

1 **Consequences of tropical forest conversion to oil palm on soil bacterial community**
2 **and network structure**

3

4 Stephen A. Wood^{1,2*}, Jack A. Gilbert^{3,4}, Jonathan W. Leff⁵, Noah Fierer⁵, Heather
5 D'Angelo⁶, Carling Bateman⁷, Seren M. Gedallovich⁷, Caitlyn M. Gillikin⁷, Mary R.
6 Gradoville⁸, Patahayah Mansor⁹, Audrey Massmann⁷, Nina Yang⁷, Benjamin L. Turner¹⁰,
7 Francis Q. Brearley¹¹, Krista L. McGuire^{6,7}

8

9 ¹ Yale School of Forestry & Environmental Studies, New Haven, CT USA 06511

10 ² The Nature Conservancy, Arlington, VA USA 22203

11 ³ The Microbiome Center, Argonne National Laboratory, Lemont, IL USA 60439

12 ⁴ Department of Surgery, University of Chicago, Chicago, IL USA 60637

13 ⁵ Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO
14 USA 80302

15 ⁶ Department of Ecology, Evolution & Environmental Biology, Columbia University,
16 New York, NY USA 10027

17 ⁷ Department of Biology, Barnard College of Columbia University, New York, NY USA
18 10027

19 ⁸ College of Earth, Ocean, and Atmospheric Sciences, Oregon State University, Corvallis,
20 OR USA 97331

21 ⁹ Forest Research Institute Malaysia, 52109 Kepong, Selangor, Malaysia

22 ¹⁰ Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancon,
23 Republic of Panama

24 ¹¹ School of Science and the Environment, Manchester Metropolitan University,
25 Manchester, UK
26 * Corresponding author: stephenawood@gmail.com; 370 Prospect St., New Haven, CT,
27 06511

28

29 **Abstract**

30 Tropical forest conversion to agriculture is a major global change process. Understanding
31 of the ecological consequences of this conversion are limited by poor knowledge of how
32 soil microorganisms respond. We analyzed the response of soil bacteria to conversion
33 from primary rain forest to oil palm plantation and regenerating logged forest in
34 Malaysia. Bacterial diversity increased by approximately 20% with conversion to oil
35 palm because of higher pH due to liming by plantation managers. Phylogenetic clustering
36 indicated that bacterial communities were determined by environmental filtering.
37 Regenerating logged forests did not have significantly different soil chemistry, which did
38 not correspond with significant differences in bacterial richness, diversity, or the relative
39 abundances of particular taxa. However, there were significant differences in the
40 structure of bacterial community networks between regenerating logged forests and
41 primary forests, highlighting previously unobserved effects of these two land uses.
42 Network analysis highlighted taxa that are potentially central to bacterial networks, but
43 have low relative abundances, suggesting that these rare taxa could play an ecological
44 role and therefore warrant further research.

45

46 **Keywords:** bacteria; microbial diversity; microbial networks; oil palm; rare microbes;
47 tropical deforestation

48 **1. Introduction**

49 Tropical forests have long been under threat of conversion to other land uses—more than
50 half of the original extent of rain forests has been converted (Asner et al., 2009). Since tropical
51 forests are home to more than two-thirds of all terrestrial plant and animal species (Brooks et al.,
52 2002; Dirzo and Raven, 2003; Gardner et al., 2009), this loss of tropical forest comes hand-in-
53 hand with a loss in biodiversity. Yet this story of conversion and species loss may or may not
54 translate to loss of the huge diversity of soil organisms found under foot.

55 Soil microorganisms, which make up the bulk of soil diversity, are widely recognized to
56 be essential to the functioning of terrestrial ecosystems. Microbial activity is responsible for
57 many biogeochemical redox reactions (Falkowski et al., 2008). Both negative and positive
58 feedbacks between soil organisms and plant communities contribute to ecological structure and
59 functioning in the tropics (Bagchi et al., 2010; Kiers et al., 2000; Mangan et al., 2010). Given the
60 importance of soil microorganisms to biogeochemical cycling and plant-soil feedbacks,
61 understanding if soil microbes are threatened by large-scale tropical land-use change is necessary
62 to understand and predict broader functional consequences of land-use change.

63 An growing body of work has documented how soil microbial communities respond to
64 human-induced environmental change (Thomas W Crowther et al., 2014; da C Jesus et al., 2009;
65 de Carvalho et al., 2016; Fierer et al., 2012; Lee-Cruz et al., 2013; Leff et al., 2015; McGuire et
66 al., 2015; Ramirez et al., 2012, 2010; Rodrigues et al., 2013; Tripathi et al., 2016; Wood et al.,
67 2015). Several consistent patterns have emerged from this work. Changes in the bacterial
68 community are largely governed by changes in soil chemical properties, mainly pH (Lauber et
69 al., 2009; Rousk et al., 2010). Bacterial diversity decreases sharply with decreases in pH, partly
70 due to an associated increase in the relative abundance of taxa such as *Acidobacteria*. By

71 contrast, fungi are less sensitive to changes in pH. Instead, the dominant control on fungi tends to
72 be a combination of factors such as soil carbon, local soil moisture, and plant composition
73 (Barberán et al., 2015; Fierer et al., 2003; Prescott and Grayston, 2013; Prober et al., 2015;
74 Toberman et al., 2008). The response of soil microbial communities to land-use change is in part
75 determined by the properties of the underlying soil, with the greatest difference between forest
76 communities and grassland communities occurring on sandier soils (Thomas W Crowther et al.,
77 2014). This constraint of soil type may be due to lower moisture and carbon holding capacity in
78 sandier soils or inability of sandier soil to buffer against changes in pH, which are dominant
79 controls of fungal and bacterial communities, respectively.

80 These now robust patterns rely on inference generated from the relative abundance of soil
81 microbes, whether directly or through abundance-weighted diversity metrics. Most microbial
82 taxa are, however, rare (Locey and Lennon, 2016)—i.e. low in relative abundance—and these
83 abundance-weighted metrics may miss possible contributions of rare species. In plant
84 communities, rare species can make important contributions to ecosystem structure and function
85 (Jain et al., 2014; Lyons and Schwartz, 2001). Whether the same is true for microbes remains
86 less well known, but evidence is mounting that loss of rare microbial taxa can play an important
87 role in community structure (Shade et al., 2014) and ecosystem functioning, especially through
88 modifying plant-soil feedbacks (Hol et al., 2015, 2010). Rare taxa, by virtue of being rare, may
89 exhibit different life history strategies than abundant taxa (Murray et al., 2002) and therefore
90 respond differently to land-use change. If this is the case, then understanding their responses may
91 highlight different trends in the response of microbial communities to land-use change. Network
92 analysis, which has been widely used to study the impacts of global change on plant and animal
93 diversity (Ings et al., 2009), may help inform understanding of the ecological role of rare bacteria

94 by highlighting how rare taxa co-occur with well-studied taxa, which could indicate similar
95 ecological roles between rare and well-studied taxa (Ma et al., 2016).

96 Based on the literature cited above showing that bacterial communities are strongly
97 structured by abiotic conditions, we expected that bacterial community composition and diversity
98 would follow land-use changes that modified soil chemical properties, particularly pH. Because
99 McGuire et al (2015) found elevated pH under oil palm—but no differences between
100 regenerating and primary forests—we expected that bacterial diversity and community
101 composition would differ between oil palm and the native forest types, but not among the native
102 forest types. For network composition, a chronosequence of abandoned agricultural land showed
103 that fungal networks became more connected in older sites with a shift towards more fungal-
104 dominated food webs (Morriën et al., 2017). Based on this we developed two competing
105 hypotheses: (H1) bacterial network structure follows patterns observed in fungi and becomes
106 more interconnected moving from disturbed to primary vegetation; (H2) because food webs shift
107 to fungal dominance under primary vegetation, bacterial networks decrease in complexity as
108 fungal communities increase in complexity.

109 To evaluate our expectations and the consequences of forest conversion on soil microbial
110 composition, we compared bacterial communities from three sites in Malaysia: a primary
111 lowland mixed dipterocarp forest, a regenerating dipterocarp forest that had been selectively
112 logged 50 years ago, and a 25-year old oil palm plantation. Over the past few decades, palm oil,
113 the commercial commodity extracted from the oil palm plant (*Elaeis guineensis*; Arecaceae) has
114 been the most rapidly growing crop in the tropics. Indonesia and Malaysia alone account for
115 more than 80% of all palm oil production and not coincidentally, this region of the world also
116 experiences the highest proportional rate of deforestation (Carlson et al., 2012; Hansen et al.,

117 2013). Thus, oil palm plantations are highly relevant for evaluating the consequences of large-
118 scale tropical deforestation on soil microbial communities.

119

120 **2. Material and methods**

121 *2.1 Site description and field sampling*

122 Soil samples were collected from lowland sites in peninsular Malaysia in the state of
123 Negeri Sembilan, as previously described (McGuire et al., 2015). Briefly, we sampled from three
124 land-use types: primary rain forest (primary forest), forest regenerating from logging 50 years
125 prior (regenerating forest) and an oil palm plantation in active cultivation for 25 years (oil palm).
126 The regenerating and primary forests area are located in the Pasoh Forest Reserve (2°5' N,
127 102°18' W, 80 m asl), with the Dipterocarpaceae family comprising nearly one-third of the basal
128 area of canopy trees (Manokaran et al., 2004). The oil palm plantation was located less than 500
129 m from the Pasoh Forest Reserve. Climate in this region is aseasonal with mean annual
130 precipitation of 1,788 mm and average minimum and maximum temperatures of 22.7 and 33.2 C,
131 respectively. The dominant soil type in the lowland forest plots sampled is Ultisols (Adzmi et al.,
132 2010).

133 Within each land-use type (primary forest, regenerating forest, and oil palm plantation),
134 three replicate plots (20 x 20 m) were established and five soil samples were collected from each
135 plot during a single sampling event. All sampling plots were at least 1 km away from each other,
136 but selected on the same underlying soil type and slope position. The collected samples were
137 divided into three sampling depths: 0-2 cm, 2-10 cm, and 10-20 cm. All plots were separated by
138 at least 500 m. Sample replicates were composited by depth to one sample per depth, per plot
139 and were placed in sterile plastic bags, sealed and frozen at -20 °C on the day of collection. In the

140 laboratory, all soil samples were passed through a 2 mm sieve, homogenized, and stored frozen
141 at -20°C until laboratory analyses were performed.

142

143 *2.2 Laboratory analyses*

144 We amplified and sequenced a portion of the 16S rRNA gene to assess bacterial
145 communities in a similar manner as described previously (Caporaso et al., 2012). Amplifications
146 were performed on DNA isolates from the MoBio PowerSoil extraction kit (MoBio, Carlsbad,
147 CA), which were the isolates used for prior analysis of soil fungi (McGuire et al., 2015). PCR
148 amplification was performed with the primers 515f and 806r, which included sequencing
149 adapters for the Illumina sequencing platform, and the reverse primer contained a 12-bp barcode
150 unique to each sample. Amplicons combined and sequenced on an Illumina MiSeq instrument
151 using a paired-end 151-bp sequencing kit. Raw amplicon sequences were demultiplexed and
152 processed with the UPARSE pipeline (Edgar, 2013) as in Ramirez et al (Ramirez et al., 2014).
153 Paired end sequence reads were merged prior to additional processing. Sequences were quality
154 filtered using a “maxee” value of 0.5 and singletons were removed. Sequences were clustered
155 into operational taxonomic units at a threshold of $\geq 97\%$ sequence similarity. Merged,
156 demultiplexed sequences were mapped against our *de novo* database of clustered OTUs to get
157 counts of sequences per OUT and sample. Taxonomy was assigned to OTUs using the RDP
158 classifier (Wang et al., 2007) with a confidence threshold of 0.5 and trained on the Greengenes
159 database (McDonald et al., 2012). Samples were rarefied to 7,000 sequences per sample prior to
160 downstream analysis. Previous analyses focused on analysis of fungal community dynamics
161 contain data on microbial biomass, enzymatic activity, fungal diversity, fungal composition, and
162 soil physical and chemical properties (D’Angelo et al., 2015; McGuire et al., 2015).

163

164 2.3 Analytic methods

165 2.3.1 Diversity

166 We calculated several common ecological diversity metrics including species richness,
167 evenness, Shannon, and Faith's Phylogenetic Diversity (PD). Shannon is a diversity metric
168 where the relative abundance of species is weighted by evenness. Faith's PD sums the branch
169 lengths of a phylogeny for a given site and uses the resulting branch length sum as a metric of
170 phylogenetic diversity. Diversity metrics were calculated for each site using the *vegan* package
171 (Oksanen et al., 2016) of R (Core, 2016), except for phylogenetic diversity, which was calculated
172 in the *picante* package (Kembel et al., 2010).

173

174 2.3.2 Phylogenetic analysis

175 Assessing the extent of phylogenetic clustering in a community can be used to infer the
176 degree to which communities are likely structured by environmental filtering or competition
177 (Cavender-Bares et al., 2009; Webb and Ackerly, 2002). Using this approach, the observed
178 phylogenetic distribution of a community is compared to a null model or randomization
179 procedure to determine whether the observed phylogeny is more or less clustered than would be
180 expected at random. Clustering suggests environmental factors structure community assembly,
181 whereas overdispersion suggests that biological interactions, such as competition, are the
182 dominant force in community assembly. To apply this approach, we used a phylogeny generated
183 from sequence OTUs to create a community dissimilarity matrix in the *picante* package in R
184 (Kembel et al., 2010). We then calculated a relative abundance-weighted standardized effect size
185 for mean pairwise distance (MPD) and mean nearest neighbor distance (MNTD), which are

186 metrics of mean pairwise phylogenetic distance within the community (Webb et al., 2008). MPD
187 calculates mean pairwise distance between all OTUs in each site. MNTD calculates the average
188 distance separating each OTU in a site from its nearest phylogenetic relative. The standardized
189 effect size of these metrics compares the observed phylogenetic distribution to an expected
190 distribution under some null model or randomized scenario. To ensure robustness of our
191 approach, we calculated MPD and MNTD using two null model scenarios, one that randomizes
192 the tips of the phylogeny (Tip Randomization) and a second that randomizes that community
193 abundances within samples, but holds richness constant (Richness Randomization).

194

195 2.3.3. Network analysis

196 To analyze network structure, we used data on the relative abundances of bacterial taxa
197 by land-use types to create a taxonomic association network. This procedure suggests an
198 association network by comparing observed taxonomic co-occurrences with a set of predicted
199 co-occurrences from null models with the same richness and relative abundances as the observed
200 community. Standardized effect-size scores are calculated for the observed vs. predicted data,
201 significant associations are retained, and scores are converted to an association network. We
202 generated association networks using the *netassoc* package (Blonder and Morueta-Holme, 2015).

203 We calculated a number of statistics to characterize the nature of networks under the
204 three land-use categories. Modularity measures the compartmentalization of a network into sub-
205 networks, or modules (Newman, 2006). High modularity scores indicate the presence of many
206 connections among vertices within a module, but few connections to vertices of different
207 modules. We calculated modularity using the *modularity* function in the *igraph* package (Csardi
208 and Nepusz, 2006). Assortativity measures the tendency for similar vertices to be linked with

209 each other (Newman, 2002). We calculated assortativity using the *assortativity_degree* function
210 in the *igraph* package. Transitivity represents the likelihood that neighboring vertices are linked,
211 and then linked to other adjacent vertices à la transitivity property (Barrat et al., 2004). We
212 calculated transitivity using the *transitivity* function in the *igraph* package. We also determine,
213 for each land-use category, which taxa (vertices) had the highest number of paths connected to
214 other vertices. This is also known as betweenness or network centrality (Freeman, 1978). We
215 calculated this using the *vertex_connectivity* function in the *igraph* package.

216 To determine whether network statistics were significantly different among the three
217 land-use categories, we generated 10,000 random networks with similar sizes and calculated the
218 mean and standard deviation of the same statistics. We then calculated a z-score for each of the
219 observed networks to determine how many standard deviations it fell away from the expected
220 value given from the network randomization procedure. The randomly generated network was a
221 regional network that had the same number of vertices and edges as the observed network that
222 includes all sites, regardless of land-use category. Comparing to this regional network therefore
223 highlights how environmental changes would affect the locally observed network.

224

225 2.3.4 Statistical analyses

226 We determined bacterial community similarity among land-use types and soil horizons
227 using ANOSIM; non-metric multi-dimensional scaling (NMDS) was used to visualize clusters.
228 We used linear models to determine the impact of land-use type on bacterial diversity. We first
229 tested response variables for normality using the Shapiro-Wilk test. In cases of non-normality,
230 response variables were transformed using a Box-Cox transformation. All differences were

231 considered significant at a 0.05 threshold and marginally significant at a 0.10 threshold (Hurlbert
232 and Lombardi, 2009).

233

234 **3. Results**

235 The soil bacterial community did not differ by sampling depth (ANOSIM $R = -0.05$, $P =$
236 0.77). We therefore pooled samples across depths to increase sample size and statistical power.

237 Because samples collected from the same site at different depths are not independent, we
238 controlled for non-independence by clustering standard errors of all samples from the same site.

239 We observed a significant difference in the soil bacterial community among land-use types
240 (ANOSIM $R = 0.59$, $P < 0.01$). Specifically, oil palm soil bacterial communities clustered

241 independently of regenerating and primary forest (Figure 1; Stress = 0.06). There was strong

242 evidence that bacterial communities from all land-use types were phylogenetically clustered (as

243 opposed to overdispersed) relative to a null model (MPD & MNTD < 0 ; $P = 0.01$; Table 1).

244 There was no evidence for significant differences in the degree of phylogenetic clustering among
245 land-use types.

246

247 *3.1 Diversity*

248 To explore the nature of the difference between bacterial communities, we assessed

249 potential differences in several ecological diversity metrics. We observed significantly elevated

250 diversity of soil bacteria in oil palm compared to regenerating and primary forests (Table 2). For

251 instance, Shannon diversity of soil bacteria increased by approximately 20% under oil palm,

252 compared to primary and regenerating forests ($p < 0.001$). This general pattern was robust to all

253 diversity indices used, including species richness ($p < 0.001$), evenness ($p = 0.001$), and Faith's

254 phylogenetic diversity ($p < 0.001$). Statistical models that included only land-use type as
255 predictor variables, explained between 50% and 77% of the variation in diversity metrics (Table
256 2).

257

258 *3.2 Community Composition*

259 We observed significant changes in the relative abundances of several key taxa among
260 land-use types (Figure 2; $p < 0.05$ for all groups shown). The most significant changes were
261 between oil palm and the two forest types, with little difference between regenerating and
262 primary forests. Most taxa increased in relative abundance under oil palm, compared to
263 regenerating and primary forest (Figure 2). A notable exception was *Acidobacteria*, which was
264 the only taxonomic group to significantly decrease in relative abundance (by approximately
265 40%) under oil palm compared to regenerating and primary forest.

266

267 *3.3 Network Structure*

268 Networks of soil bacterial communities were more modular under oil palm and logging
269 than was expected at random, given the taxa present in the regional species pool (Figure 3; Table
270 3a, b). Regenerating forests were around eight times more modular, and oil palm plantations
271 approximately five times more modular, than primary forests, but oil palm was only 0.4 times
272 less modular than regenerating forests. Similar taxa were 2.5 times less likely to be associated
273 with each other under oil palm compared to primary forests, whereas similar taxa were three
274 times more likely to be associated in regenerating forest soil compared to primary forest (Figure
275 3; Table 3a, b). All land-use types had similar values of transitivity—the likelihood that
276 neighboring vertices are linked—but were all less than expected by random (Table 3a, b).

277 For all taxa, we calculated the number of edges connecting to other vertices, for each
278 land-use type. We found that several taxa played central roles (high degree of connectivity) in
279 certain land-use networks, but were not present or were unimportant in others (Figure 3; Table
280 4). For instance, *Acidobacteria* had 244 connections under oil palm, but not under regenerating
281 or primary forest. *Actinobacteria* had 250 connections under primary forest, but none under
282 regenerating forest and oil palm. *NKB19* was not present under oil palm and regenerating forest,
283 but had the most connections under primary forest. *Planctomycetes* and *Gemmatimonadetes* were
284 two of the most central taxa under regenerating forest soils, but neither had connections in either
285 oil palm or primary forest. Some taxa were central across all land-use types, such as *GN02* and
286 *Nitrospirae*.

287 The regenerating forest network had the fewest number of taxa co-occurring, but most
288 relationships were high in magnitude—whether positive or negative (Figure 4). Oil palm had the
289 most co-occurrence relationships, but was dominated by a few strong positive interactions
290 (Figure 4). Primary forest had a mix of positive and negative interactions, both weak and strong
291 (Figure 4). The correlation between the relative abundances of two taxa was a significant
292 predictor of the co-occurrence strength between those two taxa ($P < 0.00$), but explained only
293 19% of the variance in co-occurrence scores.

294

295 **4. Discussion**

296 *4.1 Effects of oil palm on the soil bacterial community*

297 We expected that bacterial diversity would be greatest under oil palm because of greater
298 pH. We found support for this hypothesis, which conforms with other work in tropical forests
299 that find increases in measures of bacterial diversity after conversion of tropical forest (da C

300 Jesus et al., 2009; de Carvalho et al., 2016; Lee-Cruz et al., 2013; Rodrigues et al., 2013; Tripathi
301 et al., 2016). Increases in bacterial diversity were associated with significant increases in
302 evenness, suggesting a disrupted microbial community. In our study, conversion of primary
303 forest to oil palm plantation was associated with an increase in pH—from 4.7 ± 0.1 to
304 5.1 ± 0.1 (Brearley, 2015; McGuire et al., 2015). Higher pH is often associated with greater soil
305 bacterial diversity, with the slope of this relationship greatest in low pH conditions (Lauber et al.,
306 2009). Because of highly acidic tropical forest soils, oil palm plantation managers lime soils for
307 improved production (Tripathi et al., 2012). Since pH is the dominant driver of soil bacterial
308 communities across biomes (Lauber et al., 2009; Rousk et al., 2010; Tripathi et al., 2013, 2012),
309 an increase in bacterial diversity accompanying liming conforms with expectations from the
310 literature. Our observed decrease in the relative abundance of *Acidobacteria*—which tend to have
311 higher relative abundances with low pH—in oil palm soils also supports our conclusion that
312 changes in the bacterial community under oil palm cultivation were largely due to changes in pH.
313 This claim is furthermore supported by our finding that the bacterial community is highly
314 phylogenetically clustered, which is often used to infer that environmental filtering is the
315 dominant driver of community assembly (Cavender-Bares et al., 2009). Other work has found
316 evidence for abiotic stress leading to phylogenetic clustering of soil bacteria (Goberna et al.,
317 2014).

318

319 *4.2. Bacterial communities in regenerating vs. primary forest*

320 We found little evidence of differences in bacterial diversity and community composition
321 between regenerating and primary forest. Similar findings have been made in a similar system in
322 Borneo (Lee-Cruz et al., 2013; Tripathi et al., 2016, 2012). Network analysis, however,

323 illuminated previously unnoticed differences in the structure of bacterial communities between
324 primary and regenerating forest. We proposed two, competing hypotheses for differences in
325 network structure: (H1) bacterial network structure would increase in complexity towards
326 primary vegetation; (H2) bacterial network structure would become less complex as fungal
327 networks became more complex under primary forest. We found that regenerating forest
328 networks were eight times more modular than primary forest networks, providing evidence that
329 the response of bacterial networks and fungal networks could be different, given that fungal
330 networks have been shown to increase in interaction strength with primary vegetation (Morriën
331 et al., 2017). Regenerating forest and oil palm networks were also significantly more modular
332 than random. Modularity measures the compartmentalization of a network into sub-networks, or
333 modules (Newman, 2006). A lower modularity value indicates that taxa within the network tend
334 to co-occur more with a wider range of other taxa. Ecologically, modularity has been interpreted
335 to indicate partitioning into groups of ecologically similar taxa and, thus, resistance of a network
336 to disturbance and loss of individual species (Burgos et al., 2007; Ding et al., 2015). Based on
337 this interpretation, high modularity in regenerating forest could indicate that these forests include
338 more ecological types than in primary forest.

339 We also found that all land-use types had lower transitivity than random. In some cases,
340 transitivity has been shown to be an indicator that network structure is dominated by keystone
341 species—species whose removal can have a disproportionate effect on overall community
342 structure (Berry and Widder, 2014). Our observed lower-than-random transitivity across all land-
343 use types suggests that bacterial community structure is not highly sensitive to loss of particular
344 taxonomic groupings. Because lower transitivity can be indicative of weaker interactions and
345 couplings within the bacterial community, non-transitive network structure has been inferred as

346 indicative of co-existence (Narisawa et al., 2008). Our finding of lower-than-random transitivity
347 suggests fairly stable co-existence of bacterial types across land-use categories.

348 The taxa that played a key role in bacterial networks were also different between
349 regenerating and primary forests. In regenerating forests, the taxa with the most connections to
350 other taxa were *Planctomycetes*, *GN02*, *Gemmatimonadetes*, and *Nitrospirae*. By contrast, in
351 primary forest the most important taxa were *NKB19*, *ZB3*, *Actinobacteria*, and *Elusimicrobia*.
352 Thus, the network analysis highlights that land use can significantly alter the network structure
353 of the soil bacterial community, even if diversity indices do not show differences.

354 There are several important caveats to drawing ecological interpretations from network
355 topology. Because network structure shows a pattern, it is difficult to infer ecological process
356 based on assessment of the pattern alone (Bascompte, 2007). There are only a few examples of
357 systems in which it is well understood how network typology and form connects to function,
358 many of which tend to be at the cellular rather than ecological level (Ingolia, 2004; Price et al.,
359 2004). As more information becomes available on the ecological strategies of particular
360 microbial taxa—such as how they respond to abiotic conditions—making inference about
361 ecological dynamics from network structure will become more fruitful. Another limitation to co-
362 occurrence network analysis is that the nature of the interactions is vague. Much network
363 analysis in ecology focuses on well defined and quantified biotic interactions, such as food web
364 and mutualistic interactions (Ings et al., 2009). The nature of co-occurrence interactions could be
365 due to several factors, some being more ecologically meaningful than others. Methodologically,
366 network structure can be influenced by the method of network construction and null model
367 testing used (Connor et al., 2016; Weiss et al., 2016).

368 Yet, despite these limitations, network analysis may be a powerful tool to highlight
369 potential ecological roles of understudied taxa. Because many microbial taxa are hard to culture,
370 network analysis may highlight the ecological strategies of organisms that are difficult to observe
371 directly. In our study, we observed that several of the taxa that play important network roles are
372 underdescribed ecologically. For instance, taxa that strongly positively co-occur with a well-
373 studied taxon may play similar ecological roles. This inference is supported by our finding that
374 the overall bacterial community is phylogenetically clustered, meaning that environmental
375 filtering is likely important to bacterial community structure. Co-occurring taxa, therefore,
376 should be co-occurring because they have similar environmental response strategies. However,
377 we observed that correlation in relative abundance only explains 19% of the variation in co-
378 occurrence, which suggests that similar response of taxa's relative abundances to environmental
379 conditions only explains a part of the nature of complex co-occurrence patterns.

380

381 *4.3. Combining diversity, phylogenetic, and network analyses provides more insight*

382 We found many rare taxa with high network centrality highlighting potentially important,
383 but understudied, microbial taxa that are overlooked by analyses of diversity or relative
384 abundance patterns. Specifically, taxa such as *GN02*, *NKB19*, *ZB3*, *NC10*, *AD3*, *Parvarchaeota*,
385 *Armatimonadetes*, and *Fibrobacteres* all played important roles in network centrality, but had
386 low relative abundances. Identifying understudied taxa has previously focused on identifying
387 taxa with high relative abundances in novel systems, such as surprisingly high relative
388 abundances of *Verrucomicrobia* in remnant patches of native prairie across the U.S. Midwest
389 (Fierer et al., 2013). Our approach suggests that rare taxa that are low in relative abundance also
390 warrant further research effort, as they may play an important role in bacterial communities and

391 potentially connect to broader ecosystem functioning—this potential importance of rare taxa has
392 been shown for plant systems (Jain et al., 2014; Lyons and Schwartz, 2001) but not for
393 microscopic taxa that are far less well known but lend themselves well to network analysis due to
394 their high diversity.

395 Further integration of network approaches into microbial analyses requires understanding
396 how patterns between the two approaches overlap. For instance, it will be particularly important
397 to understand when and why relative abundances translate to network importance and when they
398 do not. In our analysis the relative abundance of *Acidobacteria* was lowest in oil palm soils, but
399 *Acidobacteria* had the greatest network centrality. Similarly, *Actinobacteria* relative abundance
400 was lowest in primary forest soils, but had the highest network centrality score. These patterns
401 between relative abundance and network centrality are seemingly idiosyncratic, so further
402 research into the drivers of network influence in the soil bacterial community is needed. This
403 work will likely require improved understanding of life history strategies of microbial taxa,
404 which overlaps with the research needs to develop understanding of microbial functional traits
405 (Aguilar-Trigueros et al., 2015; Thomas W. Crowther et al., 2014; Krause et al., 2014; Martiny et
406 al., 2015; Wallenstein and Hall, 2011; Wieder et al., 2014).

407

408 *4.4 Conclusion*

409 Though soil fungal communities appear to be highly responsive to changes in vegetation
410 and carbon loss (McGuire et al., 2015), changes in bacterial communities under deforestation
411 may be principally driven by changes in environmental conditions associated with land-use
412 change. This implies that diversity changes in bacterial communities may be more ephemeral

413 than changes to fungal communities, given that pH can change over shorter time periods than
414 soil carbon and dominant vegetation structure.

415 Understanding the nature of the change in these bacterial communities has largely
416 focused on shifts in relative abundances and diversity. Our finding that bacterial diversity
417 increases under oil palm aligns with previous findings, but we also shed new light on the nature
418 of bacterial community disassembly with land-use change. Network analysis highlights strong
419 differences in network structure between regenerating and primary forests that do not appear in
420 analyses of diversity or relative abundance patterns. Our analysis identified bacterial taxa that
421 play central roles in network structure, but have low relative abundances. These taxa warrant
422 further research effort to identify their functional roles in the ecosystem.

423 Our finding that the structure of bacterial networks differed between regenerating and
424 primary forests also suggests that microbial community analysis needs to go beyond assessment
425 of diversity and relative abundance patterns to unravel the nature of changes to bacterial
426 communities under land-use change. Analytic tools that go beyond diversity analyses are widely
427 applied in community ecology and our data suggests that greater application of these methods
428 could strongly benefit inference in microbial ecology.

429

430 **Author Contributions**

431 K.L.M., H.D., C.B., S.M.G, C.M.G, M.R.G, A.M, and N.Y designed the field sampling,
432 conducted field work, processed soils, and extracted DNA; B.L.T helped with study design; P.M
433 and F.Q.B helped with study design and field sampling; J.A.G amplified and sequenced DNA;
434 J.L and N.F processed sequence data; S.A.W analyzed data and wrote the first draft of the
435 manuscript; all authors provided feedback on the final version of the manuscript.

436

437 **Acknowledgements**

438 Lee Su See, Stuart Davies, and the Center for Tropical Forest Science assisted with logistical
439 support for field work. Permits were granted by the Forestry Research Institute Malaysia, the
440 Economic Planning Unit of Malaysia, and the United States Department of Agriculture. Research
441 was supported by the National Science Foundation (NSF DEB 1120011 to K.L.M).

442

443 **Conflict of Interest**

444 The authors declare no conflict of interest.

445

446 **References**

447 Adzmi, Y., Suhaimi, W.C., Husni, M.S.A., Ghazali, H.M., Amir, S.K., Baillie, I., 2010.

448 Heterogeneity of Soil Morphology and Hydrology on the 50 Ha Long-Term Ecological
449 Research Plot At Pasoh , Peninsular Malaysia. *Journal of Tropical Forest Science* 22, 21–
450 35.

451 Aguilar-Trigueros, C.A., Hempel, S., Powell, J.R., Anderson, I.C., Antonovics, J., Bergmann, J.,

452 Cavagnaro, T.R., Chen, B., Hart, M.M., Klironomos, J., Petermann, J.S., Verbruggen, E.,

453 Veresoglou, S.D., Rillig, M.C., 2015. Branching out: Towards a trait-based understanding
454 of fungal ecology. *Fungal Biology Reviews* 29, 34–41. doi:10.1016/j.fbr.2015.03.001

455 Asner, G., Rudel, T., Aide, T., DeFries, R., Emerson, R., 2009. A Contemporary Assessment of
456 Change in Humid Tropical Forests. *Conservation Biology* 23, 1386–1395.

457 doi:10.1111/j.1523-1739.2009.01333.x

458 Bagchi, R., Swinfield, T., Gallery, R.E., Lewis, O.T., Gripengberg, S., Narayan, L., Freckleton,

459 R.P., 2010. Testing the Janzen-Connell mechanism: pathogens cause overcompensating
460 density dependence in a tropical tree. *Ecology Letters* 13, 1262–1269. doi:10.1111/j.1461-
461 0248.2010.01520.x

462 Barberán, A., McGuire, K.L., Wolf, J.A., Jones, F.A., Wright, S.J., Turner, B.L., Essene, A.,
463 Hubbell, S.P., Faircloth, B.C., Fierer, N., 2015. Relating belowground microbial
464 composition to the taxonomic, phylogenetic, and functional trait distributions of trees in a
465 tropical forest. *Ecology Letters* 18, 1397–1405. doi:10.1111/ele.12536

466 Barrat, A., Barthelemy, M., Pastor-Satorras, R., Vespignani, A., 2004. The architecture of
467 complex weighted networks. *Proceedings of the National Academy of Sciences* 101, 3747–
468 3752. doi:10.1073/pnas.0400087101

469 Bascompte, J., 2007. Networks in ecology. *Basic and Applied Ecology* 8, 485–490.
470 doi:10.1016/j.baae.2007.06.003

471 Berry, D., Widder, S., 2014. Deciphering microbial interactions and detecting keystone species
472 with co-occurrence networks. *Frontiers in Microbiology* 5. doi:10.3389/fmicb.2014.00219

473 Blonder, B., Morueta-Holme, N., 2015. netassoc: Inference of Species Associations from Co-
474 Occurrence Data.

475 Brearley, F., 2015. Microbial Functioning in Response to a Simulated Drought in Malaysian
476 Rain Forest and Oil Palm Soils, in: Brearley, F., Thomas, A. (Eds.), *Land-Use Change*
477 *Impacts on Soil Processes: Tropical and Savannah Ecosystems*. CABI Publishing,
478 Oxfordshire, UK, pp. 31–40.

479 Brooks, T.M., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Rylands, A.B.,
480 Konstant, W.R., Flick, P., Pilgrim, J., Oldfield, S., Magin, G., Hilton-Taylor, C., 2002.
481 *Habitat Loss and Extinction in the Hotspots of Biodiversity*. *Conservation Biology* 16, 909–

482 923. doi:10.1046/j.1523-1739.2002.00530.x

483 Burgos, E., Ceva, H., Perazzo, R.P.J., Devoto, M., Medan, D., Zimmermann, M., María Delbue,
484 A., 2007. Why nestedness in mutualistic networks? *Journal of Theoretical Biology* 249,
485 307–313. doi:10.1016/j.jtbi.2007.07.030

486 Caporaso, J.G., Lauber, C.L., Walters, W.A., Berg-Lyons, D., Huntley, J., Fierer, N., Owens,
487 S.M., Betley, J., Fraser, L., Bauer, M., Gormley, N., Gilbert, J.A., Smith, G., Knight, R.,
488 2012. Ultra-high-throughput microbial community analysis on the Illumina HiSeq and
489 MiSeq platforms. *The ISME Journal* 6, 1621–4. doi:10.1038/ismej.2012.8

490 Carlson, K.M., Curran, L.M., Ratnasari, D., Pittman, A.M., Soares-Filho, B.S., Asner, G.P.,
491 Trigg, S.N., Gaveau, D.A., Lawrence, D., Rodrigues, H.O., 2012. Committed carbon
492 emissions, deforestation, and community land conversion from oil palm plantation
493 expansion in West Kalimantan, Indonesia. *Proceedings of the National Academy of*
494 *Sciences of the United States of America* 109, 7559–64. doi:10.1073/pnas.1200452109

495 Cavender-Bares, J., Kozak, K.H., Fine, P.V. a, Kembel, S.W., 2009. The merging of community
496 ecology and phylogenetic biology. *Ecology Letters* 12, 693–715. doi:10.1111/j.1461-
497 0248.2009.01314.x

498 Connor, N., Barberán, A., Clauset, A., 2016. Using null models to infer microbial co-occurrence
499 networks. doi:10.1101/070789

500 Core, R.T., 2016. R: A language and environment for statistical computing.

501 Crowther, T.W., Maynard, D.S., Crowther, T.R., Peccia, J., Smith, J.R., Bradford, M.A., 2014.
502 Untangling the fungal niche: the trait-based approach. *Frontiers in Microbiology* 5.
503 doi:10.3389/fmicb.2014.00579

504 Crowther, T.W., Maynard, D.S., Leff, J.W., Oldfield, E.E., McCulley, R.L., Fierer, N., Bradford,

505 M.A., 2014. Predicting the responsiveness of soil biodiversity to deforestation: a cross-
506 biome study. *Global Change Biology* 20, 2983–94. doi:10.1111/gcb.12565

507 Csardi, G., Nepusz, T., 2006. The igraph software package for complex network research.
508 *InterJournal, Complex Systems* 1695, 1–9.

509 D’Angelo, H., McGuire, K., Gillikin, C., Brearley, F., Merrer, D., 2015. Evaluating the Impact of
510 Oil Palm Agriculture and Logging on Soil Microbial Communities in South-east Asia, in:
511 Brearley, F., Thomas, A. (Eds.), *Land-Use Change Impacts on Soil Processes: Tropical and*
512 *Savannah Ecosystems*. CABI Publishing, Oxfordshire, UK, pp. 21–30.

513 da C Jesus, E., Marsh, T.L., Tiedje, J.M., de S Moreira, F.M., 2009. Changes in land use alter the
514 structure of bacterial communities in Western Amazon soils. *The ISME Journal* 3, 1004–11.
515 doi:10.1038/ismej.2009.47

516 de Carvalho, T.S., da Conceição Jesus, E., Barlow, J., Gardner, T.A., Soares, I.C., Tiedje, J.M.,
517 de Souza Moreira, F.M., 2016. Land use intensification in the humid tropics increased both
518 alpha and beta diversity of soil bacteria. *Ecology*. doi:10.1002/ecy.1513

519 Ding, J., Zhang, Y., Deng, Y., Cong, J., Lu, H., Sun, X., Yang, C., Yuan, T., Van Nostrand, J.D.,
520 Li, D., Zhou, J., Yang, Y., 2015. Integrated metagenomics and network analysis of soil
521 microbial community of the forest timberline. *Scientific Reports* 5, 7994.
522 doi:10.1038/srep07994

523 Dirzo, R., Raven, P.H., 2003. Global State of Biodiversity and Loss. *Annual Review of*
524 *Environment and Resources* 28, 137–167. doi:10.1146/annurev.energy.28.050302.105532

525 Edgar, R.C., 2013. UPARSE: highly accurate OTU sequences from microbial amplicon reads.
526 *Nature Methods* 10, 996–998. doi:10.1038/nmeth.2604

527 Falkowski, P.G., Fenchel, T., Delong, E.F., 2008. The microbial engines that drive Earth’s

528 biogeochemical cycles. *Science* 320, 1034–9. doi:10.1126/science.1153213

529 Fierer, N., Ladau, J., Clemente, J.C., Leff, J.W., Owens, S.M., Pollard, K.S., Knight, R., Gilbert,
530 J. a, McCulley, R.L., 2013. Reconstructing the microbial diversity and function of pre-
531 agricultural tallgrass prairie soils in the United States. *Science (New York, N.Y.)* 342, 621–
532 4. doi:10.1126/science.1243768

533 Fierer, N., Lauber, C.L., Ramirez, K.S., Zaneveld, J., Bradford, M.A., Knight, R., 2012.
534 Comparative metagenomic, phylogenetic and physiological analyses of soil microbial
535 communities across nitrogen gradients. *The ISME Journal* 6, 1007–1017.
536 doi:10.1038/ismej.2011.159

537 Fierer, N., Schimel, J.P., Holden, P.A., 2003. Variations in microbial community composition
538 through two soil depth profiles. *Soil Biology and Biochemistry* 35, 167–176.
539 doi:10.1016/S0038-0717(02)00251-1

540 Freeman, L.C., 1978. Centrality in social networks conceptual clarification. *Social Networks* 1,
541 215–239. doi:10.1016/0378-8733(78)90021-7

542 Gardner, T.A., Barlow, J., Chazdon, R., Ewers, R.M., Harvey, C.A., Peres, C.A., Sodhi, N.S.,
543 2009. Prospects for tropical forest biodiversity in a human-modified world. *Ecology Letters*
544 12, 561–582. doi:10.1111/j.1461-0248.2009.01294.x

545 Goberna, M., Navarro-Cano, J.A., Valiente-Banuet, A., García, C., Verdú, M., 2014. Abiotic
546 stress tolerance and competition-related traits underlie phylogenetic clustering in soil
547 bacterial communities. *Ecology Letters* 17, 1191–1201. doi:10.1111/ele.12341

548 Hansen, M.C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau,
549 D., Stehman, S. V., Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L.,
550 Justice, C.O., Townshend, J.R.G., 2013. High-Resolution Global Maps of 21st-Century

551 Forest Cover Change. *Science* 342, 850–853. doi:10.1126/science.1244693

552 Hol, W.H.G., de Boer, W., de Hollander, M., Kuramae, E.E., Meisner, A., van der Putten, W.H.,
553 2015. Context dependency and saturating effects of loss of rare soil microbes on plant
554 productivity. *Frontiers in Plant Science* 6. doi:10.3389/fpls.2015.00485

555 Hol, W.H.G., de Boer, W., Termorshuizen, A.J., Meyer, K.M., Schneider, J.H.M., van Dam,
556 N.M., van Veen, J.A., van der Putten, W.H., 2010. Reduction of rare soil microbes modifies
557 plant-herbivore interactions. *Ecology Letters* 13, 292–301. doi:10.1111/j.1461-
558 0248.2009.01424.x

559 Hurlbert, S., Lombardi, C., 2009. Final collapse of the Neyman-Pearson decision theoretic
560 framework and rise of the neoFisherian. *Annales Zoologici Fennici* 46, 311–349.

561 Ingolia, N.T., 2004. Topology and Robustness in the *Drosophila* Segment Polarity Network.
562 *PLoS Biology* 2, e123. doi:10.1371/journal.pbio.0020123

563 Ings, T.C., Montoya, J.M., Bascompte, J., Blüthgen, N., Brown, L., Dormann, C.F., Edwards, F.,
564 Figueroa, D., Jacob, U., Jones, J.I., Lauridsen, R.B., Ledger, M.E., Lewis, H.M., Olesen,
565 J.M., van Veen, F.J.F., Warren, P.H., Woodward, G., 2009. Review: Ecological networks -
566 beyond food webs. *Journal of Animal Ecology* 78, 253–269. doi:10.1111/j.1365-
567 2656.2008.01460.x

568 Jain, M., Flynn, D.F.B., Prager, C.M., Hart, G.M., Devan, C.M., Ahrestani, F.S., Palmer, M.I.,
569 Bunker, D.E., Knops, J.M.H., Jouseau, C.F., Naeem, S., 2014. The importance of rare
570 species: A trait-based assessment of rare species contributions to functional diversity and
571 possible ecosystem function in tall-grass prairies. *Ecology and Evolution* 4, 104–112.
572 doi:10.1002/ece3.915

573 Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D.,

574 Blomberg, S.P., Webb, C.O., 2010. Picante: R tools for integrating phylogenies and
575 ecology. *Bioinformatics* 26, 1463–1464. doi:10.1093/bioinformatics/btq166

576 Kiers, E.T., Lovelock, C.E., Krueger, E.L., Herre, E.A., 2000. Differential effects of tropical
577 arbuscular mycorrhizal fungal inocula on root colonization and tree seedling growth:
578 implications for tropical forest diversity. *Ecology Letters* 3, 106–113. doi:10.1046/j.1461-
579 0248.2000.00126.x

580 Krause, S., Le Roux, X., Niklaus, P.A., Van Bodegom, P.M., Lennon, J.T., Bertilsson, S.,
581 Grossart, H.-P., Philippot, L., Bodelier, P.L.E., 2014. Trait-based approaches for
582 understanding microbial biodiversity and ecosystem functioning. *Frontiers in Microbiology*
583 5. doi:10.3389/fmicb.2014.00251

584 Lauber, C.L., Hamady, M., Knight, R., Fierer, N., 2009. Pyrosequencing-based assessment of
585 soil pH as a predictor of soil bacterial community structure at the continental scale. *Applied
586 and Environmental Microbiology* 75, 5111–20. doi:10.1128/AEM.00335-09

587 Lee-Cruz, L., Edwards, D.P., Tripathi, B.M., Adams, J.M., 2013. Impact of Logging and Forest
588 Conversion to Oil Palm Plantations on Soil Bacterial Communities in Borneo. *Applied and
589 Environmental Microbiology* 79, 7290–7297. doi:10.1128/AEM.02541-13

590 Leff, J.W., Jones, S.E., Prober, S.M., Barberán, A., Borer, E.T., Firn, J.L., Harpole, W.S.,
591 Hobbie, S.E., Hofmockel, K.S., Knops, J.M.H., McCulley, R.L., La Pierre, K., Risch, A.C.,
592 Seabloom, E.W., Schütz, M., Steenbock, C., Stevens, C.J., Fierer, N., 2015. Consistent
593 responses of soil microbial communities to elevated nutrient inputs in grasslands across the
594 globe. *Proceedings of the National Academy of Sciences* 201508382.
595 doi:10.1073/pnas.1508382112

596 Locey, K.J., Lennon, J.T., 2016. Scaling laws predict global microbial diversity. *Proceedings of*

597 the National Academy of Sciences 113, 5970–5975. doi:10.1073/pnas.1521291113

598 Lyons, K.G., Schwartz, M.W., 2001. Rare species loss alters ecosystem function - invasion
599 resistance. *Ecology Letters* 4, 358–365. doi:10.1046/j.1461-0248.2001.00235.x

600 Ma, B., Wang, H., Dsouza, M., Lou, J., He, Y., Dai, Z., Brookes, P.C., Xu, J., Gilbert, J.A.,
601 2016. Geographic patterns of co-occurrence network topological features for soil microbiota
602 at continental scale in eastern China. *The ISME Journal* 10, 1891–1901.
603 doi:10.1038/ismej.2015.261

604 Mangan, S.A., Schnitzer, S.A., Herre, E.A., Mack, K.M.L., Valencia, M.C., Sanchez, E.I., Bever,
605 J.D., 2010. Negative plant–soil feedback predicts tree-species relative abundance in a
606 tropical forest. *Nature* 466, 752–755. doi:10.1038/nature09273

607 Manokaran, N., Seng, Q., Ashton, P., LaFrankie, J., Noor, N., Ahmad, W., Okuda, T., 2004.
608 Pasoh forest dynamics plot, peninsular Malaysia, in: *Tropical Forest Diversity and
609 Dynamics: Findings from a Large-Scale Plot Network*. pp. 585–598.

610 Martiny, J.B.H., Jones, S.E., Lennon, J.T., Martiny, A.C., 2015. Microbiomes in light of traits: A
611 phylogenetic perspective. *Science* 350, aac9323–aac9323. doi:10.1126/science.aac9323

612 McDonald, D., Price, M.N., Goodrich, J., Nawrocki, E.P., DeSantis, T.Z., Probst, A., Andersen,
613 G.L., Knight, R., Hugenholtz, P., 2012. An improved Greengenes taxonomy with explicit
614 ranks for ecological and evolutionary analyses of bacteria and archaea. *The ISME Journal* 6,
615 610–618. doi:10.1038/ismej.2011.139

616 McGuire, K.L., D’Angelo, H., Brearley, F.Q., Gedallovich, S.M., Babar, N., Yang, N., Gillikin,
617 C.M., Gradoville, R., Bateman, C., Turner, B.L., Mansor, P., Leff, J.W., Fierer, N., 2015.
618 Responses of Soil Fungi to Logging and Oil Palm Agriculture in Southeast Asian Tropical
619 Forests. *Microbial Ecology* 69, 733–747. doi:10.1007/s00248-014-0468-4

620 Morriën, E., Hannula, S.E., Snoek, L.B., Helmsing, N.R., Zweers, H., de Hollander, M., Soto,
621 R.L., Bouffaud, M.-L., Buée, M., Dimmers, W., Duyts, H., Geisen, S., Girlanda, M.,
622 Griffiths, R.I., Jørgensen, H.-B., Jensen, J., Plassart, P., Redecker, D., Schmelz, R.M.,
623 Schmidt, O., Thomson, B.C., Tisserant, E., Uroz, S., Winding, A., Bailey, M.J., Bonkowski,
624 M., Faber, J.H., Martin, F., Lemanceau, P., de Boer, W., van Veen, J.A., van der Putten,
625 W.H., 2017. Soil networks become more connected and take up more carbon as nature
626 restoration progresses. *Nature Communications* 8, 14349. doi:10.1038/ncomms14349

627 Murray, B.R., Thrall, P.H., Gill, A.M., Nicotra, A.B., 2002. How plant life-history and
628 ecological traits relate to species rarity and commonness at varying spatial scales. *Austral*
629 *Ecology* 27, 291–310. doi:10.1046/j.1442-9993.2002.01181.x

630 Narisawa, N., Haruta, S., Arai, H., Ishii, M., Igarashi, Y., 2008. Coexistence of Antibiotic-
631 Producing and Antibiotic-Sensitive Bacteria in Biofilms Is Mediated by Resistant Bacteria.
632 *Applied and Environmental Microbiology* 74, 3887–3894. doi:10.1128/AEM.02497-07

633 Newman, M.E.J., 2006. Modularity and community structure in networks. *Proceedings of the*
634 *National Academy of Sciences* 103, 8577–8582. doi:10.1073/pnas.0601602103

635 Newman, M.E.J., 2002. Assortative Mixing in Networks. *Physical Review Letters* 89, 208701.
636 doi:10.1103/PhysRevLett.89.208701

637 Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., Minchin, P.R.,
638 O’Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H.H.,
639 2016. *vegan: Community Ecology Package*.

640 Prescott, C.E., Grayston, S.J., 2013. Tree species influence on microbial communities in litter
641 and soil: Current knowledge and research needs. *Forest Ecology and Management*.
642 doi:10.1016/j.foreco.2013.02.034

643 Price, N.D., Reed, J.L., Palsson, B.Ø., 2004. Genome-scale models of microbial cells: evaluating
644 the consequences of constraints. *Nature Reviews Microbiology* 2, 886–897.
645 doi:10.1038/nrmicro1023

646 Prober, S.M., Leff, J.W., Bates, S.T., Borer, E.T., Firn, J., Harpole, W.S., Lind, E.M., Seabloom,
647 E.W., Adler, P.B., Bakker, J.D., Cleland, E.E., DeCrappeo, N.M., DeLorenze, E., Hagenah,
648 N., Hautier, Y., Hofmockel, K.S., Kirkman, K.P., Knops, J.M.H., La Pierre, K.J.,
649 MacDougall, A.S., McCulley, R.L., Mitchell, C.E., Risch, A.C., Schuetz, M., Stevens, C.J.,
650 Williams, R.J., Fierer, N., 2015. Plant diversity predicts beta but not alpha diversity of soil
651 microbes across grasslands worldwide. *Ecology Letters* 18, 85–95. doi:10.1111/ele.12381

652 Ramirez, K.S., Craine, J.M., Fierer, N., 2012. Consistent effects of nitrogen amendments on soil
653 microbial communities and processes across biomes. *Global Change Biology* 18, 1918–
654 1927. doi:10.1111/j.1365-2486.2012.02639.x

655 Ramirez, K.S., Lauber, C.L., Knight, R., Bradford, M.A., Fierer, N., 2010. Consistent effects of
656 nitrogen fertilization on soil bacterial communities in contrasting systems. *Ecology* 91,
657 3463–70.

658 Ramirez, K.S., Leff, J.W., Barbera, A., Bates, S.T., Betley, J., Crowther, T.W., Kelly, E.F.,
659 Oldfield, E.E., Shaw, E.A., Steenbock, C., Bradford, M.A., Wall, D.H., Fierer, N., 2014.
660 Biogeographic patterns in below-ground diversity in New York City’s Central Park are
661 similar to those observed globally. *Proceedings of the Royal Society B*.

662 Rodrigues, J.L.M., Pellizari, V.H., Mueller, R., Baek, K., Jesus, E.D.C., Paula, F.S., Mirza, B.,
663 Hamaoui, G.S., Tsai, S.M., Feigl, B., Tiedje, J.M., Bohannan, B.J.M., Nüsslein, K., 2013.
664 Conversion of the Amazon rainforest to agriculture results in biotic homogenization of soil
665 bacterial communities. *Proceedings of the National Academy of Sciences of the United*

666 States of America 110, 988–93. doi:10.1073/pnas.1220608110

667 Rousk, J., Bååth, E., Brookes, P.C., Lauber, C.L., Lozupone, C., Caporaso, J.G., Knight, R.,
668 Fierer, N., 2010. Soil bacterial and fungal communities across a pH gradient in an arable
669 soil. *The ISME Journal* 4, 1340–51. doi:10.1038/ismej.2010.58

670 Shade, A., Jones, S.E., Caporaso, J.G., Handelsman, J., Knight, R., Fierer, N., Gilbert, J.A.,
671 2014. Conditionally Rare Taxa Disproportionately Contribute to Temporal Changes in
672 Microbial Diversity. *mBio* 5, e01371-14-e01371-14. doi:10.1128/mBio.01371-14

673 Toberman, H., Freeman, C., Evans, C., Fenner, N., Artz, R.R.E., 2008. Summer drought
674 decreases soil fungal diversity and associated phenol oxidase activity in upland Calluna
675 heathland soil. *FEMS Microbiology Ecology* 66, 426–436. doi:10.1111/j.1574-
676 6941.2008.00560.x

677 Tripathi, B.M., Edwards, D.P., Mendes, L.W., Kim, M., Dong, K., Kim, H., Adams, J.M., 2016.
678 The impact of tropical forest logging and oil palm agriculture on the soil microbiome.
679 *Molecular Ecology* 25, 2244–2257. doi:10.1111/mec.13620

680 Tripathi, B.M., Kim, M., Lai-Hoe, A., Shukor, N.A.A., Rahim, R.A., Go, R., Adams, J.M., 2013.
681 pH dominates variation in tropical soil archaeal diversity and community structure. *FEMS*
682 *Microbiology Ecology*. doi:10.1111/1574-6941.12163

683 Tripathi, B.M., Kim, M., Singh, D., Lee-Cruz, L., Lai-Hoe, A., Ainuddin, a N., Go, R., Rahim,
684 R.A., Husni, M.H. a, Chun, J., Adams, J.M., 2012. Tropical Soil Bacterial Communities in
685 Malaysia: pH Dominates in the Equatorial Tropics Too. *Microbial Ecology*.
686 doi:10.1007/s00248-012-0028-8

687 Wallenstein, M.D., Hall, E.K., 2011. A trait-based framework for predicting when and where
688 microbial adaptation to climate change will affect ecosystem functioning. *Biogeochemistry*

689 35–47. doi:10.1007/s10533-011-9641-8

690 Wang, Q., Garrity, G.M., Tiedje, J.M., Cole, J.R., 2007. Naive Bayesian Classifier for Rapid
691 Assignment of rRNA Sequences into the New Bacterial Taxonomy. *Applied and*
692 *Environmental Microbiology* 73, 5261–5267. doi:10.1128/AEM.00062-07

693 Webb, C., Ackerly, D., 2002. Phylogenies and community ecology. *Annual Review of Ecology*
694 ... 33, 475–505.

695 Webb, C.O., Ackerly, D.D., Kembel, S.W., 2008. Phylocom: software for the analysis of
696 phylogenetic community structure and trait evolution. *Bioinformatics* 24, 2098–2100.
697 doi:10.1093/bioinformatics/btn358

698 Weiss, S., Van Treuren, W., Lozupone, C., Faust, K., Friedman, J., Deng, Y., Xia, L.C., Xu,
699 Z.Z., Ursell, L., Alm, E.J., Birmingham, A., Cram, J.A., Fuhrman, J.A., Raes, J., Sun, F.,
700 Zhou, J., Knight, R., 2016. Correlation detection strategies in microbial data sets vary
701 widely in sensitivity and precision. *The ISME Journal* 10, 1669–1681.
702 doi:10.1038/ismej.2015.235

703 Wieder, W.R., Grandy, a. S., Kallenbach, C.M., Bonan, G.B., 2014. Integrating microbial
704 physiology and physiochemical principles in soils with the Microbial-MIneral Carbon
705 Stabilization (MIMICS) model. *Biogeosciences Discussions* 11, 1147–1185.
706 doi:10.5194/bgd-11-1147-2014

707 Wood, S.A., Bradford, M.A., Gilbert, J.A., McGuire, K.L., Palm, C.A., Tully, K.L., Zhou, J.,
708 Naem, S., 2015. Agricultural intensification and the functional capacity of soil microbes on
709 smallholder African farms. *Journal of Applied Ecology* 52, 744–752. doi:10.1111/1365-
710 2664.12416

711

713 **Figure Headings**

714 **Figure 1.** NMDS plot of soil bacterial communities under primary rainforest, regenerating
715 rainforest, and oil palm plantation in peninsular Malaysia.

716 **Figure 2.** Bar plot of relative abundances of bacterial taxa among the three land-use categories.
717 Taxa were included for which there was significant differences in relative abundances among at
718 least two of the categories. For visualization, plots are broken up by taxa with high relative
719 abundances (a) and low relative abundances (b).

720 **Figure 3.** Association network maps of soil bacterial communities under the three land-use
721 categories: regenerating forest (a), oil palm (b), and primary forest (c). The size of vertices is
722 proportional to the number of edges connecting each vertex.

723 **Figure 4.** Heat map of significant ($p < 0.05$) co-occurrence values among individual taxa under
724 the three land-use categories: regenerating forest (a), oil palm (b), and primary forest (c). Red
725 indicates negative co-occurrence scores and blue indicates positive co-occurrence scores.

726 Correlation of species taxonomic relative abundances is a significant explanatory variable of co-
727 occurrence scores, but only explains a small portion of the overall variation (d).

