.org/10.1186/s13104-016-1900-2
739 Seibold, S., Bässler, C., Baldrian, P., Reinhard, L., Thorn, S., Ulyshen, M. D., Weiß, I., & Müller, J. (2016a). Dead-wood
740 addition promotes non-saproxylic epigeal arthropods but effects are mediated by canopy openness. *Biological*
741 *Conservation*, *204*, 181–188. https://doi.org/10.1016/j.biocon.2016.09.031
742 Seibold, S., Bässler, C., Brandl, R., Büche, B., Szallies, A., Thorn, S., Ulyshen, M. D., & Müller, J. (2016b). Microclimate
743 and habitat heterogeneity as the major drivers of beetle diversity in dead wood. *Journal of Applied Ecology*, *53*, 934–943.
744 https://doi.org/10.1111/1365-2664.12607
745 Seibold, S., Gossner, M. M., Simons, N. K., Blüthgen, N., Müller, J., Ambarlı, D., Ammer, C., Bauhus, J., Fischer, M., Habel,
746 J. C., Linsenmair, K. E., Nauss, T., Penone, C., Prati, D., Schall, P., Schulze, E. D., Vogt, J., Wöllauer, S., & Weisser, W.
747 W. (2019). Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature*, *574*, 671-+.
748 https://doi.org/10.1038/s41586-019-1684-3
749 Seibold, S., Hagge, J., Müller, J., Gruppe, A., Brandl, R., Bässler, C., & Thorn, S. (2018). Experiments with dead wood reveal
750 the importance of dead branches in the canopy for saproxylic beetle conservation. *Forest Ecology and Management*, *409*,
751 564–570. https://doi.org/10.1016/j.foreco.2017.11.052
752 Seidl, R., Donato, D. C., Raffa, K. F., & Turner, M. G. (2016). Spatial variability in tree regeneration after wildfire delays and
753 dampens future bark beetle outbreaks. *Proceedings of the National Academy of Sciences of the United States of America*,
754 *113*, 13075–13080. https://doi.org/10.1073/pnas.1615263113
755 Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi,
756 J., Lexer, M. J., Trotsiuk, V., Mairota, P., Svoboda, M., Fabrika, M., Nagel, T. A., & Reyer, C. P. O. (2017). Forest
757 disturbances under climate change. *Nature Climate Change*, *7*, 395–402. https://doi.org/10.1038/nclimate3303
758 SFA (State Forestry Administration). (2006, August). Standard of forset pests occurrence and disaster, LY/T 1681-2006.
759 SFA (State Forestry Administration). (2016, June). National forest management plan 2016-2050.

760 Stadelmann, G., Bugmann, H., Meier, F., Wermelinger, B., & Bigler, C. (2013). Effects of salvage logging and sanitation
761 felling on bark beetle (*Ips typographus* L.) infestations. *Forest Ecology and Management, 305*, 273–281.
762 https://doi.org/10.1016/j.foreco.2013.06.003
763 Swanson, M. E., Franklin, J. F., Beschta, R. L., Crisafulli, C. M., DellaSala, D. A., Hutto, R. L., Lindenmayer, D. B., &
764 Swanson, F. J. (2011). The forgotten stage of forest succession: Early-successional ecosystems on forest sites. *Frontiers*
765 *in Ecology and the Environment, 9*, 117–125. https://doi.org/10.1890/090157
766 Thom, D., Rammer, W., & Seidl, R. (2017). The impact of future forest dynamics on climate: interactive effects of changing
767 vegetation and disturbance regimes. *Ecological Monographs*, *87*, 665–684. https://doi.org/10.1002/ecm.1272
768 Thom, D., & Seidl, R. (2016). Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal
769 forests. *Biological Reviews of the Cambridge Philosophical Society*, *91*, 760–781. https://doi.org/10.1111/brv.12193
770 Thorn, S., Bässler, C., Brandl, R., Burton, P. J., Cahall, R., Campbell, J. L., Castro, J., Choi, C. Y., Cobb, T., Donato, D. C.,
771 Durska, E., Fontaine, J. B., Gauthier, S., Hebert, C., Hothorn, T., Hutto, R. L., Lee, E. J., Leverkus, A. B., Lindenmayer,
772 D. B., … Müller, J. (2018). Impacts of salvage logging on biodiversity: A meta-analysis. *Journal of Applied Ecology*, *55*,
773 279–289. https://doi.org/10.1111/1365-2664.12945
774 Thorn, S., Chao, A., Bernhardt-Römermann, M., Chen, Y. H., Georgiev, K. B., Heibl, C., Müller, J., Schäfer, H., & Bässler,
775 C. (2020). Rare species, functional groups, and evolutionary lineages drive successional trajectories in disturbed forests.
776 *Ecology*, *101*, e02949. https://doi.org/10.1002/ecy.2949
777 Thorn, S., Müller, J., & Leverkus, A. B. (2019). Preventing European forest diebacks. *Science*, *365*, 1388.
778 https://doi.org/10.1126/science.aaz3476
779 Trzcinski, M. K., & Reid, M. L. (2008). Effect of management on the spatial spread of mountain pine beetle (*Dendroctonus*
780 *ponderosae*) in Banff National Park. *Forest Ecology and Management*, *256*, 1418–1426.
781 https://doi.org/10.1016/j.foreco.2008.07.003
782 Viña, A., McConnell, W. J., Yang, H., Xu, Z., & Liu, J. (2016). Effects of conservation policy on China's forest recovery.
783 *Science Advances*, *2*, e1500965. https://doi.org/10.1126/sciadv.1500965
784 Wang, H., Zhao, Y., Pu, R., & Zhang, Z. (2015). Mapping Robinia pseudoacacia forest health conditions by using combined
785 spectral, spatial, and textural information extracted from IKONOS imagery and random forest classifier. *Remote Sensing,*
786 *7*, 9020–9044. https://doi.org/10.3390/rs70709020
787 Wang, J., Zhang, Z., Kong, X., Wang, H., & Zhang, S. (2015). Intraspecific and interspecific attraction of three *Tomicus* beetle
788 species during the shoot-feeding phase. *Bulletin of Entomological Research, 105*, 225–233.
789 https://doi.org/10.1017/S0007485315000048
790 Wang, Q., Garrity, G. M., Tiedje, J. M., & Cole, J. R. (2007). Naïve Bayesian classifier for rapid assignment of rRNA
791 sequences into the new bacterial taxonomy. *Applied and Environmental Microbiology*, 73, 5261–5267.
792 https://doi.org/10.1128/AEM.00062-07

793 Wang, X., Hua, F., Wang, L., Wilcove, D. S., & Yu, D. W. (2019). The biodiversity benefit of native forests and mixed-species
794 plantations over monoculture plantations. *Diversity and Distributions*, *25*, 1721–1735. https://doi.org/10.1111/ddi.12972
795 Wang, Y., Naumann, U., Wright, S. T., & Warton, D. I. (2012). Mvabund- an R package for model-based analysis of
796 multivariate abundance data. *Methods in Ecology and Evolution*, *3*, 471–474. https://doi.org/10.1111/j.2041-
797 210X.2012.00190.x
798 Xinhua News Agency (2019, July 23). The general office of the CPC central committee issued the Natural forest protection
799 and restoration system program. Retrieved from http://www.gov.cn/zhengce/2019-07/23/content_5413850.htm
800 Xu, J., Yin, R., Li, Z., & Liu, C. (2006). China's ecological rehabilitation: Unprecedented efforts, dramatic impacts, and
801 requisite policies. *Ecological Economics*, *57*, 595–607. https://doi.org/10.1016/j.ecolecon.2005.05.008
802 Yin, R., Yin, G., & Li, L. (2009). Assessing China's ecological restoration programs: What's been done and what remains to
803 be done? *Environmental Management*, *45*, 442–453. https://doi.org/10.1007/978-90-481-2655-2_2
804 Yang, C., Wang, X., Miller, J. A., De Blécourt, M., Ji, Y., Yang, C., Harrison, R. D., & Yu, D. W. (2014). Using metabarcoding
805 to ask if easily collected soil and leaf-litter samples can be used as a general biodiversity indicator. *Ecological Indicators*,
806 *46*, 379–389. https://doi.org/10.1016/j.ecolind.2014.06.028
807 Yang, C., Bohmann, K., Wang, X., Cai, W., Wales, N., Ding, Z., Gopalakrishnan, S., & Yu, D. (2020). Biodiversity Soup II:
808 A bulk-sample metabarcoding pipeline emphasizing error reduction. *bioRXiv.* https://doi.org/10.1101/2020.07.07.187666
809 Yang, C., Schaefer, D. A., Liu, W., Popescu, V. D., Yang, C., Wang, X., Wu, C., & Yu, D. W. (2016). Higher fungal diversity
810 is correlated with lower CO 2 emissions from dead wood in a natural forest. *Scientific Reports*, *6*, 1–10.
811 https://doi.org/10.1038/srep31066
812 YNFA (Yunnan Forestry Administration). (2018, August) Yunnan forest management plan 2017-2050.
813 Yu, D. W., Ji, Y., Emerson, B. C., Wang, X., Ye, C., Yang, C., & Ding, Z. (2012). Biodiversity soup: Metabarcoding of
814 arthropods for rapid biodiversity assessment and biomonitoring. *Methods in Ecology and Evolution*, *3*, 613–623.
815 https://doi.org/10.1111/j.2041-210X.2012.00198.x
816 Yue, F., Yang, B., Feng, D., & Zhou, X. W. (2011). A study on the effect of resistance of *Pinus yunnanensis* mixed forest
817 against *Tomicus yunnanensis*. *Jiangsu agricultural sciences, 39*, 159-161. https://doi.org/10.15889/j.issn.1002-
818 1302.2011.04.100
819 Zhang, K., Lin, S., Ji, Y., Yang, C., Wang, X., Yang, C., Wang, H., Jiang, H., Harrison, R. D., & Yu, D. W. (2016). Plant
820 diversity accurately predicts insect diversity in two tropical landscapes. *Molecular Ecology*, *25*, 4407–4419.
821 https://doi.org/10.1111/mec.13770
822 Zhao, T., & Långström, B. (2012). Performance of *Tomicus yunnanensis* and *Tomicus minor* (Col., Scolytidae) on *Pinus*
823 *yunnanensis* and *Pinus armandii* in Yunnan Southwestern China. *Psyche A Journal of Entomology, 6*.
824 https://doi.org/10.1155/2012/363767

825 Zepeda-Mendoza, M. L., Bohmann, K., Carmona Baez, A., & Gilbert, M. T. P. (2016). DAMe: A toolkit for the initial
826 processing of datasets with PCR replicates of double-tagged amplicons for DNA metabarcoding analyses. *BMC Research*
827 *Notes*, *9*, 1–13. https://doi.org/10.1186/s13104-016-2064-9
828 Zhai, D. L., Xu, J. C., Dai, Z. C., Cannon, C. H., & Grumbine, R. E. (2014). Increasing tree cover while losing diverse natural
829 forests in tropical Hainan, China. *Regional Environmental Change*, *14*, 611–621. https://doi.org/10.1007/s10113-013-
830 0512-9
831 Zinger, L., Taberlet, P., Schimann, H., Bonin, A., Boyer, F., De Barba, M., Gaucher, P., Gielly, L., Giguet-Covex, C., Iribar,
832 A., Réjou-Méchain, M., Rayé, G., Rioux, D., Schilling, V., Tymen, B., Viers, J., Zouiten, C., Thuiller, W., Coissac, E.,
833 & Chave, J. (2019). Body size determines soil community assembly in a tropical forest. *Molecular Ecology, 28*, 528–543.
834 https://doi.org/10.1111/mec.1491

Title: The ecological impact of pest-induced tree dieback on insect biodiversity in Yunnan pine plantations, China: **Supplementary Information**

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Table S1. Sampling sites and elevations.

Site	Elevation (m)	Longitude	Latitude
lah1	2719	100° 3'13.08"E	26°52'25.63"N
lah2	2682	100° 3'19.70"E	26°52'7.15"N
lal1	2578	100° 5'46.44"E	26°49'22.79"N
lal2	2640	100° 5'15.78"E	26°50'13.90"N
lam1	2769	100° 2'48.38"E	26°51'44.03"N
lam2	2673	100° 2'39.97"E	26°51'19.45"N
luh1	2792	100°45'22.37"E	27°44'4.44"N
luh2	2758	100°44'39.00"E	27°44'15.41"N
lul1	3052	100°48'22.72"E	27°39'23.82"N
lul2	2980	100°47'42.07"E	27°39'22.08"N
lum1	2770	100°44'36.66"E	27°44'16.89"N
lum2	2761	100°46'3.87"E	27°44'42.32"N
puh1	2196	100°55'2.25"E	25°19'1.63"N
puh2	2318	100°54'18.51"E	25°18'20.51"N
pul1	2101	100°53'13.66"E	25°22'59.68"N
pul2	2192	100°52'45.36"E	25°22'6.92"N
pum1	2132	100°54'7.89"E	25°21'14.56"N
pum2	2173	100°52'21.61"E	25°19'43.28"N
toh1	2019	102°45'2.58"E	24° 6'14.94"N
toh2	2017	102°45'7.29"E	24° 6'23.23"N
tol1	1905	102°38'28.14"E	24° 8'14.78"N
tol2	1886	102°38'32.20"E	24° 8'9.39"N
tom1	2043	102°44'54.25"E	24° 6'4.46"N
tom2	2020	102°44'59.78"E	24° 6'8.84"N
yuh1	1808	102°34'24.84"E	24°18'36.22"N
yuh2	1800	102°34'16.76"E	24°18'26.81"N
yul1	1757	102°35'43.85"E	24°20'45.53"N
yul2	1768	102°35'47.46"E	24°20'35.40"N
yum1	1779	102°34'28.70"E	24°19'10.84"N
yum2	1805	102°34'37.47"E	24°18'46.23"N

S2. Phylogenetic tree construction for iNextPD

We used *RAxML* 8.0.0 (Stamatakis, 2014) to build a maximum-likelihood (ML) tree with an alignment of the OTU-representative sequences (used MAFFT alignment function in Geneious 11.0.3 with default parameters). The ML tree used a general time-reversible (GTR) model of nucleotide substitution and a gamma model of rate heterogeneity estimating the proportion of invariable sites (-m GTRGAMMAI). The algorithm used a rapid bootstrap analysis and searched for the best-scoring ML tree (-f a), with -N 1,000 times bootstrap and -p 12,345 as the parsimony random seed. Two OTU sequences were removed because produced very long branches in the ML tree.

Figure S3. Histogram of sample read depth, and the relationship between read depth and species richness. There is no correlation between read depth and species richness after removal of eight samples that had < 25,000 reads (Pearson, sample size = 22, p = 0.68).

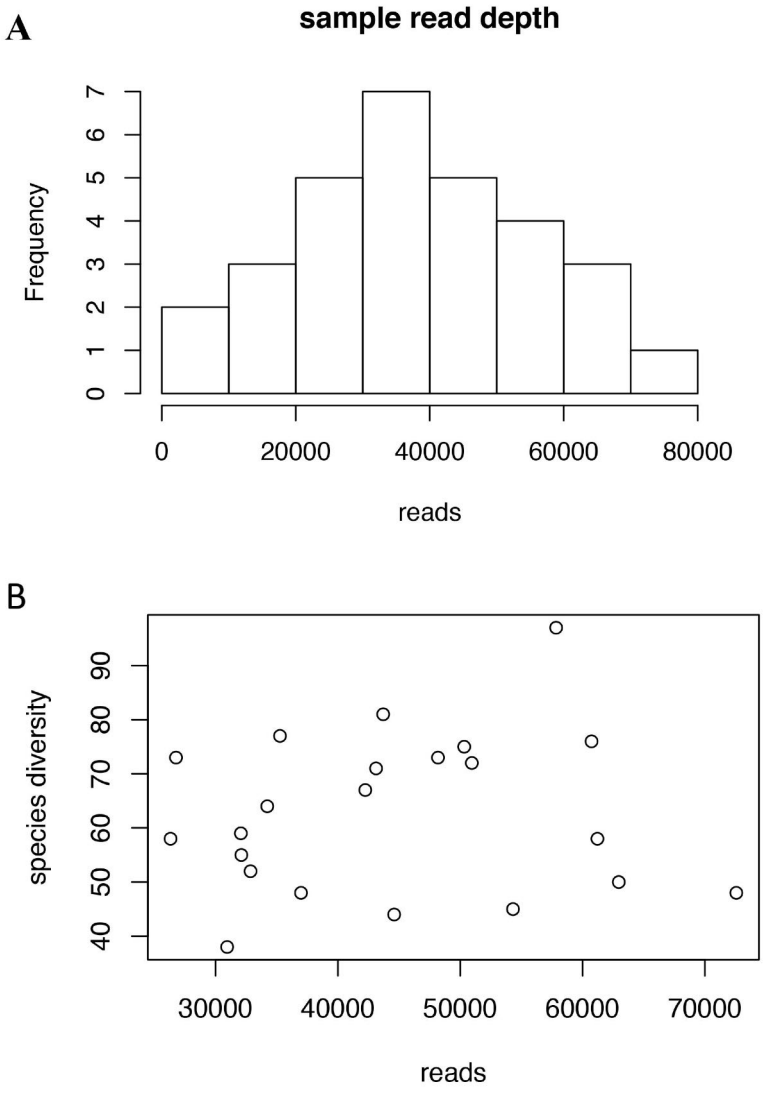

Figure S4. 'Boral' ordination of beta diversity by disturbance type after removal of eight low-read-depth samples. Color codes for outbreak severity as in Figure 1 (main text), and points represent samples.

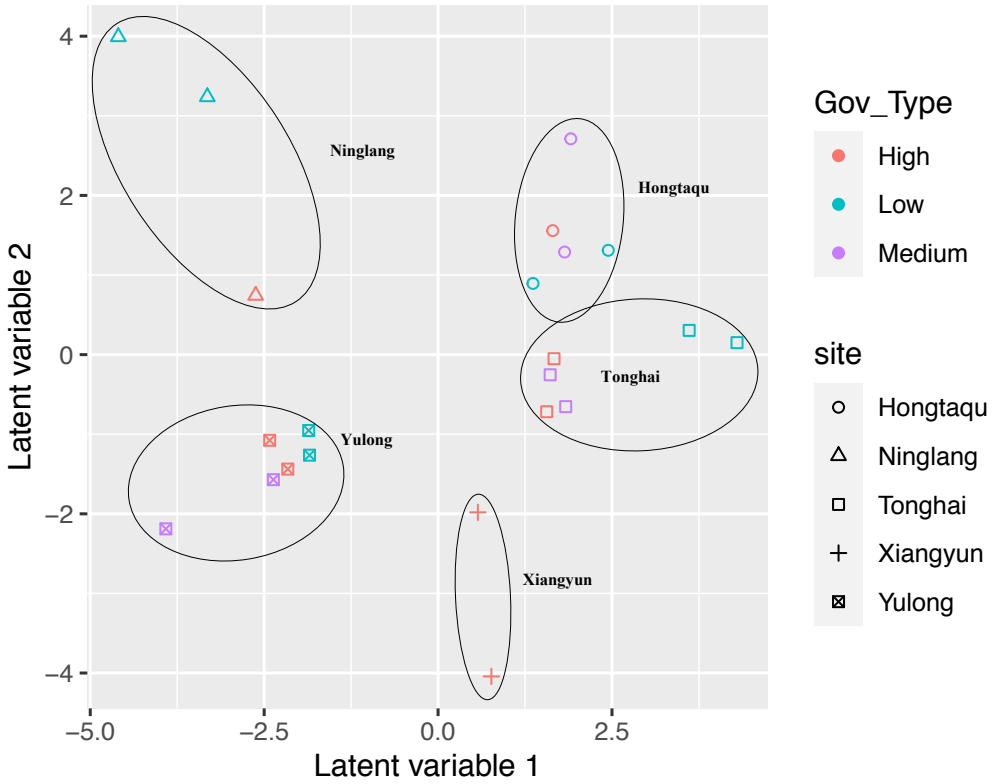

Figure S5. Residual plots of the Boral model fit in Fig. 2.

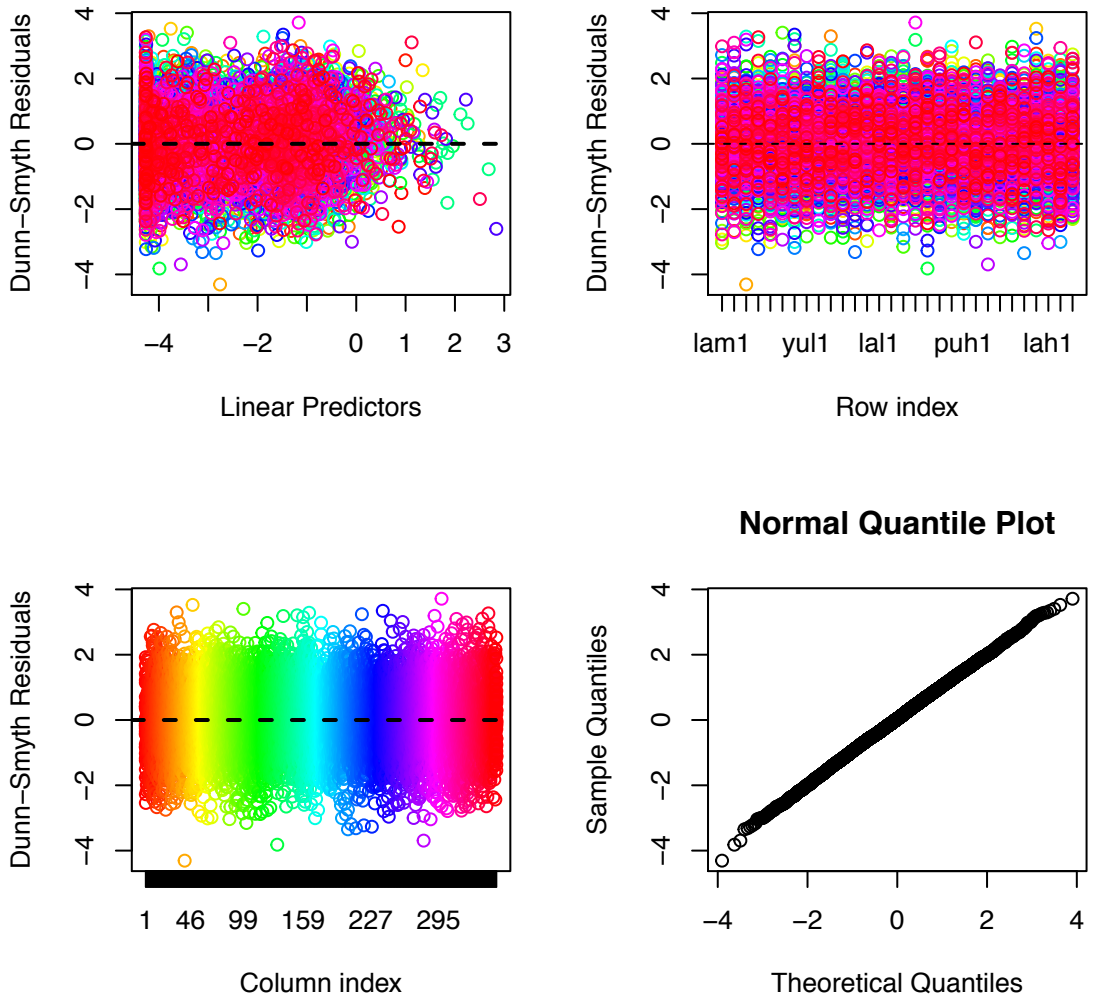

Figure S6. Multi-Site Generalised Dissimilarity Modelling (MS-GDM) analysis after removal of eight low-read-depth samples. A. Contributions of five environmental covariates and distance to explaining zeta diversity and B. variation partitioning. Environmental covariates were rescaled between 0 and 1. The vertical axes indicate the relative contributions of each environmental variable, at each order. Geographic distance is most important at low zeta orders, canopy openness and then infestation rate become increasingly more important. Overall, with zeta order >4, environmental covariates explain more compositional change than does distance.

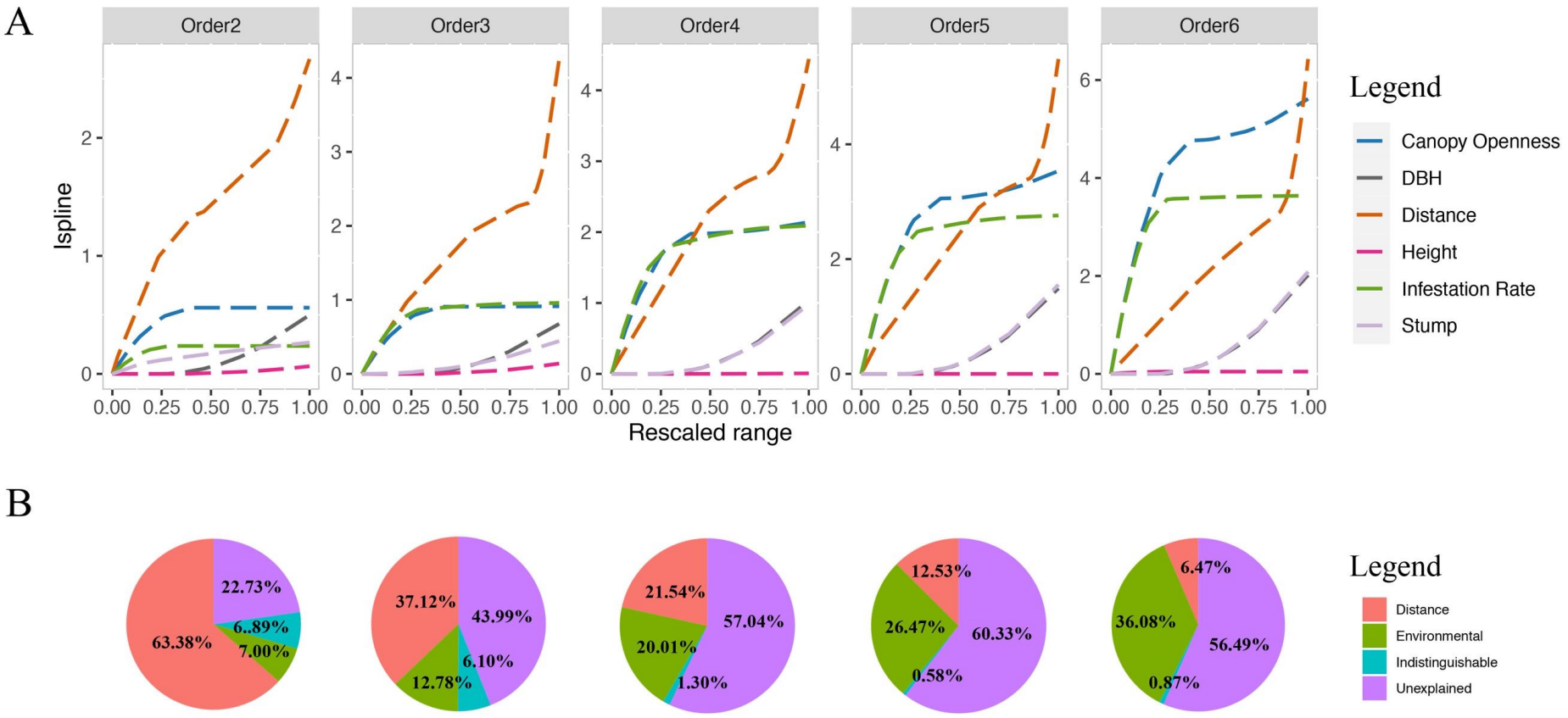

Figure S7. A. Multi-Site Generalized Dissimilarity Modeling (MS-GDM) with all six environmental covariates including elevation and B. variation partitioning. Canopy openness and infestation rate become relatively more important for explaining compositional change at zeta orders ≥4. Unlike the model without elevation (Figure 3), distance alone explains little variance at low zeta orders, while the category of indistinguishable (non-separable distance & environment) increases correspondingly, indicating that elevation and distance are correlated.

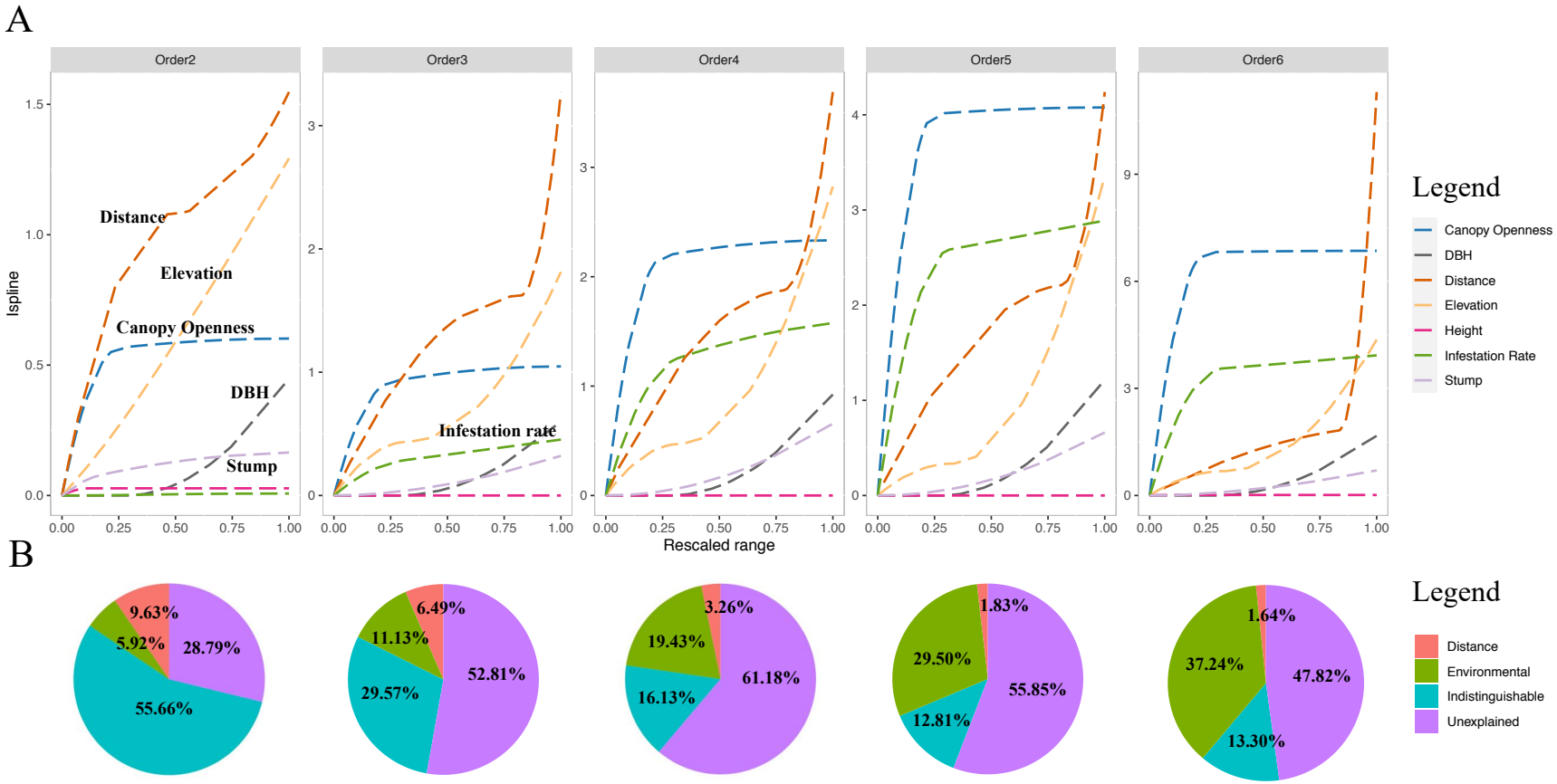

Figure S8. Histogram of infestation rates. Sites are categorized into 'low' (infestation rate ≤ 0.25, n = 14) and 'high' (>0.25, n = 16) infestation rate, used in Figs. 4 and 5.

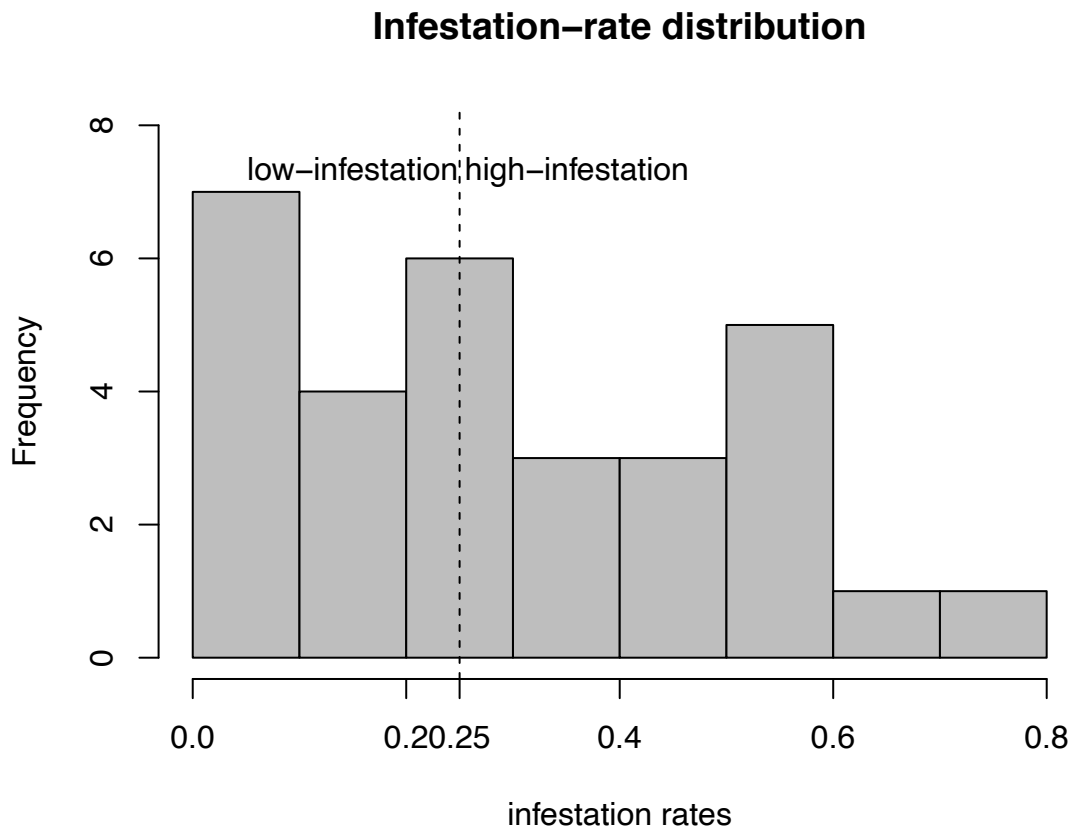

Figure S9. Comparison of zeta diversity decline (left) and retention rate (right) between low- and high-infestation forests after removal of eight low-read-depth samples. Zeta orders 1 to 7 are shown, as zeta diversity equals zero for orders >7. High-infestation sites are characterized by (left) a power-law decline and (right) share more common species, consistent with a niche-differentiated community. Low-infestation sites are characterized by (left) an exponential zeta decline and (right) share relatively fewer common species, consistent with a stochastic community-assembly process.

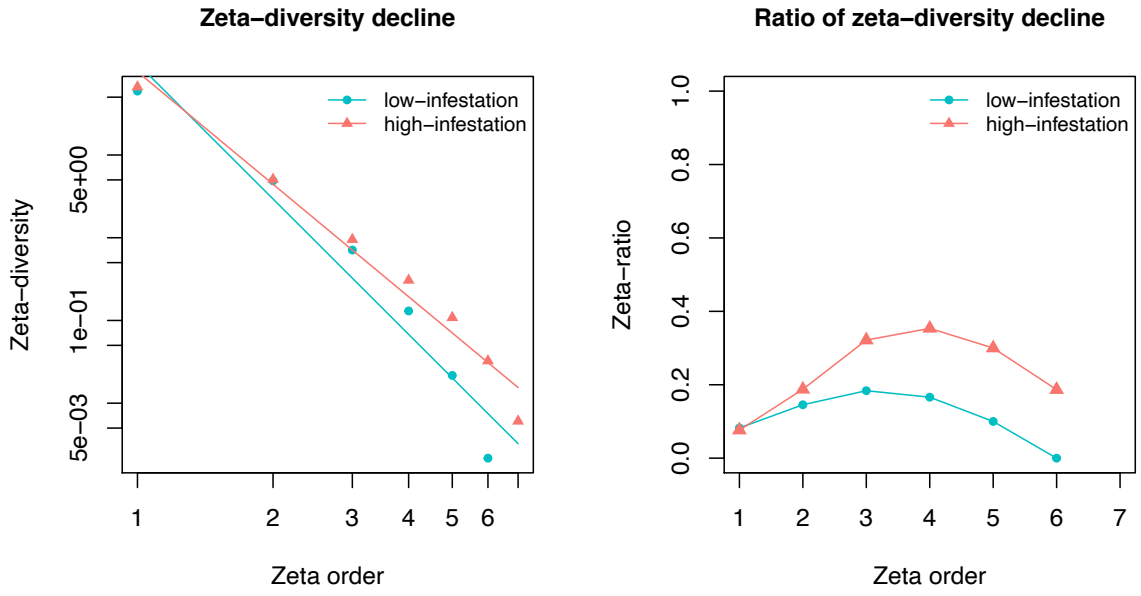

Figure S10. Alpha diversity analysis after removal of eight low-read-depth samples. A. iNEXT and B. iNextPD. Sample-size-based rarefaction (solid lines) and extrapolation (dashed lines) sampling curves for three measures of A. species diversity and B. phylogenetic diversity in low-infestation and high-infestation forests. Shaded areas represent 95% confidence intervals. Symbols indicate sample size per forest type. Overlapping confidence intervals indicate no evidence for difference between forest types. Sites are categorized into 'low' (infestation rate ≤ 0.25, n = 11) and 'high' (>0.25, n = 11) infestation.