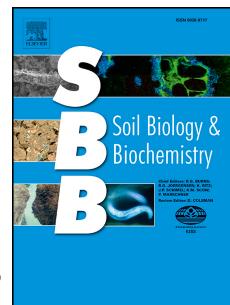


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Straw chemistry links the assembly of bacterial communities to decomposition in paddy soils

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1 **Title Page**

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4 paddy soils

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18

19 **Abstract**

20 Although increasing number of studies have shown that microorganisms play important
21 roles in plant residue decomposition, an important process for crop productivity and soil
22 fertility in agroecosystems, the underlying ecological processes of microbial community
23 assembly as well as the associated governing factors remain elusive. As such, we conducted
24 three replicate paddy straw decomposition experiments, located across subtropical China. We
25 used ecological null modeling to quantify assembly processes governing bacterial community
26 turnover during straw decomposition. Consistent observations emerged across the
27 experiments that indicated significant associations between bacterial community assembly
28 processes and straw chemistry. Specifically, according to our framework, shifts in straw
29 chemistry were associated with variable selection, which was inferred to drive community
30 turnover between soil and straw surfaces. This resulted in bacterial subgroups from soil being
31 deterministically selected to degrade straw. In turn, patterns were consistent with
32 homogeneous selection governing community composition within straw decomposition stages
33 and ecological drift being important across decomposition stages. Subsequently, shifts in
34 community composition and assembly processes were linked to variation in functional aspects
35 of straw decomposition. This study indicates that straw chemistry strongly influenced
36 assembly processes governing microbial community turnover during straw decomposition.
37 These outcomes are important for mechanistically understanding and predicting
38 microbial-driven plant residue decomposition in terrestrial ecosystem.

39

40 **Keywords:** Straw decomposition; Null models; Deterministic; Stochastic; Ecosystem
41 function

42

43 **1. Introduction**

44 Globally, 2.5 billion tons of crop straw are estimated to be produced annually (FAO,
 45 2017). Straw is one of the main exogenous sources of organic carbon and nutrients in arable
 46 soil (Liu et al., 2014). Its amendment not only increases soil C budgets but also mediates
 47 nitrogen, phosphorous and sulfur nutrient pools, thereby improving soil fertility and plant
 48 growth (Lu et al., 2009; Fan et al., 2014). Therefore, straw decomposition in soils attracts
 49 great interests of agricultural, ecological and soil scientists (Marschner et al., 2011; Bernard et
 50 al., 2012; Ji et al., 2018). Straw decomposition can be generally parsed into several stages.
 51 The fast decomposition of easily degradable components is the initial step, followed by
 52 decomposition of recalcitrant compounds and subsequent produced biopolymers, and
 53 mineralization of final monomers to CO₂ and/or CH₄ (Conrad, 1993; Glissmann and Conrad,
 54 2002).

55 Soil-dwelling microorganisms are the major drivers for straw decomposition
 56 (Chidthaisong et al., 1999; Chidthaisong and Conrad, 2000). Due to different life strategies
 57 and substrate preferences, distinct microbial community successions have been observed
 58 across decomposition stages in previous studies (Rui et al., 2009; Marschner et al., 2011;
 59 Wegner and Liesack, 2016). In addition, although microbial communities (especially core
 60 microbial taxa) involved in straw decomposition are differentiated among sites (Rui et al.,
 61 2009), microbial communities with similar functional genes involved in plant residue
 62 decomposition have been observed (Hollister et al., 2010; Mula-Michel and Williams, 2013).
 63 This coherence may be due to species-by-environment interactions. For example, Maynard et
 64 al. (2018) found that species associations overwhelmed abiotic conditions to govern the
 65 structure and function of wood-decaying fungal communities in a forest ecosystem. These
 66 investigations imply that consistent assembly processes underlie shifts in microbial
 67 community composition during straw decomposition. To our best knowledge, however, this
 68 expectation has not been evaluated.

69 A central goal of microbial ecology is to unravel microbial community assembly
 70 processes as well as their underlying governing factors. A conceptual and
 71 null-modeling-based framework (Vellend, 2010; Stegen et al., 2012; Stegen et al., 2015)
 72 based on community ecology theory was developed to disentangle ecological processes
 73 governing community assembly. These processes include deterministic (i.e., homogeneous
 74 selection plus variable selection) and stochastic (i.e., homogenizing dispersal plus dispersal

75 limitation coupled with ecological drift) factors (Stegen et al., 2013; Dini-Andreote et al.,
 76 2015; Stegen et al., 2015). Although the null modeling framework has limitations (e.g.,
 77 possible violations of assumptions and statistical uncertainties), it has been shown to provide
 78 robust statistical proxies for ecological assembly processes (Stegen et al., 2015; Zhou and
 79 Ning, 2017). As such, it has furthered our understanding of the ecological processes
 80 governing temporal and/or spatial community assembly in groundwater (Danczak et al., 2016;
 81 Graham et al., 2017; Stegen et al., 2018), shrimp guts (Xiong et al., 2017), soils
 82 (Dini-Andreote et al., 2015; Feng et al., 2018; Tripathi et al., 2018), and other environments
 83 (e.g., Wang et al. (2013)).

84 Here we use null models to study assembly processes during straw decomposition. We
 85 hypothesize that deterministic over stochastic assembly processes underlie shifts in microbial
 86 communities during straw decomposition. In addition, existing evidence indicates that the
 87 quantity and/or properties (e.g., chemical components and/or functional groups) of organic
 88 matter play important roles into structuring microbial communities (Nemergut et al., 2010;
 89 Dini-Andreote et al., 2015; Bhatnagar et al., 2018; Feng et al., 2018;) and likely impose
 90 deterministic selection on microbial communities (Ferrenberg et al., 2013). Thus, we further
 91 hypothesize that straw chemistry governs assembly processes that influence
 92 straw-decomposing microbial communities and in turn decomposition.

93 To test our hypotheses, we used ditch-buried rice straw in anoxic paddy fields at three
 94 experimental sites across subtropical China. Due to anoxic conditions, we expect that bacteria
 95 were largely responsible for straw decomposition, whereby the activities of aerobic fungi and
 96 fauna were strongly limited (Nakamura et al., 2003; Kyuma, 2004). Thus, we focused on
 97 bacterial communities in this study. We leveraged a null-modeling framework based on
 98 community ecology theory (Vellend, 2010; Stegen et al., 2012; Stegen et al., 2015) to reveal
 99 the ecological processes governing community assembly within and across decomposition
 100 stages. We further evaluated factors driving community assembly processes, through detailed
 101 molecular analysis.

102 **2. Material and methods**

103 **2.1. Experimental sites and the field straw decomposition experiment**

104 The ditch-buried straw decomposition experiment was conducted using litter bags at three
 105 replicated rice field experimental sites in Chongqing, Changshu, and Yingtan across

106 subtropical China. Annual average temperature and precipitation at the three experimental
107 sites were collected from the website of Weather China (<http://www.weather.com.cn>). Each
108 experimental site had a similar long-term NPK (mineral N, P and K fertilizers) fertilization
109 strategy. Details of the experimental sites are described in Tables S1 and S2 (Wu et al., 2019).

110 Rice straw materials were collected after rice harvesting in 2014 and air-dried. Twenty
111 grams of rice straw was cut to 5 cm length and put into nylon litter bags, which were then
112 sealed via heat-sealing. Bags were 12 cm×20 cm in size and were made of 300 mesh (41 µm
113 pore size) nylon fabric, which permitted the free transfer of microorganisms between litter
114 bags and paddy soils. Before rice cultivation at each experimental site, litter bags containing
115 rice straw were buried at 10 cm depth in a 48 m² area (with bamboo poles as marks for
116 sampling) in a spatially random design to avoid bags associated with a given decomposition
117 stage being placed together in space. The litter bags were collected at 1, 2, 4, 8 and 16 weeks
118 after they were buried; these time points are referred to as ‘decomposition stages’. Each
119 decomposition stage had 12 replicates, and a total of 60 litter bags were collected for each
120 experimental site. On each day of litter bag sampling, corresponding soil samples adjacent to
121 bags were collected using a 30-mm-diameter auger. Thus, each soil collection also had 12
122 replicates, and a total of 60 soil samples were collected for each experimental site. In total,
123 there were 180 straw samples and 180 soil samples in this investigation. Subsamples of soil
124 and straw for DNA extraction were stored at -80°C, and subsamples for straw chemistry and
125 decomposition assays were stored at -20°C.

126 The straw decomposition ratio was calculated on the basis of dry weight loss as (dry
127 initial mass - dry final mass) / dry initial mass. In brief, following field collection the
128 remaining straw from each litter bag was taken out and weighed. Then, a subsample from
129 each bag was oven-dried at 60°C for a minimum of 72 h and weighed to determine the total
130 dry final mass. In this case, soil particles with sizes less than 41 µm may have been included
131 and/or part of the decomposed straw debris may have leached out. However, these potential
132 sources of error should not cause significant deviations between estimated and actual
133 decomposition ratios. Part of the remaining subsample was used to further analyze the
134 structure of straw by stereoscopic microscopy (VH-S30B, KEYENCE) at the magnification of
135 100×. Another part of the remaining subsample was used for genomic DNA extraction to
136 determine bacterial community composition. To prepare for DNA extraction, 5 g of remaining
137 straw from each bag was cut to 0.5 cm length, combined with 40 mL of phosphate buffered

138 saline in a 200-mL tube and vortexed at 180 rpm for 1 h. The straw was washed three times.
 139 All suspensions were collected and centrifuged at 5,000 g for 10 min at 4°C. The precipitates
 140 were then stored at -80°C prior to DNA extraction. In this case, bacteria closely adhered to
 141 straw might be under-sampled.

142 **2.2. Straw chemical properties measurement**

143 The chemical functional groups of straw at different decomposition stages were assessed
 144 with solid-state CPMAS ^{13}C NMR spectroscopy. The spectra were obtained on a Bruker
 145 AVANCE 400MHz (BrukerBioSpin, Rheinstetten, Germany). Subsamples of remaining straw
 146 in litterbags were ground into powder and passed through 0.074 mm sieve. Powdered samples
 147 were analyzed in a 4 mm Wide Bore MAS probe. The ^{13}C resonating frequency was set at 100
 148 MHz. The spinning rate was 10000 Hz, acquisition time was 33 ms, the recycle delay was 1.0
 149 s, and carried on 6000 scans. The spectra were integrated into 7 chemical-shift regions (Mao
 150 et al., 2000; Mao et al., 2008), with assignments as the following C-types: alkyl (0-45 ppm);
 151 O-CH₃/NCH (45-60 ppm); O-alkyl (60-93 ppm); O-C-O anomeric (93-110 ppm); aromatic
 152 (110-142 ppm); aromatic C-O (142-165 ppm); carbonyl (165-190 ppm).

153 The straw chemical components of hemicellulose, cellulose and lignin were determined
 154 according to the Van Soest analysis (Van Soest, 1963) with some modifications (Wilk et al.,
 155 2019). The content of water soluble polysaccharides (WSP) was estimated, following
 156 extraction with distilled water and precipitation with ethanol (Chapman and Lynch, 1985).

157 **2.3. DNA extraction**

158 Genomic DNA was extracted from straw slurries and from soil. In brief, 0.5 g slurry or
 159 sieved soil was pulverized by MP FastPrep® at a speed of 6 m/s for 45s and then extracted
 160 using a FastDNA® SPIN Kit for soil (MP Biomedicals, Santa Ana, CA). A negative control
 161 was conducted following the same protocol. The extracted DNA was eluted in 50 μL of TE
 162 buffer, quantified by Nanodrop 2000 (ThermoFisher, USA) and stored at -20°C until further
 163 use.

164 **2.4. Preparation of the amplicon libraries for high-throughput sequencing**

165 Bacterial communities were assayed by high-throughput sequencing. For each DNA
 166 sample, the primer set 519F/907R was used to amplify approximately 400 bp of bacterial 16S
 167 rRNA gene V4-V5 fragments (Feng et al., 2015). Briefly, the unique 5-bp barcoded
 168 oligonucleotide sequence was fused to the forward primer to distinguish different samples.

169 PCR was carried out in 50- μ L reaction mixtures with the following components: 4 μ L (initial:
 170 2.5 mM each) of deoxynucleoside triphosphates, 2 μ L (initial: 10 mM each) of forward and
 171 reverse primers, 2 U of Taq DNA polymerase (0.4 μ L; TaKaRa, Japan), and 1 μ L of template
 172 containing approximately 50 ng of genomic community DNA as a template. Thirty-five cycles
 173 (95°C for 45 s, 56°C for 45 s, and 72°C for 60 s) were performed with a final extension at
 174 72°C for 7 min. The purified bar-coded PCR products from all of samples were normalized in
 175 equimolar amounts, prepared using a TruSeq™ DNA Sample Prep LT Kit and sequenced
 176 using a MiSeq Reagent Kit v2 (500 cycles) following manufacturer's protocols with Illumina
 177 MiSeq sequencing platform (Illumina Inc., CA, USA). Negative controls were always run for
 178 each experimental step to guarantee the effectiveness of the results. The sequences were
 179 deposited into the NCBI SRA database (accession no., PRJNA591776).

180 **2.5. Processing of high-throughput sequencing data**

181 Raw sequence data were processed using the Quantitative Insights Into Microbial
 182 Ecology (QIIME, USA) pipeline (<http://qiime.sourceforge.net>) (Caporaso et al., 2010). Sequences
 183 with a quality score below 25 and the length fewer than 300 bp were trimmed and the rest
 184 then assigned to samples based on unique 5-bp barcodes. Sequences were denoised using the
 185 denoise_wrapper.py script with default settings (Reeder and Knight, 2010) and the quality
 186 reads were then binned into operational taxonomic units (OTUs) using UCLUST (Edgar,
 187 2010) at 97% identity threshold, and the most abundant sequence from each OTU was
 188 selected as a representative sequence. Taxonomy was assigned to bacterial OTUs with
 189 reference to a subset of the SILVA 119 database (Pruesse et al., 2007)
 190 (<http://www.arb-silva.de/download/archive/qiime/>). A phylogenetic tree was constructed using
 191 FastTree to support phylogenetic analyses. In total, we obtained 6,528,688 quality sequences
 192 of the bacterial 16S rRNA gene and between 8,081 and 39,732 sequences per sample, with a
 193 median value of 17,228 sequences per sample. Because of the high-variance sequences
 194 between samples and a required even depth of sampling for alpha (α) and beta (β) diversity
 195 comparisons, all samples were randomly rarified to 8,000 sequences for downstream analyses
 196 (Shaw et al., 2008; Port et al., 2016).

197 **2.6. Phylogenetic analysis**

198 We conducted incidence analysis for species at each experimental site. It was found that
 199 the majority of species were shared across decomposition stages (Fig. S1), thus one species

200 pool for each experimental site was considered. Mantel correlograms (Diniz-Filho et al., 2010)
 201 were used as in Stegen et al. (2012) to evaluate phylogenetic signal across a range of
 202 phylogenetic distances using the R function “mantel.correlog” (package “vegan” (Oksanen et
 203 al., 2007), Version 2.2-1). The significant positive correlations between phylogenetic
 204 distances and OTU niche differences were strongest at short phylogenetic distances
 205 (approximately 0%-3.5% (for Chongqing), 0%-5.5% (for Changshu), and 0%-6.5% (for
 206 Yingtan) of the maximum phylogenetic distances, respectively; Fig. S2). This indicated that
 207 OTU environmental preferences were phylogenetically conserved across relatively short
 208 phylogenetic distances.

209 Phylogenetically conserved environmental preferences are an assumption of the null
 210 modeling framework we use here (Stegen et al., 2012). Our observation of phylogenetic
 211 conservatism across relatively short phylogenetic distances (Fig. S2) is consistent with
 212 numerous other microbial studies across diverse ecosystems (e.g., Wang et al. (2013)). Lack
 213 of phylogenetic conservatism should lead to phylogenetic null model outcomes that do not
 214 deviate from a stochastic expectation, potentially leading to underestimation of the influences
 215 of deterministic assembly processes. We minimized any such biases by using phylogenetic
 216 null model analyses that focus on relatively short phylogenetic distances among nearest
 217 relatives. This approach minimizes—but cannot fully eliminate—violations of the assumption
 218 of phylogenetic conservatism. More specifically, we quantified phylogenetic turnover
 219 (phylogenetic β -diversity) between communities using between-community
 220 β -Mean-Nearest-Taxon-Distance (β MNTD) (Fine and Kembel, 2011) and the β -Nearest
 221 Taxon Index (β NTI) (Stegen et al., 2012) metrics. β MNTD quantifies the phylogenetic
 222 distance between each OTU in one community and its closest relative in another community
 223 using the R function “comdistnt” (abundance.weighted = TRUE; package “picante”, Version
 224 1.8 (Kembel et al., 2010)). β NTI measures the difference between observed β MNTD and the
 225 null β MNTD distribution. The null distribution was generated through 1000 randomizations
 226 in which a null value of β MNTD was calculated after shuffling OTU labels randomly across
 227 the tips of the phylogeny of all taxa investigated. This null modeling approach has been
 228 shown via simulation modeling to generate a null distribution of β MNTD values expected
 229 when community assembly is dominated by stochastic processes (Dini-Andreote et al., 2015;
 230 Stegen et al., 2015). β NTI measures the deviation between observed β MNTD and the mean of
 231 the null β MNTD distribution in units of standard deviation. As such, β NTI values < -2 or > +2

232 respectively indicate phylogenetic turnover that is less than or greater than expected under
 233 stochastic assembly, thereby indicating a primary role of deterministic assembly processes
 234 (Stegen et al., 2012).

235 **2.7. Quantitative estimation of ecological assembly processes**

236 As in Stegen et al. (2013), the β NTI metric was used in combination with
 237 Bray-Curtis-based Raup-Crick (RC_{bray}) to quantify contributions of four ecological assembly
 238 processes governing bacterial community turnover between the soil matrix and straw surface
 239 (by comparing all taxa between soil and straw samples), as well as within and across
 240 decomposition stages (by comparing all taxa among straw samples) within each experimental
 241 site. RC_{bray} is based on a comparison between observed and expected levels of taxonomic
 242 turnover (Stegen et al., 2015). The deviation between empirically observed Bray-Curtis and
 243 the null distribution is then standardized to vary between -1 and +1, and the resulting metric is
 244 referred to as RC_{bray} . Values of RC_{bray} below -0.95 or above +0.95 indicate significant
 245 deviations from the null model expectation.

246 Following established methods described in Stegen et al. (2012; 2013; 2015) and
 247 Dini-Andreote et al. (2015), the relative contributions of community turnover that were
 248 governed by homogeneous or variable selection were estimated as the fraction of pairwise
 249 comparisons with β NTI < -2 or β NTI > +2, respectively. The relative contributions of
 250 dispersal limitation or homogenizing dispersal for spatial turnover in community composition
 251 were estimated as the fraction of pairwise comparisons with $|\beta$ NTI| < 2 and $RC_{bray} > +0.95$ or
 252 $RC_{bray} < -0.95$, respectively. Dispersal does not occur through time such that the interpretation
 253 of null model outcomes is slightly different for temporal analyses. Specifically, pairwise
 254 comparisons *through time* with $|\beta$ NTI| < 2 and $RC_{bray} > +0.95$ were interpreted as indicating a
 255 strong role of ecological drift, leading to stochastic divergence in community composition
 256 through time. In addition, pairwise comparisons *through time* with $|\beta$ NTI| < 2 and $RC_{bray} <$
 257 -0.95 were interpreted as communities (in a given location) being assembled due to high rates
 258 of dispersal from another spatial location. That is, $|\beta$ NTI| < 2 combined with $RC_{bray} < -0.95$
 259 indicate that temporally-consistent high rates of dispersal from a temporally-consistent source
 260 can homogenize community composition through time. Lastly, if $|\beta$ NTI| < 2 and $|RC_{bray}| <$
 261 0.95, then neither deterministic nor stochastic processes dominate. This condition has been
 262 referred to as “undominated” (Stegen et al., 2015). Ecological assembly processes were
 263 calculated by pairwise comparison across all samples from all time points within each

264 experimental site.

265 **2.8. Random Forest Model**

266 To evaluate the performance of different taxa across straw decomposition stages, we
 267 regressed the relative abundances of bacterial taxa at the genus level against straw
 268 decomposition stages using default parameters of the R implementation of the Random Forest
 269 (RF) algorithm (R package “randomForest” (Liaw and Wiener, 2002), ntree=1,000, using
 270 default mtry of 1/3 of the data, which are withheld during its construction (out-of-bag or OOB
 271 cases)). The importance of each predictor variable was determined by evaluating the decrease
 272 in prediction accuracy (that is, increase in the mean square error between observations and
 273 OOB predictions) when the data for that predictor was randomly permuted. Lists of taxa
 274 ranked by RF in order of importance were determined over 100 iterations. The number of
 275 marker taxa was identified using 10-fold cross-validation implemented in R “rfcv” function.

276 We further applied the RF approach to estimate the importance of biomarker taxa for
 277 explaining changes in straw chemical properties (Jiao et al., 2018). A multiple regression
 278 model with variance decomposition analysis was used to validate the outcome of RF analyses
 279 by using the lm and calc.relimp function in the “relaimpo” package (Grömping, 2006).

280 **2.9. Statistical analysis**

281 Succession of straw-associated bacterial communities along 5 decomposition stages
 282 within each experimental site was visualized by nonmetric multidimensional scaling analyses
 283 (NMDS), based on weighted β MNTD distance. Permutational multivariate analysis of
 284 variation (PERMANOVA) (Anderson and Walsh, 2013) and permutational analysis of
 285 multivariate dispersions (PERMDISP) tests were respectively conducted to test for
 286 statistically significant differences in community composition and heterogeneity among stages,
 287 using R software (the “vegan” package (Oksanen et al., 2007), Version 2.2-1). The separation
 288 of mean values among samples was evaluated with one-way ANOVA followed by post-hoc
 289 Tukey’s HSD tests using the IBM Statistical Product and Service Solutions (SPSS) Statistics
 290 for Windows (Version 13). $P < 0.05$ was considered significant.

291 Correspondence analyses (redundancy analysis, RDA) were conducted to determine
 292 associations between straw chemical properties and bacterial phylogenetic composition in R
 293 using the “vegan” package (Oksanen et al., 2007) (Version 2.2-1). The significance of models
 294 was tested by ANOVA based on 999 permutations. Mantel tests between β NTI and changes in

straw functional groups and chemical components were conducted to determine the relationship between assembly processes and straw chemical properties. The changes in chemical properties were calculated using 7 functional groups and 4 chemical components of straw samples (Tables S3 and S4 (Bao et al., 2020)) based on Euclidean distances. Variation partitioning analyses (VPA) were used to estimate the amount of variation in straw decomposition explained by community composition (the first axis of PCoA based on β MNTD distance) and assembly processes (the first axis of PCoA based on β NTI distance). VPA was conducted within each experimental site, using R software with the package “permute” (Simpson, 2012) and “vegan” (Oksanen et al., 2007). Venn diagram analysis was used to compare the observed OTUs between the soil matrix and straw within each experimental site by using R packages “VennDiagram” (Version 1.6.20) (Chen and Boutros, 2011).

3. Results

3.1. Dynamics of straw decomposition and chemical properties

Generally, the straw decomposition ratio at each experimental site increased with incubation time ($P < 0.05$) (Fig. 1A). As shown in Fig. 1B, the decomposition of the straw was not visible by stereoscopic microscopy until the partial decomposition of the thin membrane that covered the epidermal layer at week four. The area of decomposition increased and many parts of the thin membrane were peeled off by week eight. Further decomposition was observed on week sixteen, at which time nearly all the thin membrane that covered epidermal cells had disappeared and the internal structure of the straw was exposed. The decomposition rates (characterized by the slope between two adjacent time points; the inset of Fig. 1A) before week four were greater than others, implying that easily degradable substances were being consumed during these periods. Then the reduced decomposition rates after week four imply that recalcitrant substances were being consumed during these periods.

For straw chemical components, the remaining mean percentages of cellulose, lignin, hemicellulose and WSP in different stages are shown in Fig. 1C and Table S4. Their concentrations decreased gradually with decomposition time, indicating that these substances were degraded to intermediates. The proportions of functional groups in the total spectral area showed systematic changes with decomposition stages (Fig. 1D and Table S3). In general, the relative proportions of recalcitrant functional groups, including alkyl C, aromatic C, and

326 aromatic C-O tended to increase with decomposition stage. O-alkyl C and O-C-O anomeric C
 327 representing easily decomposed chemical functional groups decreased with decomposition
 328 stages, while carbonyl increased and O-CH₃/NCH did not change (Table S3).

329 **3.2. Variation in community composition between soil matrix and straw-associated, as**
 330 **well as among straw-associated across decomposition stages**

331 The straw-associated communities were significantly different from those of soils ($P =$
 332 0.001) (Figs. 2A-C and Table S5), which is likely the consequence of large differences in
 333 chemical properties between the soil matrix and straw. Venn diagrams revealed that the
 334 majority of soil taxa (70.7%-79.6%) were filtered out and were not found associated with
 335 straw (Fig. S3). The additional 20.4%-29.3% of taxa in litter bags (Fig. S3) could be those
 336 already on straw and/or rare taxa in soils that were enriched by straw amendments. We further
 337 visualized shifts in straw-associated communities in terms of phylogenetic compositions
 338 among five decomposition stages, based on β MNTD distances (Figs. 2D-F). This showed that
 339 bacterial community composition grouped based on decomposition stage, which was
 340 confirmed by PERMANOVA ($P = 0.001$) (Table S5). The shift in heterogeneity of
 341 within-stage community composition across decomposition stages was evaluated using
 342 PERMDISP in each experimental site (Figs. 2G-I). Generally, the level of heterogeneity was
 343 lower during the first two stages, increased at week four, decreased at week eight, and
 344 increased at week sixteen (one-way ANOVA, $P < 0.05$).

345 **3.3. Ecological assembly processes governing community composition**

346 The ecological assembly processes governing straw degrading bacterial communities
 347 were similar for the three experimental sites (Fig. 3). Variable selection played a dominant
 348 role (consistently ~50%) in shifting community composition between the soil matrix and
 349 straw (Figs. 3A-C). When examining straw-associated communities on their own within
 350 decomposition stages (Figs. 3D-F), homogeneous selection was dominant (ranging from a
 351 high of 98.5% (Chongqing) and 100.0% (Changshu) at week eight and 100.0% (Yingtan) at
 352 week one, to a low of 42.4% (Chongqing) and 69.7% (Yingtan) at week sixteen and 56.1%
 353 (Changshu) at week four). With respect to community turnover across decomposition stages,
 354 homogeneous selection (39.6%-62.9%) and ecological drift (28.8%-33.1%) simultaneously
 355 played important roles regardless of experiment site (Figs. 3G-I).

356 **3.4. Associations among straw chemical properties and community composition and**

357 **assembly processes**

358 Correlation analyses consistently revealed that straw-associated bacterial communities
 359 formed clusters that were related to different straw chemical functional groups and
 360 components in each experimental site (Fig. 4). With respect to functional groups, along axis 1,
 361 easily degraded O-alkyl C and O-C-O anomeric C groups were associated with bacterial
 362 communities in the first three decomposition stages, while the final two decomposition stages
 363 were associated with both recalcitrant and easily degraded groups, including alkyl C, aromatic
 364 C, aromatic C-O and carbonyl (Figs. 4A-C). For straw chemical components, axis 1 mainly
 365 separated cellulose from hemicellulose, lignin and WSP across decomposition stages (Figs.
 366 4D-F).

367 For associating ecological assembly processes to straw chemistry, we estimated
 368 functional group distances and component distances using all straw chemical groups or
 369 components (“all factors combined” in Table S6) (Fig. 5). This was done because the vast
 370 majority of functional groups and components of straw had significant correlations with β NTI
 371 (except for O-CH₃/NCH and WSP of Yingtan) (Mantel test, $P < 0.05$) (Table S6). Linear
 372 Mantel tests revealed significant associations between β NTI and both functional groups and
 373 components in each experimental site (Fig. 5; $P < 0.05$). Specifically, as the change in
 374 functional groups and components increased, there was a continuous transition from β NTI <
 375 -2 when functional groups and components were most similar between samples towards -2 <
 376 β NTI < +2 at intermediate differences and further towards β NTI > +2 when functional groups
 377 and components were most dissimilar between samples (Fig. 5). This indicates that increasing
 378 variations in straw chemistry led to changes in assembly processes by transitioning from
 379 homogeneous selection, to stochasticity, and to variable selection.

380 **3.5. Potential key bacterial taxa for straw decomposition**

381 We further examined important bacterial genera as biomarker taxa for decomposition at
 382 different stages (Fig. 6). The RF model explained 93.92% of bacterial variances related to
 383 straw decomposition stages. The minimum cross-validation error was obtained when using 56
 384 important genera (Fig. S4). The top 20 bacterial biomarkers were then chosen as the
 385 representative biomarker taxa because the cross-validation error curve had stabilized when
 386 these taxa were used (Fig. S4). The majority of biomarker taxa showed high relative
 387 abundances in the corresponding decomposition stages. We further evaluated the potential

388 contributions of these biomarkers to decomposition of straw chemical functional groups and
 389 components at different stages via RF analysis (Supplementary data). In particular, the genera,
 390 *Aeromonas* (for changes in O-CH₃/NCH, O-alkyl C, O-C-O anomeric C, cellulose and WSP)
 391 and *Enterobacter* (for changes in O-C-O anomeric C, cellulose and WSP) had higher relative
 392 abundances in the first three decomposition stages. Unclassified *Ruminococcaceae* (for
 393 changes in cellulose, hemicellulose and lignin), *Sporobacter* (for the change in cellulose),
 394 *Anaeromyxobacter* (for the change in alkyl C), Unclassified BRC1 (for changes in cellulose
 395 and hemicellulose), and Unclassified *Prolixibacteraceae* (for changes in aromatic C, aromatic
 396 C-O, cellulose, lignin and WSP) started to accumulate at week eight, while *Phenylobacterium*
 397 (for changes in alkyl C, O-CH₃/NCH, O-alkyl C, O-C-O anomeric C, aromatic C, aromatic
 398 C-O, carbonyl, lignin and WSP), Unclassified *Rhizobiales* and *Aquicella* (for the change in
 399 hemicellulose), *Bradyrhizobium* (for changes in alkyl C and O-alkyl C), Unclassified
 400 *Planctomycetaceae* (for changes in O-C-O anomeric C, carbonyl, cellulose, lignin and WSP)
 401 and *Hyphomicrobium* (for changes in O-alkyl C, alkyl C, O-C-O anomeric C, aromatic C,
 402 aromatic C-O and carbonyl), had higher relative abundances at week sixteen (Supplementary
 403 data).

404 **3.6. Variation in straw decomposition explained by assembly processes and community 405 composition**

406 The VPA indicated that together, bacterial community composition and assembly
 407 processes largely explained (70% (Chongqing), 57% (Changshu) and 47% (Yingtan)) straw
 408 decomposition within each experimental site (Fig. 7). In addition, bacterial community
 409 composition alone explained 11% and 35% in Chongqing and Yingtan, respectively (Figs. 7A
 410 and C), whereas the contributions of assembly processes alone were less than 3%. These
 411 results indicate that straw decomposition was influenced by bacterial community composition,
 412 which was further determined by ecological assembly processes mediated by straw chemistry
 413 (Figs. 4 and 5).

414 **4. Discussion**

415 **4.1. Deterministic over stochastic assembly processes underpin bacterial communities 416 during straw decomposition**

417 The null model analyses showed a strong link between both deterministic and stochastic
 418 assembly processes and patterns of community composition (Fig. 3). More specifically, our

419 results were consistent with deterministic variable selection (consistently around 50% of
 420 assembly processes (Figs. 3A-C)) being responsible for shifts in community composition
 421 *between* soil and straw (Figs. 2A-C). Our results further indicate that another deterministic
 422 homogeneous selection strongly constrained (accounting for 42.4%-100% of assembly
 423 processes) straw-associated community composition *within* stages (Figs. 3D-F). We infer that
 424 both variable and homogeneous selections were due to a subgroup of the initial soil
 425 community being able to metabolize specific substrates, especially recalcitrant components in
 426 straw. This inference is corroborated by data showing that straw functional groups such as
 427 O-alkyl C and O-C-O anomeric C decreased first, resulting in the increase of the proportion of
 428 recalcitrant groups along decomposition stages, for example at week eight (Fig. 1D and Table
 429 S3). The accumulation of recalcitrant groups at week eight (Table S3) may have resulted in
 430 fewer niches being available such that only species that could degrade recalcitrant compounds
 431 were deterministically selected for (Figs. 3D-F). Furthermore, sudden decreases in
 432 community heterogeneity occurred at week eight (Figs. 2G-I).

433 The increase in stochastic processes at week sixteen (Figs. 3D-F) is an “exception that
 434 proves the rule.” At week sixteen, monomers were released from the decomposition of
 435 recalcitrant components (Tables S3). For example, increases in the content of carbonyl groups
 436 (Fig. 1D and Table S3) indicated increases in easily degradable intermediates of lignin
 437 decomposition (Kirk et al., 1986). The high content of these substances may result in a less
 438 selective environment that allowed a broader range of taxa to colonize (Chase, 2010), and
 439 thus lead to an increase in the influence of stochasticity and greater community heterogeneity
 440 (Figs. 2G-I).

441 While homogeneous selection was dominant across decomposition stages, ecological
 442 drift also played an important role (Figs. 3G-I). This null model-based result is supported by
 443 clear temporal community succession (Figs. 2D-F) and the predominance of different
 444 bacterial genera at different stages (Fig. 6). We therefore infer that community assembly
 445 processes influencing community composition within and across decomposition stages
 446 included a combination of stochastic and deterministic processes. This is highly consistent
 447 with previous work in microbial ecology (Zhang et al., 2016), as well as in plant (Romme et
 448 al., 2016; Alcantara et al., 2018) and animal (Budischak et al., 2016) ecologies, which
 449 supports the general perspective that stochastic and deterministic processes operate
 450 simultaneously.

451 **4.2. Straw chemistry is linked to decomposition via assembly processes that govern**
 452 **community composition**

453 Null model analyses combined with other statistical analysis further revealed that straw
 454 chemistry imposed deterministic processes that, in turn, influence community composition
 455 (Figs. 4 and 5). Specifically, our results indicate that similar straw chemistry within stages
 456 deterministically constrained community composition to be similar within stages, while
 457 divergence in straw chemistry across stages deterministically drove divergence in community
 458 composition across stages (Fig. 5). Our results are similar to those in previous work
 459 associated with wood-decaying fungi (Rajala et al., 2012; Ottosson et al., 2014), which found
 460 that the variation of wood chemistry during decomposition served as an environmental filter
 461 governing the wood-inhabiting fungi community composition. Other work also demonstrated
 462 that the abundance and quality of compounds released from straw drove variation in bacterial
 463 communities (Baumann et al., 2009; Marschner et al., 2011). In addition, similar patterns in
 464 which deterministic assembly processes were linked to organic matter chemistry have been
 465 observed in the hyporheic zone (Stegen et al., 2018), which is a very different type of
 466 ecosystem. Common outcomes across different systems point to a broad influence of organic
 467 matter chemistry on microbial community assembly.

468 We further find that assembly processes were linked to ecosystem function, but that this
 469 link was indirectly mediated through community composition. VPA indicated that the
 470 assembly processes and community compositions largely explained straw decomposition
 471 within each experimental site (Figs. 7A-C). However, assembly processes alone did not
 472 explain a significant amount, which is not surprising given the consistently dominant
 473 influence of homogeneous selection at each stage (Figs. 3D-F). Under deterministic selection,
 474 taxa succeed or fail in a given ecosystem based on how well their functional traits align with
 475 environmental conditions (Webb, 2000; Horner-Devine and Bohannan, 2006). In our study,
 476 communities contained taxa that have been reported to possess functional traits involved in
 477 straw decomposition (Fig. 6 and Supplementary data). Particularly, at week eight, the
 478 community appeared to possess functional traits for decomposition of cellulose (mainly
 479 contributed by Unclassified *Ruminococcaceae* (Schmidt et al., 2015), *Sporobacter*
 480 (Grech-Mora et al., 1996), Unclassified BRC1 and Unclassified *Prolixibacteraceae* (Huang et
 481 al., 2014)), hemicellulose (mainly contributed by Unclassified *Ruminococcaceae* (Li et al.,
 482 2012) and Unclassified BRC1), and lignin (mainly contributed by Unclassified

483 *Ruminococcaceae* (Wu and He, 2013) and Unclassified *Prolixibacteraceae*). We infer that
 484 straw decomposition may have been facilitated by the deterministic assembly of taxa that
 485 were well-adapted to degrade straw (Figs. 2, 6 and S3).

486 In contrast to determinism favoring particular microorganisms that are functionally
 487 optimized for their environment, stochasticity can result in more diversified functional traits
 488 of microorganisms, but at the cost of suppressing their ecosystem function (Knelman and
 489 Nemergut, 2014; Graham et al., 2016; Graham and Stegen, 2017). Consistent with this
 490 influence of stochasticity, we observed decreased decomposition rates at week sixteen (the
 491 inset of Fig. 1A), during which stochastic assembly was more influential (Figs. 3D-F). As
 492 discussed above, our results indicate that this release from determinism (i.e., increase in
 493 stochasticity) was due to an increase in labile monomers that could be degraded by a broader
 494 range of taxa. Taken together, the above outcomes strongly suggest that straw chemistry
 495 heavily influences assembly processes, in some cases increasing determinism and in other
 496 cases increasing stochasticity, which is indirectly linked to straw decomposition via shifts in
 497 community composition.

498 **4.3. Caveats**

499 Our results align with previous studies across different ecosystem types, which in
 500 encouraging in terms of collectively building generalizable understanding of ecological
 501 assembly processes and the factors that influence these processes. As with all studies, there
 502 are nonetheless caveats to consider and build upon in future investigations. For example, the
 503 OTU richness of straw-decomposing bacteria increased across decomposition stages (Fig. S5).
 504 While this may influence null modeling outcomes, changes in richness result from assembly
 505 processes. Any connection between richness and null model outcomes would therefore reflect
 506 real changes in assembly processes, not a methodological artefact. Another consideration is
 507 the potential for a systematic increase in bacterial cell density across decomposition stages
 508 due to colonization and growth. While we did not measure cell density, if it had increased
 509 systematically, we would have observed a decrease in OTU richness and a decrease in β NTI
 510 (i.e., more negative) due to progressively under-sampling the community. Neither of these
 511 patterns were observed, indicating that our results were not significantly influenced by
 512 progressive increases in cell density. It should be noted, however, that our analyses focused
 513 on dominant taxa due to the relatively limited sequencing depth; we encourage future studies
 514 to sequence more deeply to understand the role of less abundant taxa. Furthermore, our

515 inferences linking assembly processes to straw degradation make the implicit assumption that
 516 taxa associated with straw were involved in straw decomposition. While we cannot directly
 517 evaluate this assumption, it is supported by large compositional differences between soils and
 518 straw (Figs. 2A-C and Table S5; Fig. S3) and among stages (Figs. 2D-F and Table S5). All
 519 studies have caveats, and those discussed above should be considered in the design of future
 520 studies. However, none of the caveats discussed above should alter the conceptual inferences
 521 drawn from our results. Because individual elements of our results align with previous studies,
 522 we suggest that our findings provide potentially generalizable insights into relationships
 523 among microbial assembly processes, community composition, and organic matter
 524 decomposition.

525 **5. Conclusion**

526 Our results indicate that variable selection resulted in divergence between soil and straw
 527 microbial communities via selection for bacterial subgroups from soils during straw
 528 decomposition, while homogeneous selection constrained community composition within
 529 decomposition stages, and ecological drift had important influences on community succession
 530 across decomposition stages. Such patterns of ecological assembly processes appear to be
 531 strongly influenced by straw chemistry, and indirectly linked to decomposition via shifts in
 532 microbial community composition.

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772 **Figure legends**

773 **Figure 1.** Patterns of the decomposition ratio of rice straw (A), the stereoscopic pictures (B)
 774 and straw chemical components (based on proportions of initial material) (C) and functional
 775 groups (based on relative proportions of remaining material) (D). The inset of A is the
 776 decomposition rate at different decomposition stages. The insets of C are the changing
 777 patterns of WSP among decomposition stages in the three experimental sites. Means indicate
 778 average values of dry mass loss and vertical error bars indicate standard deviations of means
 779 ($n = 12$). Different letters over error bars denote significant differences ($P < 0.05$).

780 **Figure 2.** Nonmetric multidimensional (NMDS) analysis of bacterial communities, based on
 781 β MNTD distance, between the soil matrix and straw (A-C, $n=120$, each plot) as well as
 782 among straw-associated (D-F, $n=60$, each plot) across decomposition stages. Permutational
 783 analysis of multivariate dispersions (PERMDISP) showing mean \pm SD distance to the group
 784 centroid based on β MNTD distance (G-I, $n=60$, each plot) of the straw-associated community
 785 across decomposition stages within each experimental site. Different letters over error bars
 786 denote significant differences ($P < 0.05$).

787 **Figure 3.** Contributions of ecological assembly processes governing bacterial community
 788 turnover between the soil matrix and straw (A-C) as well as among straw-associated
 789 community composition within decomposition stages (D-F) and across decomposition stages
 790 (G-I), within each experimental site.

791 **Figure 4.** Redundancy analysis (RDA) relating bacterial community composition to straw
 792 chemical properties based on β MNTD distance. A-C use straw chemical function groups and
 793 D-F use straw chemical components.

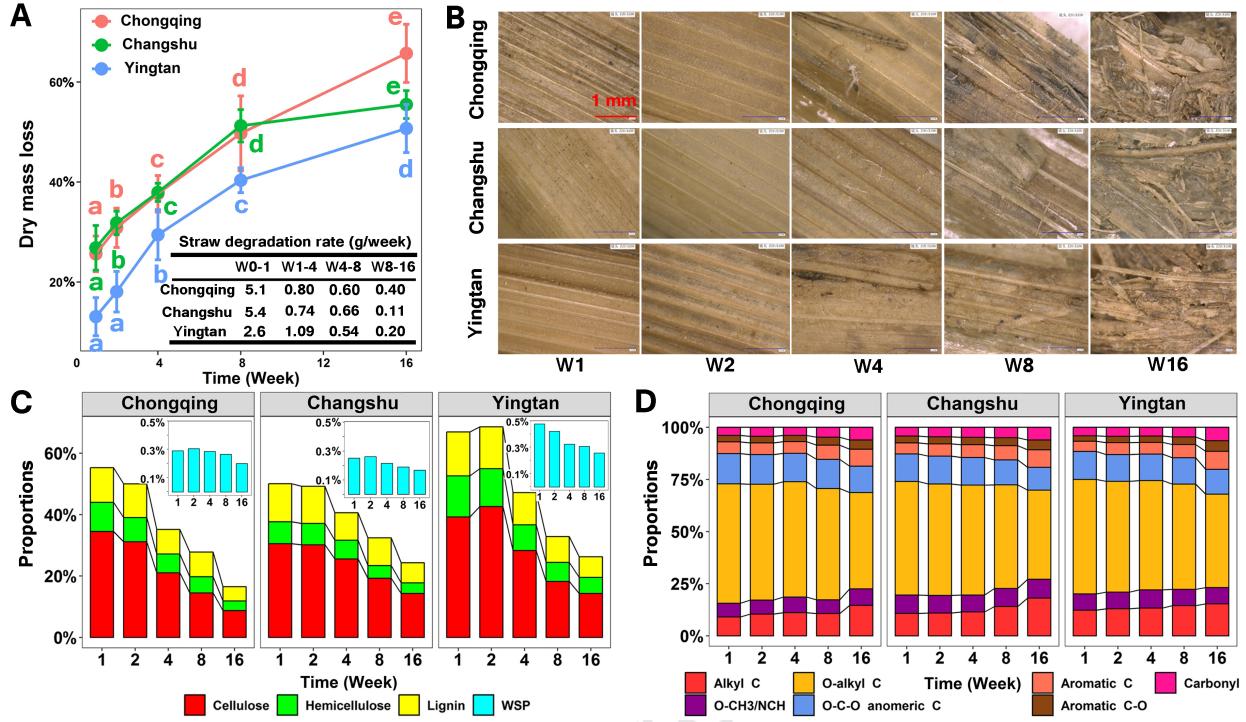
794 **Figure 5.** Distance matrix regressions between β NTI and variations in straw chemistry during
 795 decomposition within each experimental site. Horizontal axes indicate Euclidean distances
 796 based on all straw functional groups (A-C) or components (D-F). Linear relationships were
 797 evaluated by Mantel test (p -value provided on each panel). Linear models (shown as blue
 798 lines) and associated correlation coefficients are provided on each panel. Horizontal dashed
 799 lines indicate the β NTI significance thresholds of +2 and -2.

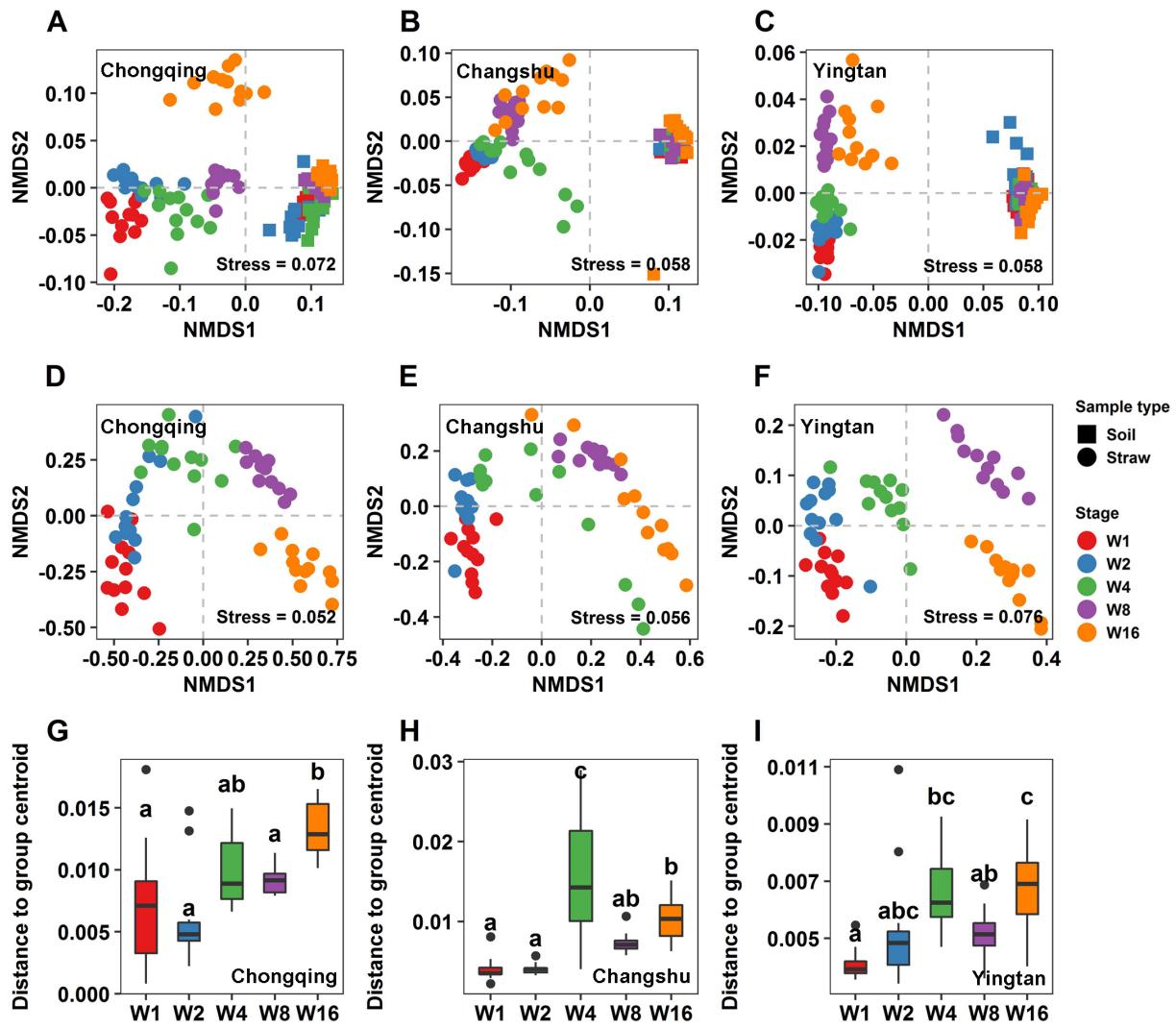
800 **Figure 6.** Predictor importance (percentages of increase in mean square error (MSE) between
 801 observations and OOB predictions) of the top 20 bacterial taxonomic biomarkers and their
 802 relative abundances (standardized by Z-score transformation) within straw decomposition

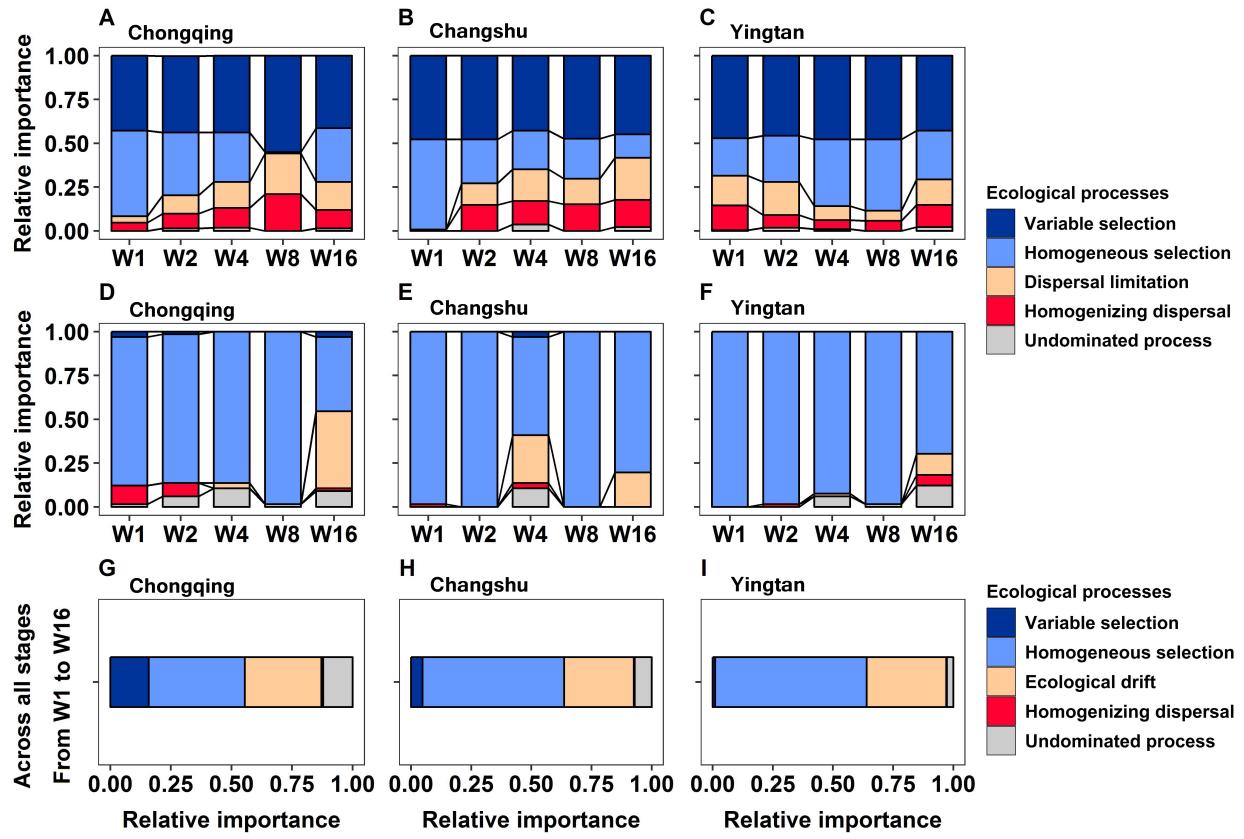
803 stages across three experimental sites.

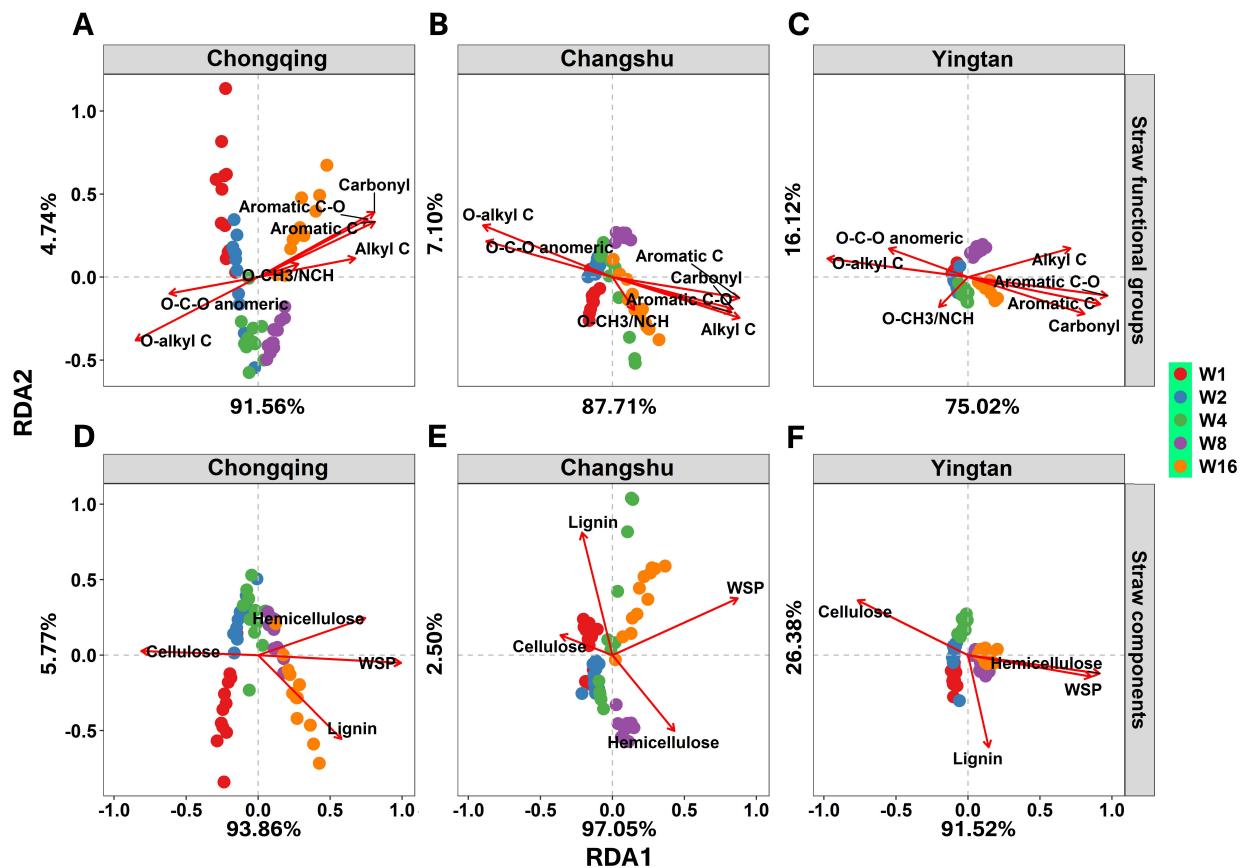
804 **Figure 7.** Variation partitioning analysis (VPA) differentiating contributions of bacterial
805 community composition (the first axis of PCoA based on β MNTD distance) and assembly
806 processes (the first axis of PCoA based on β NTI distance) on straw decomposition within
807 each experimental site.

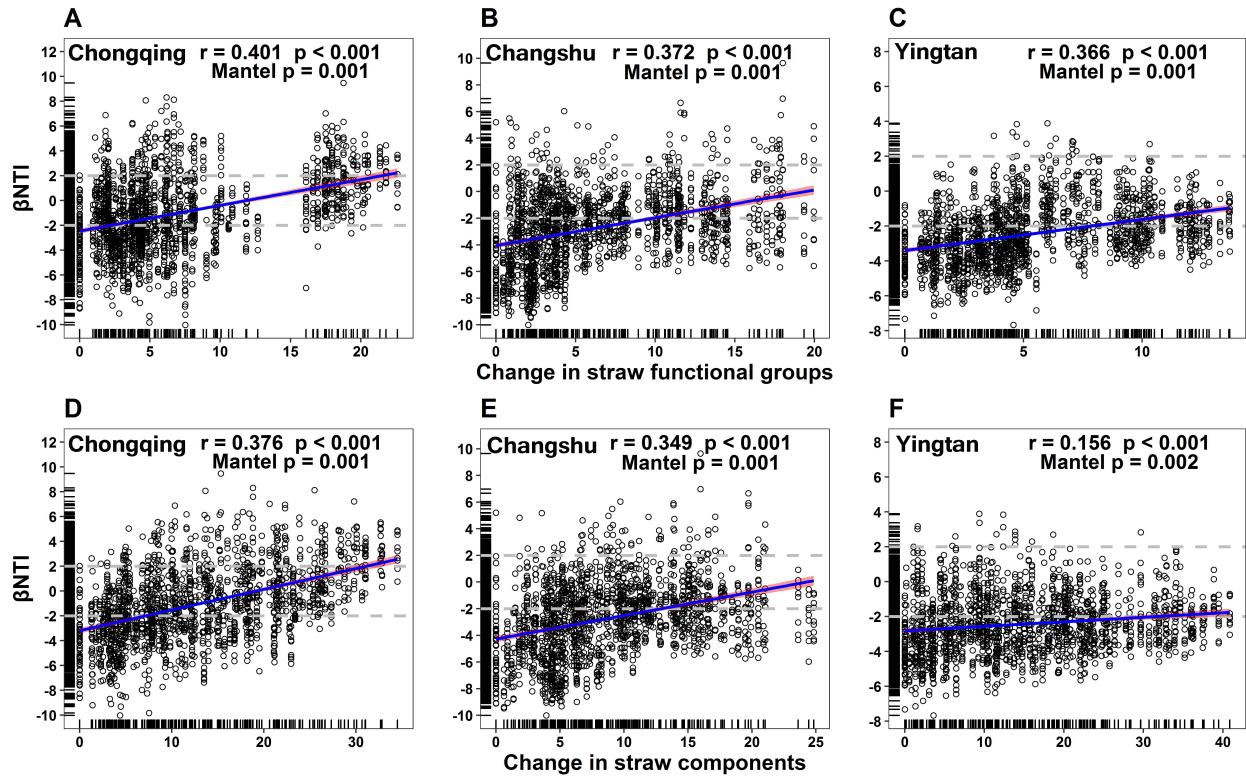
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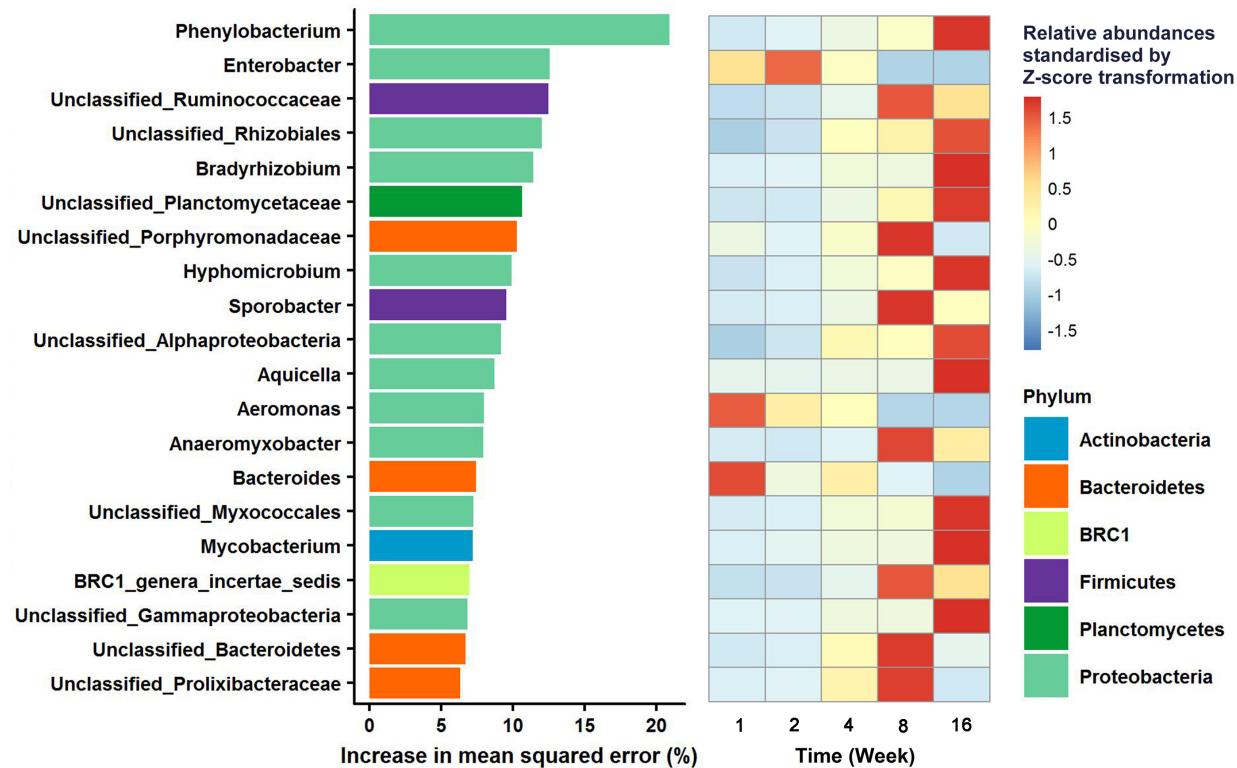


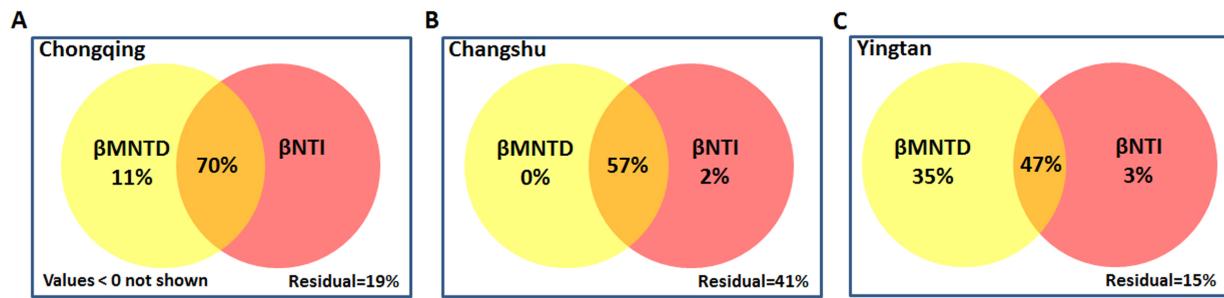












Highlights

- Variable selection selects bacterial subgroups from soils for straw decomposition
- Homogeneous selection governs community composition within decomposition stages
- Ecological drift has important influences across decomposition stages
- Assembly processes influence decomposition via shifts in community composition
- Straw chemistry governs assembly processes of community for straw decomposition

Declaration of Interest Statement

We confirm that this manuscript has not been published elsewhere, is not under consideration by another journal, and that all authors have seen this manuscript and approve its submission to *Soil Biology and Biochemistry*. The authors declare no conflicts of interest.