1) Mosaic forest has higher species richness and higher Shannon richness than the monospecies plantations: JC, EC, and BB (marginal diff over BB)

2) Mosaic forest composition is more similar to Native forest than any of the monospecies plantations are to Native forest

3) The source of the beta diversity in this system is entirely turnover, which means that each of the monospecies plantations has its own set of species

**Title:** The biodiversity benefit of a diversity of managed forests

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**Abstract**

**Aim:** China’s Grain-for-Green Program (GFGP) is the largest reforestation program in the world and has been operating since 1999. However, because the GFGP has promoted the establishment of monoculture plantations over the preservation of natural forest, GFGP-funded forests support low levels of biodiversity. In a previous study (Hua et al. 2016, *Nat Comms* 7:12717), we showed that GFGP monocultures supported considerably lower bird and bee species richness than do native, natural forest and farmland. However, we also found that ‘mosaic GFGP forests, which are made up of 2-5 neighboring monoculture stands of different species, planted in checkboard fashion, could support nearly the same bird (but not bee) species richness as native, natural forest and farmland. Here, we use metabarcoding to test whether arthropod biodiversity, sampled with pan traps, also show higher levels of species richness in mosaic GFGP forests, both to generalize the previous finding and to provide a potential explanation for higher bird species richness.

**Location:** Sichuan province of China.

**Methods:** We used COI-amplicon sequencing of bulk samples of arthropods that were collected with pan traps (‘metabarcoding’) in monoculture, mosaic, and natural forest stands and in cropland.

**Results:** GFGP mosaic forest supports arthropod species richness and diversity at a level that is statistically indistinguishable from natural forest and significantly higher than found in monoculture stands of Japanese cedar, Eucalyptus, or bamboo forests, paralleling the results with birds. The mosaic-forest arthropod community is composed of subsets from the individual monocultures and also native forest, but the monocultures are not simply nested subsets of the mosaic forest; each monoculture also supports its own (small) arthropod community.

**Main conclusion:** Our new results show that the simple management intervention of promoting checkerboard arrangements of monocultures (‘mosaic forests’) boosts not only bird diversity but also the portion of arthropod biodiversity that is sampled by pan traps. These results strengthen our original GFGP-policy recommendations of (1) promoting the conservation and expansion of natural forest and (2) promoting mosaic-forest planting arrangements. Finally, the surprising observation that even monocultures support small but unique arthropod communities exemplifies Lindenmayer et al.’s insight that ‘management of diversity calls for diversity of management.’

**KEYWORDS:** Arthropod, biodiversity, China, forest management, Grain-for-Green Program, metabarcoding, reforestation

1 INTRODUCTION

China’s Grain-for-Green Program (GFGP) has been processed 19 years and still continuing. It is initiated in 1999 and aimed to maintain water and prevent soil erosion (Zhai, Xu, Dai, Cannon, & Grumbine, 2013; Delang & Yuan, 2015; Ren et al., 2014). Many researchers have done lots of studies about the basic ecosystem service like soil maintain (Deng, Shangguan, Li, 2012; Wang, Jiao, Rayburg, Wang, & Su, 2016; Wang, Peng, Zhao, Liu, & Chen, 2016; Yang et al., 2017), vegetation coverage (Zhou, Rompaey, & Wang, 2009) and carbon storage (Deng, Liu, & Shangguan, 2014) and so on. Recently, we did a research to reveal the impact of Grain-for-Green Program (GFGP) to biodiversity (Hua et al., 2016). In our previous study, we chose birds and bees as representative taxa to value biodiversity in different GFGP forest type, and mainly focus on monoculture forests and simply mixed plantation to see if there are different in biodiversity. The birds’ results show that simply mixed plantation has higher diversity than other three monospecies plantations (bamboo, Eucalyptus, Japanese cedar), but bees’ results did not show a positive effect of mixed forest. Thus, does it mean that lack of response by bees also indicate the general insect response to mixed forest? or other insect will get different results because bees are strongly dependent on floral plants which are found at a general low level in both the monoculture and mixed forests, while a wider range of insect species should be able to exploit a wider range of food and other resources (via direct consumption of plants and fungi, and via decomposition, parasitism, and predation of other animals, including other arthropods) and thus might be more likely to get more biodiversity information.

In order to test whether mixed forest might provide a biodiversity boost to insect diversity, we introduced an efficient technology – metabarcoding, which combined traditional DNA barcode with high-throughput sequencing technology to generate vast barcodes of mass samples in one sequencing run (Yu et al., 2012; Yang, Ji, Wang, Yang, & Yu, 2012; Baird & Hajibabaei, 2012; Bik et al., 2012; Cristescu, 2014). Bioinformatic pipelines have been developed to get operational taxonomy units (OTUs) and their taxonomic information (Yu et al., 2012; Fonseca et al., 2010; Hajibabaei, Shokralla, Zhou, Singer, & Baird, 2011; Zhou et al., 2013; Coissac, Riaz, & Puillandre, 2012; Balint, Schmidt, Sharma, Thines, & Schmitt, 2014; Yang et al., 2014). This method has been proved to be reliable, verifiable and efficient in biodiversity monitoring (Ji et al., 2013; Yang et al., 2014), and has been used in many ecology studies of fungi, botany and zoology (Hiiesalu et al., 2012; Thomsen et al., 2012; Ovaskainen et al., 2013; Gibson et al., 2014; Bik, 2014; Bik, Halanych, Sharma, & Thomas, 2012; Zhang et al., 2016; Leray & Knowlton, 2015; Yang et al., 2016). Another advantage of this method is we can just use environmental DNA (eDNA, DNA extracted from soil, leaf litter, water and feces et al.) and invertebrate DNA (iDNA) to get indirect information of those animals we concerned (Bohmann et al., 2014; Yang et al., 2014; Calvignac, Leendertz, Gilbert, & Schubert, 2013; Schnell et al., 2012; Thomsen et al., 2012; Jerde, Mahon, Chadderton, & Lodge, 2011; Thomsen & Willerslev, 2014; Yoccoz et al., 2012).

The purpose of this study is to interrogate the ‘rest of the biodiversity’ captured in the same sites analyzed by Hua et al. (2016) whether mixed forests are indeed more biodiverse than the individual component monoculture forests? Here we use metabarcoding to processed ‘other insect’ caught by the same pan traps that had been used to trap the bees, analyzed alpha diversity, beta diversity and phylogenetic diversity. We got some similar results to Hua et al. (2016), native forest performed best in all diversity indices and it is the ideal model as a target of reforestation; comparing different plantation type of GFGP: simply mixed forest and monospecies plantation, mosaic forest has significantly higher species richness, higher Shannon richness and higher phylogenetic diversity than other three monocultures (bamboo forest, eucalyptus forest and Japanese cedar forest); mosaic forest has more similar species composition to native forest than other three monocultures. In our study, beta diversity is dominated by turnover, which means each single monospecies plantation has its own species.

2 METHODS

2.1 Study location

The study region and sampling locations are the same as those in Hua et al. (2016), where further details can be found. In short, our study region was a 7,949 km2 area in south-central Sichuan province (Fig. MAP) spanning an elevation range of 315 – 1,715 m above sea level, historically forested and then heavily deforested starting in the 1950s. The GFGP established ~54,800 ha of forest between 1999 and 2014, dominated by the following four types: short-rotation (6-20 years) monocultures of (1) eucalyptus (EC), (2) bamboo (BB), and (3) Japanese cedar (JC), and compositionally simple, short-rotation (4) ‘mosaic’ forest (MF) consisting of two to ﬁve tree species (including the three monoculture plantations). Monoculture forests are created by households planting the same tree species in neighboring stands of median 0.4 ha size. Correspondingly, mosaic forests are created by households planting different species in neighboring stands, mostly resulting in a checkerboard structure. although about a quarter of mosaic forests do consist of individual-level mixtures. In Hua et al. (2016), we used the term ‘mixed’ forests, but we now use the term ‘mosaic’ forests, since we want to emphasize that this forest type is mostly neighboring but different monoculture stands.

The two other surveyed habitats were cropland (CL) and native forests (NF). Cropland mostly consists of low-intensity plantings of rice, corn, and vegetables and is the land type that has been most displaced by GFGP forest. Native forest is broadleaf, subtropical, evergreen forest that has been subject to selective logging and other forms of extraction, especially since the 1950s, but note that this region of China has been inhabited for millennia. Cropland is typically located on flatter land than are the forest plots, since GFGP reforestation targeted sloped land, and native forests are concentrated toward the southern end of the study region, near Emei Mountain. For sampling, we chose larger expanses (> 60 ha) of each of these six land-cover types (EC, BB, JC, MF, NF, CL).

2.2 Sampling design

Each land-cover type was represented by at least two locations set ≥15 km apart. All forest stands chosen were closed canopy. For each land-cover type, we sampled with at least ten one-ha quadrats within which we operated 40 fluorescent pan traps for 24 hrs (Bartholomew et al. 2005) (Fig. S\_PANTRAP). In total, 74 quadrats were sampled (BB: n = 10 quadrats, EC: 10, JC: 12, MF: 10, NF: 16, CL: 16). Quadrats were separated by ≥ 300 m if placed in the same forest stand. All individual samples were stored in 100% ethanol and stored at ambient temperature until shipment back to the Kunming Institute of Zoology, where they were stored in a -20 ℃ freezer before DNA extraction. The original reason for using pan traps was to trap bees, which we genotyped individually for analysis in Hua et al. (2016). Here we use metabarcoding to analyze the pan-trap bycatch.

2.2 Amplicon preparation

For each of the 74 quadrats, we first pooled all 40 pan traps into a single sample. In this part, 3 quadrats had very few individuals, and we pooled them into their nearest-neighbor quadrat (EC02 and EC03 were pooled with EC01, NF03 was pooled with NF02). Thus, we were left with 71 bulk samples in total. Storage ethanol was removed by air drying on single-use filter papers. Our samples were dominated by Diptera and Hymenoptera, as expected with pan traps. We equalized input template DNA across species by using one leg of every *individual* larger than a mosquito and the whole body if smaller (e.g. midges). This was to reduce the effect of large-biomass individuals outcompeting small-biomass individuals during PCR, which improves taxon detection (Elbrecht, Peinert, & Leese, 2017). DNA extraction followed the protocols of Qiagen DNeasy Blood & Tissue Kits (Hilden, Germany), followed by quantification via Nanodrop 2000 spectrophotometer (Thermo Fisher Scientific, Wilmington, DE).

We amplified a 319 bp fragment of COI using forward primer LCO1490 (5’- GGTCAACAAATCATAAAGATATTGG-3’) and reverse primer mlCOIintR (5’- GGNGGRTANANNGTYCANCCNGYNCC-3’) (Leray et al. 2013). All samples were carried out with two rounds of PCR. In the first round, both forward and reverse primers (12 ~ 17 bp) were tailed with the same tag (‘twin-tags’) to allow sample identification. Twin-tagging allows identification and subsequent removal of tag-jumping events (Schnell et al. 2015). In the second round PCR, we added Illumina adapters to the amplicons produced in the first PCR. A table of the primers with tags and the second-round PCR primers is in Supplementary Information. All PCRs were performed on a Mastercycler Pro (Eppendorf, Germany) in 20-µl reaction volumes, each containing 2 µl 10 x buffer (Mg2+ plus), 0.2 mM dNTPs, 0.4 µM of each primer, 1 µl DMSO, 0.4 µl BSA (bovine serum albumin) (TaKaRa Biotechnology (Dalian, China) Co. Ltd), 0.6 U exTaq DNA polymerase (TaKaRa Biotechnology), and approximately 60 ng genomic DNA. Both rounds of PCR started with an initial denaturation process at 94 ℃ for 4 mins, followed by 35 cycles of 94 ℃ for 45s, 45 ℃ for 45s, 72 ℃ for 90s, and finishing at 72 ℃ for 10 mins. PCR products were gel-purified with QIAquick PCR Purification Kit (Qiagen). In this part, one sample failed to amplify target gene. For the remaining 70 samples, we pooled purified PCR products into two libraries, then sequenced on the Illumina MiSeq platform (Reagent Kit v3 600 cycles, 300PE) at the Southwest Biodiversity Institute Regional Instrument Center.

2.3 Data analyses

The bioinformatic and R scripts (including parameter values) for the analyses below are provided in Supplementary Information and will also be archived in datadryad.org, along with the raw sequence data and metadata.

2.3.1 Bioinformatic processing

*Initial processing*. – We first removed remnant Illumina adapter sequences from the MiSeq output files with *AdapterRemoval* 2.2.0 (Schubert, Lindgreen, & Orlando, 2016), followed by Schirmer et al.’s (2015) recommended pipeline to filter, trim, denoise, and merge read pairs. Specifically, we trimmed low-quality ends using *sickle* 1.33 (Joshi & Fass, 2011), corrected sequence errors using the *BayesHammer* module in *SPAdes* 3.10.1 (Nikolenko, Korobeynikov, & Alekseyev, 2013), and merged reads using *PandaSeq* 2.11 (Masella, Bartram, Truszkowski, Brown, & Neufeld, 2012). In all cases, we used default parameters.

*Demultiplexing and Clustering*. – We then used *qiime* 1.9.1’s *split\_libraries.py* function (Caporaso et al., 2010) to demultiplex reads by samples, and we used *usearch* 9.2.64 (Edgar, 2010) to keep only reads between 300 and 330 bp, inclusive, since our target amplicon is 319 bp. We used *vsearch* v2.4.3 (Rognes, Flouri, Nichols, Quince, & Mahé, 2016) to carry out *de-novo* chimera removal and clustered the reads into 3,507 97% Operational Taxonomic Units (OTUs) using *CROP* 1.33 (Hao, Jiang, & Chen, 2011).

*OTU filtration and taxonomic assignment*. – From the resulting OTU table, we used the *lulu* 0.1.0 (Frøslev et al., 2017) to combine OTUs that are likely from the same species but which CROP failed to cluster. *lulu* infers (and combines) such ‘parent-daughter’ sets by first calculating pairwise similarities of all OTU representative sequences (here, using *vsearch*) to identify sets of high-similarity OTUs and then combining OTUs within such sets that show nested distributions across samples. For example, four OTUs might show high pairwise similarities, and within this set of four, one OTU contains the most reads and is observed in ten samples. This OTU is designated the parent, and daughter OTUs are inferred if they are only present in a subset of the parent OTU’s ten samples. We ended with 1,506 OTUs.

A common filtering step is to remove ‘small’ OTUs (made up of few reads, e.g. 1-read OTUs), as these are more likely to be artefactual. For instance, PCR errors can generate clusters of sequences that form their own OTUs and are sufficiently different from the parent that they cannot be identified as daughters by *lulu*. Such OTUs are more likely to be small because they can arise in a later PCR cycle and thus be amplified less often than the original true OTUs. There is no reason for such PCR errors to be sequenced at low quality, so they cannot be filtered out by phred score. However, the definition of ‘small’ is inherently subjective and necessarily differs by the size of the sequence dataset (and other aspects of the lab and bioinformatic pipeline). We therefore used the *phyloseq* 1.19.1 (McMurdie & Holmes, 2013) to plot the number of OTUs that would be filtered out at different minimum OTU sizes (example in http://evomics.org/wp-content/uploads/2016/01/phyloseq-Lab-01-Answers.html, accessed 19 July 2018), and we chose a minimum OTU size of 44 reads, which is roughly the inflection point of the above graph and is the size that filters out the most (small) OTUs for the smallest minimum size. This removed about 60% of the original 1,506 OTUs, and we ended this step with 594 OTUs.

We then used *PyNAST* 1.2.2 to align the 594 remaining OTU representative sequences to a reference alignment of Arthropoda COI sequences (from Yu et al. 2012) at a minimum similarity of 60%; one sequence failed to align and was deleted. The remaining sequences were translated to amino acids using the invertebrate mitochondrial codon table, and we removed 32 OTUs with representative sequences that contain stop codons. We carried out taxonomic assignment of the OTUs using the Naïve Bayesian Classifier (Wang, Garrity, Tiedje, & Cole, 2007) that had been trained on the Midori UNIQUE COI dataset (Machida, Leray, Ho, & Knowlton, 2016). 16 OTUs assigned to non-Arthropoda taxa and 2 OTUs assigned to Collembola were removed. We ended this step with 543 OTUs.

Finally, we inspected the OTU table and removed cells that had < 5 reads representing that OTU in that sample, since these are likely to be the result of double tag jumps or sequencing error. Also, we removed two samples that contained ≤100 reads total (i.e. samples with very little data) and removed seven samples with ≤5 number of OTUs (species) because these samples are potentially overly influential (‘ecological outliers’) in analyses of species richness. After these sample removals, some OTUs were rendered small, and OTUs with <20 reads were removed. Because we do not consider read numbers per OTU to be reliable measures of biomass or abundance (Yu et al., 2012; Piñol, Mir, Gomez-Polo, & [Agustí](%20%20%20%20%20%20%20%20%20%20%20%20%20%20%20%20%20%20%20%20%20%20%20%20%20%20%20%20/s?wd=author%3A%28Agust%C3%AD%20N%29%20&tn=SE_baiduxueshu_c1gjeupa&ie=utf-8&sc_f_para=sc_hilight%3Dperson), 2015; Nichols et al., 2018), we converted read numbers to absence/presence (0/1). Throughout, our bias was to remove possible false positive detections even at the expense of losing true positive detections, thereby resulting in a dataset with less, but more reliable, data. Even so, we ended with 536 OTUs and 61 samples.

2.3.2 Community analysis

*Alpha diversity*. – All community analyses were performed in R 3.3.3 (R Core Team, 2017). We plotted observed species richnesses using *beanplot* 1.2 (Kampstra, 2008) and estimated alpha diversity using two incidence-based estimators: function *specpool* in *vegan* 2.4-5 (Chiu, Wang, Walther, & Chao, 2014) and *iNEXT* 2.0.12 (Hsieh, Ma, & Chao, 2016).

Because we had used a combination of *lulu* and *phyloseq* to combine and remove, respectively, small OTUs that are likely to be artefactual, the OTUs that remained are more likely to be true presences. Nonetheless, it remains possible that we have still over-split some biological species into multiple OTUs, since there is no single correct similarity threshold for species delimitation, and this oversplitting might have occurred more often for some taxa in some habitats, leading to artefactual differences in species richness. However, such oversplit OTUs should cluster more closely together in a phylogenetic tree and thus contribute less to estimates of *phylogenetic* diversity than will OTUs from multiple, true biological species. To estimate sample phylogenetic diversities, we used *iNextPD* 0.3.2 (Hsieh & Chao, 2017). We built a maximum-likelihood tree in *RaxML* 8.0.0 (Stamatakis, 2014) with an alignment of the OTU representative sequences (ML tree building using a General Time Reversible (GTR) model of nucleotide substitution and gamma model of rate heterogeneity and estimating the proportion of invariable sites (-m GTRGAMMAI). The algorithm used a rapid bootstrap analysis and search for the best-scoring ML tree (-f a), with 1000 times bootstrap (-N 1000) and 12345 set to be the parsimony random seed (-p 12345)). Three of the sequences produced very long branches in the resulting ML tree, which would skew estimates of phylogenetic diversity, and we removed these three OTUS and their representative sequences from the *iNextPD* analysis.

*Beta diversity*. – To visualize community compositions, we ran a Bayesian ordination using *boral* 1.5 (Hui, 2016), which is more statistically robust than running non-metric multidimensional analysis. We used a binomial error distribution and no row effect to fit the model since we were using presence/absence data (Fig. S\_BORALRESID). We also used the *mvabund* 3.12.3 (Wang, Naumann, Wright, & Warton, 2012) to test whether the compositions of native forest and mosaic forest are significantly different from each other, and whether these two habitats are significantly different from the other habitats (cropland, bamboo forest, eucalyptus, Japanese cedar).

We also visualized beta diversity with a heatmap using the *tabasco* function in *vegan*. We then partitioned the beta diversity into turnover and nestedness components using *betapart* 1.4-1 (Baselga & Orme, 2012) with binary Jaccard dissimilarities, and we visually compared these two components using the *metaMDS* function in *vegan*. Finally, we used *metacoder* 0.2.0 (Foster et al., 2017) to generate taxonomic ‘heat trees’ (instead of barcharts) to visualize and pairwise-compare the taxonomic compositions of the six land-cover types. The *metacoder* analysis also used the presence/absence OTU table.

3 RESULTS

3.1 Alpha diversity

*Species diversity*. – Observed species richnesses (Fig. BEANPLOT) did not differ significantly between any pair of forest types, after correction for multiple tests, but observed species richness was significantly lower in eucalyptus and Japanese cedar forests than in cropland. Of course, observed species richness ignores potential undetected species. We thus first used the Chao2 estimator (Chao, 1987) and found that cropland, native forest, and mosaic forest have the highest estimated species richnesses and do not differ significantly from each other (Figure SPECPOOL). In contrast, and importantly, the monoculture forests (bamboo, eucalyptus, and Japanese cedars) are estimated to contain half or less the species richnesses of mosaic forest, and after correction for multiple pairwise tests, these differences achieve formal statistical significance for the contrast between mosaic and eucalyptus forest (p = 0.0455).

Finally, we checked the robustness of this finding with *iNEXT* and *iNextPD*. Both methods concurred with the Chao2 finding. Using *iNEXT*, natural forest has the highest estimated species richness and species diversities (Shannon, Simpson), followed by cropland and mosaic forest, which overlap in their 95% confidence intervals, followed by the three monocultures (Fig. INEXT). Using *iNextPD*, the estimators Faith’s phylogenetic diversity and Phylogenetic Entropy show the same pattern (natural forest, followed by cropland and mosaic forest, followed by the three monocultures). The final estimator, Rao’s quadratic entropy, shows confidence-interval overlap of mosaic forest with two of the three monocultures, but the rank order of phylogenetic diversities remains the same. In summary, two table-based estimators and one phylogenetic-diversity estimator all find that mosaic forest has an elevated species diversity relative to the monocultures, and nearly to the same level as natural forest.

We can also use *iNextPD* to visualize phylogenetic coverage by habitat (Fig. INEXTPDTREE), and we see that the three monocultures, and mosaic forest to a lesser extent, exhibit multiple deficits in phylogenetic coverage, while cropland and native forest have almost complete phylogenetic coverage. In the next section, we explore these compositional differences between habitats.

3.2 Beta diversity

We carried out a model-based unconstrained ordination with *boral* to visualize compositional differences amongst the six land-cover types (Fig. BORAL). Not surprisingly, the primary separation was between cropland and forests, which were arranged at different ends of the first latent-variable axis. The cropland sites themselves also separated by elevation. A non-metric multidimensional scaling (NMDS) ordination showed very similar patterns but failed to separate cropland sites into high and low elevation clusters (data not shown).

Latent variables can be thought of as ‘unmeasured predictor variables’ that are revealed by correlations amongst species in their distributions across samples (Warton et al., 2015), and in this case, latent variable 1 is correlated with altitude (r = -0.457, df = 59, p = 0.0002). Latent variable 2 largely separates eucalyptus forests from the other forest types, which might reflect eucalyptus’ distinct phytochemistry. Finally, we observe that the mosaic forest sites cluster closely together and are encircled by the other forest types, which indicates that mosaic forests share species with all of the other forest types, especially Japanese cedar, eucalyptus, and native forests. A heatmap (Fig. HEATMAP) is another way to see these patterns, with two clear ‘compartments’ of communities sharing species, one dominated by forests (eucalyptus, Japanese cedar, bamboo, mosaic forest, and native forest), the other dominated by cropland. Despite being encircled by the monoculture forests (Fig. BORAL), mosaic and natural forest are still compositionally distinct from the monocultures (and from cropland), according to *mvabund* analysis (Table MVABUND).

*Turnover versus nestedness*. – We now ask whether the compositional difference amongst forest types is driven by turnover or nestedness. *betapart* analysis shows that turnover, not nestedness, dominates compositional differences (Fig. BETAPART). The heatmap (Fig. HEATMAP) also shows this pattern. In other words, even though mosaic forest shares species with the other forest types, mosaic forest is not simply a superset of the monocultures, or, put another way, the monoculture forests are not nested within the mosaic forest but contain their own monoculture-specific sets of species.

*Taxonomic differences between forest types*. – The ordination (Fig. BORAL) shows a high degree of compositional similarity between the mosaic and natural forests, but which taxa are most responsible for this similarity, and for the differences with the other forest types? The *metacoder* heat trees (Fig. METACODER, inset box) show that the mosaic and natural forests are similar in how they differ from each of the three monocultures. Relative to bamboo, mosaic and natural forest both show little taxonomic difference, which is consistent with how bamboo also overlaps mosaic and natural forest (Fig. BORAL). Relative to eucalyptus, mosaic and natural forest both have more Diptera-assigned OTUs in general and fewer of three OTUs (assigned to genera *Mycetophila*, *Sonema*, and *Homaloxestis*), which can be taken as eucalyptus indicator species. And relative to Japanese cedar, mosaic and natural forest both have more Araneae- and Lepidoptera-assigned OTUs, fewer Hemiptera-assigned OTUs, and fewer of one OTU assigned to *Mycetophila*. Heat tree differences at higher taxonomic levels (e.g. more Araneae-assigned OTUs) mean that the species which separate two forest types differ across sample pairs but nonetheless tend to be in the Araneae and Diptera.

Interestingly, when we include cropland (Fig. S\_METACODER), the heat trees flag up the largest number of species-level differences that are responsible for separating cropland from the forest types. In other words, there are particular species that serve as indicators of cropland (or in the case of the *Mycetophila* OTU, an indicator of Japanese cedar and eucalyptus).

4 DISCUSSION

To recap, our overall question is whether a mosaic plantation forest, which is merely checkerboard arrangement of monoculture plantations from individual households, can boost local biodiversity. Our previous results (Hua et al. 2016) found contradictory results, in that bird diversity was higher in mosaic forest, nearly at the level of natural forest, while bee diversity was not boosted at all. Birds and bees are clearly not representative of each other, which raises the possibility that neither birds nor bees are representative of other taxa in these forests. Thus, we metabarcoded the arthropod bycatch of the pan traps used to catch the bees, and we find results that are consistent with the bird response. The bees appear to be an exception.

In short, all three estimators used (*specpool*, *iNEXT*, and *iNextPD*) support the conclusion that, like in Hua et al. (2016), natural forest supports the highest species diversity, but mosaic forest supports a species diversity that is close to natural forest and higher than any of the monocultures (Figs. iNEXT, INEXTPD, INEXTPDTREE). In other words, a seemingly simple policy adjustment of encouraging checkboard plantings of household stands with different tree species could indeed provide a low-cost method for boosting biodiversity in Grain-for-Green plantations, at least in western China, where we conducted this study. We also re-affirm the biodiversity value of natural forest and reinforce our other policy recommendation of encouraging the retention and expansion of natural forest in the Grain-for-Green program.

The reason why bee’s results are so different with others is that bees’ tracking depends on floral plants, which are very few under the GFGP forests. Local people cut redundant plants when they planted trees, and the herbaceous layer under GFGP forests mainly dominated by fern under mosaic forest, Japanese cedar and bamboo, few grass under eucalyptus. Also, using traps collect bees normally has bias on different family (Geroff, Gibbs & McCravy, 2014).

The value of using metabarcoding is that these policy prescriptions are now based on a dataset that includes approximately 500 species-resolution taxa, ranging across the Arthropoda and representing a wide range of ecological functions, including predation (Araneae, Formicidae), spiders are the most abundant predatory natural enemies of many pests, they play an important role in maintaining the stability of agricultural and forest ecosystems, parasitism and parasitoidism (Tachinidae, Phoridae, Braconidae), most genus of Tachinidae and Braconidae are the natural enemies of pests like some Lepidoptera and sawfly, detritivory, pollination (Thysanoptera), xylophagy (Isoptera), and various modes of frugivory and herbivory (Lepidoptera, Hemiptera, Diptera, Formicidae).

Interestingly, we found that compositional differences amongst forest types is almost entirely dominated by species turnover, not nestedness, meaning that some species were only detected in the larger monocultures (Figs. HEATMAP, BETAPART). One interpretation is that overall landscape biodiversity (gamma diversity) would be maximized by including stretches of monocultures, but we think a more parsimonious explanation is that these monoculture-specific species are probably just rare in more diverse forests and thus less likely to be detected in diverse forests. After all, Japanese cedar and eucalyptus are not native to Sichuan.

Why should mosaic forest support more diverse arthropod and bird communities? The simplest explanation is that the different tree monocultures complement each other in resource availability, probably across the seasons, which would allow more species to persist in mosaic forests. This could be tested by sampling different parts of a mosaic forest through a year, to test if the arthropod and bird communities migrate around and/or consume different plant resources. Another, non-mutually exclusive possibility is that mosaic forests might allow a more diverse herb and shrub understory because the monocultures differ in height and structure and thus allow sunlight to penetrate from different angles, as opposed to the uniform canopies of tree monocultures. We note of course that a more diverse, and presumably higher biomass, arthropod community itself would also support a richer bird community.

One potential explanation that is not supported is that mosaic forests achieve higher species diversities by support arthropods from cropland (Figs. BORAL, HEATMAP). This was also the result for birds, where cropland and forest avifauna differed (Hua et al. 2016).

*Metabarcoding, alpha diversity, and beta diversity*. – Metabarcoding provides an efficient method for interrogating highly diverse biodiversity samples, such as the pan-trap samples that we found here, but because of its reliance on PCR, metabarcoding datasets tend to contain a non-trivial amount of noise mixed in with data. This noise manifests as a large number of false-positive OTUs, which are filtered out heuristically. Such false OTUs especially complicate efforts to estimate species richness and diversity. Here, we applied several filtering steps to remove false OTUs, and we also used *iNextPD* to generate more robust estimates of phylogenetic diversity, which we propose can compensate for possible oversplitting of true species into multiple OTUs. (Also, in Yu et al. (2012), we showed that metabarcoding can accurately recover the phylogenetic diversities of mock samples of known composition.)

Another approach, which we learned of after we had completed the wet lab portion of our study, is to subject each sample to multiple PCRs (typically 3) and to bioinformatically filter out sequences that fail to appear in at least two of the PCRs above some minimum number of reads. Such sequences are more likely to be PCR or sequencing errors. This is the DAMe protocol of Zepeda-Mendoza et al. (2016, see also Alberdi et al. 2017). Our experiments using this protocol on mock samples of known composition (data not shown) show that almost all false-positive OTUs are removed with only a small loss of true-positive OTUs, improving the reliability of alpha diversity estimates.

That said, biodiversity conservation studies should focus less on explaining changes in species *diversity* per se and more on explaining changes in taxonomic *composition* as a function of natural and anthropogenic causes (Magurran et al. 2015, Magurran 2016). One important reason is because anthropogenically disturbed communities can maintain species richness and diversity, even as local species go extinct and are replaced by cosmopolitan species. On the other hand, the same change leads to biotic homogenization, which is detectable as a reduction in beta diversity. Fortunately, metabarcoding’s biases are well suited to estimating changes in composition. For instance, Xiong and Zhan (2018) have shown that beta diversity estimates are robust to different OTU-clustering thresholds. In our study, cropland supports a species diversity similar to mosaic forest and also just below natural forest (Fig. INEXT, INEXTPD), but cropland species are compositionally distinct from natural forest species (Fig. BORAL), so we obviously would not recommend cropland expansion as a conservation measure. Instead, our combined analyses of alpha and beta diversity support our previous policy-relevant conclusion that (unsurprisingly) natural forests support the most biodiversity, followed by (surprisingly) fine-scale, checkboard plantings of a few tree monocultures.

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