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ABSTRACT

Soil microbial communities are dominated by a relatively small number of taxa that may play outsized roles in ecosystem functioning, yet little is known about their capacities to resist and recover from climate extremes such as drought, or how environmental context mediates those responses. Here, we imposed an *in situ* experimental drought across 30 diverse UK grassland sites with contrasting management intensities and found that: 1) the majority of dominant bacterial (85 %) and fungal (89 %) taxa exhibit resistant or opportunistic drought strategies, likely contributing to their ubiquity and dominance across sites; and 2) intensive grassland management decreases the proportion of drought-sensitive and non-resilient dominant bacteria – likely via alleviation of nutrient limitation and pH-related stress under fertilisation and liming – but has the opposite impact on dominant fungi. Our results suggest a potential mechanism by which intensive management promotes bacteria over fungi under drought with implications for soil functioning.

INTRODUCTION

Soil microbial communities mediate ecosystem functions including nutrient cycling, organic matter decomposition, and pathogen control [1–3], but their functioning can be impacted by climate extremes [4,5] which are becoming increasingly common. Recent evidence shows that despite very high diversity of soil microbial taxa, a small proportion can be considered dominant, i.e., they are found across most soils and are highly abundant relative to other taxa [6,7]. These dominant taxa may be drivers of ecosystem responses to climate extremes (i.e., the mass-ratio hypothesis; Grime, 1998; de Vries et al., 2018), an idea supported by studies of plant communities linking ecosystem responses to the abundances of dominant plant species [10,11]. Therefore, understanding how dominant microbial taxa respond to climate extremes and how these responses are shaped by environmental factors and land management, will enable better predictions of ecosystem behaviour into the future [12,13].

Soil microbial taxa can be categorised by life history strategies [14,15] to inform on their capacity to resist and recover from climate extremes such as drought [12,16]. These life history strategies are thought to emerge from correlated sets of traits (e.g., related to resource acquisition, growth yield, and stress tolerance), which are favoured under different environmental conditions [15]. For example, soil microbial communities subjected to moisture

69 pulses had greater proportions of taxa exhibiting a stress-resistant strategy, whereas those under

70 ambient conditions had higher abundances of drought-sensitive taxa [14]. Land management may

71 also shift microbial life history strategies by changing resource availability and plant

72 communities – environmental factors known to shape microbial community structure and

73 function [17–22]. However, the interacting effects of land management and climate extremes such as

74 drought have not been studied in the context of microbial life history strategies. This is a

75 necessary step towards using ecological knowledge of soil microbes to predict and understand

76 the consequences of land management decisions on soil functioning and sustainability in the face

77 of climate change.

78   Here, we carried out a large-scale field experiment across a broad range of grassland sites

79 to explore how the relative abundances of dominant microbial taxa with different drought-

80 response strategies are shaped by soil conditions, climate, and land management intensity. We

81 imposed a simulated drought on 15 pairs of grasslands under contrasting management (i.e.,

82 intensive and extensive) in three geographically distinct regions of the UK representing a range

83 of soil and climatic conditions (Fig. S1, Table S1). Using an operational approach, we identified

84 dominant microbial taxa and classified them into three broad drought-response strategies (i.e.,

85 resistant [no detectable response], opportunistic [positive response], or sensitive [negative

86 response])[14]. We examined the interacting effects of climate, soil properties, and historical

87 grassland management on dominant microbial taxa by drought-response strategy immediately

88 following the drought and after a 60-day post-drought period[23], to capture both microbial

89 resistance (lack of response to a perturbation) and resilience (recovery to an un-perturbed state)

90 to drought[24,25].

91   We hypothesised that: (1) dominant soil microbial taxa largely display resistant or

92 opportunistic strategies under drought, because a capacity to withstand variable moisture

93 conditions would partly explain their ubiquity and abundance across sites; (2) intensive grassland

94 management, characterized by regular fertiliser and lime application and higher plant

95 productivity (Table S1), favours taxa that are maladapted to low resource availability and stress,

96 and therefore will be sensitive to drought; and (3) intensive grassland management favours

97 microbial taxa that recover after drought (i.e., resilient), because more favourable soil conditions

98 allow drought-affected taxa to rebound quickly with rewetting.

99   Our results show that most dominant soil microbial taxa were resistant to drought, as
100 expected. We further show that intensive grassland management increases the proportion of
101 dominant bacterial taxa that are resistant or opportunistic in the face of drought relative to those
102 that are sensitive, and increases the proportion of taxa that are resilient relative to those that are
103 not resilient. However, intensive management has the opposite effect on dominant fungal taxa,
104 increasing the proportions of sensitive and non-resilient taxa. Our finding that land management
105 shapes the drought-response strategies of dominant soil microbial taxa has important
106 implications for microbial community structure and function. Intensive grassland management is
107 known to broadly favour bacteria over fungi, impacting key functions including soil carbon and
108 nitrogen cycling[26,27]; our results suggest this pattern may be exacerbated as droughts become
109 more frequent and intense with climate change.
110
111 **RESULTS**
112 **Most dominant soil microbial taxa are resistant to drought**
113 We found that a relatively small number of bacteria and fungi dominate soils across the
114 grassland sites, and that these taxa were highly resistant to an imposed drought event. For
115 bacteria, dominant taxa (defined as present across all 15 sites and in the top 10 % of relative
116 abundance ranked by 16S rRNA reads[7]) represented 1269 out of 19224 total operational
117 taxonomic units (OTUs), which accounted for approximately 7 % of total OTUs but 76 % of all
118 reads. For fungi, dominant taxa (present across all three regions and in the top 10 % by ITS
119 rRNA reads) made up 209 out of 12837 total OTUs, accounting for approximately 2 % of total
120 OTUs but 53 % of all reads. Overall, the majority of dominant bacterial (66 %) and fungal (64
121 %) taxa were classified as displaying a resistant drought strategy, as they showed no response to
122 drought in our hierarchical model using all data across sites and management regimes
123 immediately after the simulated drought (Table S2). Opportunistic taxa, whose relative
124 abundances increased in response to drought, represented 19 % of dominant bacteria and 25 % of
125 dominant fungi; sensitive taxa, whose relative abundances decreased with drought, represented
126 12 % of dominant bacteria and 7 % of dominant fungi.
127 Dominant bacterial phyla in our dataset comprised primarily (by reads) *Proteobacteria*
128 (32 %), *Acidobacteria* (21 %), *Verrucomicrobia* (13 %), *Bacteroidetes* (11 %), *Firmicutes* (9 %),
129 *Actinobacteria* (7 %), *Chloroflexi* (3 %), and several other globally distributed taxa. Of these
130 phyla, most contained taxa representing each of the three drought-response strategies (Fig. 1).

131   However, members of *Firmicutes* and *Bacteroidetes* tended to display resistant or sensitive

132   drought-response strategies, with few or no taxa identified as opportunistic (zero out of 47 in

133   *Firmicutes;* five out of 175 in *Bacteroidetes*). Members of *Acidobacteria, Actinobacteria,* and

134   *Chloroflexi* tended to display resistant or opportunistic drought-response strategies, with few taxa

135   identified as sensitive (nine out of 227 in *Acidobacteria*, one out of 118 in *Actinobacteria*, and

136   one out of 65 in *Chloroflexi*). Dominant fungal phyla comprised (by reads) *Mortierellomycota*

137   (48 %), *Ascomycota* (22 %), *Basidomycota* (15 %), *Glomeromycota* (1 %), and several other

138   known and globally distributed or unidentifiable taxa. Members of *Ascomycota* tended to display

139   resistant or opportunistic drought-responses strategies, with only six of 94 taxa identified as

140   having a drought-sensitive strategy. Members of *Mortierellomycota, Basidiomycota*, and

141   *Glomeromycota* tended to display resistant or sensitive drought-response strategies, with only

142   one or no taxa identified as opportunistic in each phylum (Fig. 1). Overall, dominant taxa

143   resistant to drought belonged to different taxonomic groups dispersed across every major lineage

144   of the phylogeny, suggesting that this capability is not limited to specific phylogenetic groups of

145   microbes.

146

147   **Management affects dominant bacteria and fungi differently**

148   We used structural equation models to infer potential mechanisms through which grassland

149   management affected opportunistic, sensitive, and resistant dominant microbial taxa across sites

150   (Fig. 2). Except for sensitive bacterial taxa, intensive management increased the relative

151   abundances of all dominant microbial drought-response groups. Opportunistic and resistant

152   bacterial taxa were positively impacted by intensive management at both timepoints (both

153   directly and via increased pH; Fig. 2a, b), while sensitive bacterial taxa were either unaffected

154   (following drought) or negatively affected (after the recovery period). Opportunistic and resistant

155   fungal taxa were also positively affected by intensive management (either directly or via

156   increased pH; Fig. 2c, d), but in contrast to sensitive bacterial taxa, sensitive fungal taxa were

157   positively and directly affected by intensive management at both timepoints. As a result, the ratio

158   of opportunistic:sensitive dominant taxa increased under intensive management for bacteria but

159   decreased for fungi (Fig. 3a).

160   Of the environmental variables we considered in the SEMs (total C and N, temperature,

161   texture, moisture, and pH), pH played the most important role. There were strong positive

162   indirect effects of management intensity via increased soil pH for opportunistic and resistant

163   bacterial taxa at both timepoints (Fig. 2a, b). Further investigation revealed unimodal

164   relationships between pH and resistant and resilient bacterial taxa that peaked ca. pH 5.7 (Fig.

165   S4). Fungal taxa were less impacted by pH overall, but there was a positive effect on

166   opportunistic fungal taxa after the drought (Fig. 2c), and a negative effect on resistant fungal taxa

167   after the recovery period (Fig. 2d). While the inclusion of pH did account for one mechanism by

168   which management impacts microbial taxa, the fact that direct paths from the management

169   variable manifested in the SEMs indicates that other mechanisms related to management (and

170   not captured by total soil C and N, soil temperature, texture, and soil water content) are also

171   impacting dominant microbial taxa in these soils. Intensive management did impact other key

172   variables including above-ground plant biomass and plant-available N (Fig. 3) that are implicitly

173   represented by our management variable in the SEM. In general, dominant fungal groups were

174   impacted more strongly by the management variable in our SEMs, while dominant bacterial

175   groups were impacted more strongly by pH and other soil characteristics (total soil C and N, soil

176   temperature, texture, and soil water content).

177

178   **Drought treatment and soil moisture effects on dominant microbes**

179   Drought treatment was the best predictor of soil moisture immediately after the simulated

180   drought (day 0), with latitude and soil properties captured in the composite soil variable (total C

181   and N, temperature, texture) also playing important roles (Fig. 2a, c). The drought treatment

182   effect on the different microbial drought-response strategy groups was not fully captured by the

183   field measurements of soil moisture – which only provided a snapshot of soil moisture conditions

184   at the time of sampling – indicated by the direct paths from drought treatment for several

185   microbial groups at that timepoint at day 0 (Fig. 2a, c). After the 60-day post-drought period, the

186   drought treatment no longer predicted soil moisture or microbial drought-response strategy

187   groups. Instead, latitude was a very strong predictor of soil moisture, and soil properties

188   (composite soil variable) were an important predictor for bacterial drought response groups, but

189   not fungal drought response groups (Fig. 2b, d). The absence of drought treatment effects on

190   sensitive and opportunistic bacterial or fungal taxa after the 60-day post-drought period indicates

191   group-level recovery within that time (Fig. 2b, d).

192

193   **Most drought-affected dominant bacteria and fungi are resilient**

194   We categorized individual opportunistic and sensitive dominant taxa as resilient or not based on

195   their abundances relative to ambient control plots after the 60-day post-drought recovery period.

196   While most of the 503 drought-affected (opportunistic or sensitive) taxa were found to be

197   resilient after 60 days, we identified 110 taxa that were not (Fig. 1). Of these, 34 were sensitive

198   bacterial taxa and 8 were sensitive fungal taxa that differed from ambient control plot levels after

199   the 60-day post-drought recovery period. Analyses of resilient bacterial and fungal taxa groups in

200   control plots across both timepoints revealed that the relative proportion of resilient taxa (ratio of

201   resilient:not resilient taxa; Fig. 3b) was higher for bacteria but lower for fungi under intensive

202   compared to extensive grassland management.

203

204

205   **DISCUSSION**

206   Our study provides novel evidence, from a broad range of grassland sites varying in

207   climatic and soil conditions (Table S1), that dominant soil microbial taxa are highly resistant to

208   drought. Despite significant and sizable reductions in soil moisture under experimental drought

209   across sites within three geographically distinct regions of the UK (Fig. S2), the majority of

210   dominant soil microbial taxa either did not respond or responded positively. Of the taxa that were

211   negatively impacted by the drought treatment (drought-sensitive strategies), the majority were

212   resilient (i.e., did not differ from ambient control levels within the 60-day post-drought period).

213   The resistance and resilience of these soil microbial taxa to drought, observed here across three

214   geographically distinct regions of the UK, may in part explain why they are present and highly

215   abundant (i.e., dominant) across sites [7]. The use of a distributed landscape design combined with

216   an *in situ* experimental drought treatment uniquely demonstrates that responses of dominant soil

217   microbial to drought are consistent at a large spatial scale. Though drought severity can be

218   difficult to quantify [28], especially at the microscale most relevant to microbiota [29], we observed

219   significant effects of the drought treatment on ecosystem respiration and microbial community

220   structure (including non-dominant taxa) at the plot scale across all regions, indicating that our

221   drought treatment was ecologically significant (Fig. S2, Fig. S3, Table S3). Our findings align

222   with recent studies showing that abundant microbial taxa are more resistant to perturbations [30],

223   are adapted to broader ranges of environmental conditions [31,32], and display higher frequencies of

224   genomic traits associated with stress-tolerance and competitive abilities [6] than rare microbial

225   taxa. These results suggest that dominant microbial taxa in grassland soils are generalists adapted

226   to varying environmental conditions, allowing them to withstand perturbations and thrive across

227   a broad range of sites.

228   We found that environmental context and land management did affect the relative

229   abundances of dominant microbial taxa with different drought response strategies, but not in

230   ways we expected. We expected that the impacts of grassland management on the resistance and

231   resilience (i.e., the capacity to recover) of dominant microbial taxa to drought would be inversely

232   related[33,34], and that bacterial and fungal communities would respond similarly. More

233   specifically, we hypothesised that microbial communities in intensively managed grasslands

234   would be more sensitive to drought due to lower stress-tolerance but be more resilient due to

235   higher available nutrients and more ideal pH levels enabling recovery. However, our findings

236   suggest that resistance and resilience of dominant soil microbial taxa are positively related in the

237   context of grassland management, and that bacterial and fungal communities respond to

238   intensive and extensive grassland management in divergent ways. Compared to communities

239   under extensive management, dominant bacterial communities under intensive management

240   shifted toward less sensitive and more resilient drought strategies, while dominant fungal

241   communities shifted toward more sensitive and less resilient drought strategies (Fig. 3). This

242   suggests that across these grassland sites, dominant bacterial communities under more intensive

243   management are better able to withstand and recover from drought than those under extensive

244   management, while dominant fungal communities are not. Again, these findings were apparent

245   when data were aggregated across all three UK regions, which cover a broad range of climatic

246   and soil conditions.

247   The divergence between bacterial and fungal responses to more intensive management

248   may be explained by differences in their sensitivities to prevailing conditions including pH,

249   nutrients, and plant productivity. The intensively managed grasslands used in our study all

250   receive regular inputs of inorganic fertilisers to reduce nutrient limitation along with lime, which

251   increases pH toward neutral levels and leads to increased plant productivity (Fig. 4). For the

252   dominant bacterial communities at these sites, liming likely alleviates pH-related stress, allowing

253 opportunistic taxa to succeed under the drought treatment relative to other taxa. These

254 opportunistic taxa may have traits related to high growth yields or efficient resource acquisition

255 [35] that enable them to take rapid advantage of abundant resources under changing conditions.

256 Indeed, the higher soil pH observed in the intensively managed grasslands (due to lime

257 application) positively affected resistant and resilient bacterial taxa relative to the extensive

258 grasslands with more acidic soils (Fig. S4). This finding agrees with previous work on similar

259 soils suggesting that relief from acidic conditions allows bacterial communities to shift from

260 maintenance to growth strategies [36]. In that study, the key pH threshold for shifts in microbial

261 strategies was found to be pH ca. 6.2, however, in our study the pH in intensively managed fields

262 rarely surpassed that threshold, suggesting the pH threshold could be lower for many of our sites.

263 In addition to higher pH, the higher soil nutrient availability and plant productivity in the

264 intensively managed grasslands likely further favoured copiotrophic or high-yield bacterial taxa

265 [37] capable of taking advantage of changing conditions under drought, or capitalizing on flushes

266 of nutrients upon rewetting of the droughted plots [35,38]. Indeed, *Actinobacteria* had the highest

267 proportion of opportunistic taxa in our study (consistent with a previous large-scale study of

268 drought effects on microbial communities in grasslands [4]) and this phylum is thought to comprise

269 primarily copiotrophs or high-yield strategy taxa favoured by N additions [21,37,39,40]. Further,

270 *Verrucomicrobia* and *Acidobacteria*, which that are thought to be comprised of mainly

271 oligotrophs (taxa that grow slowly and perform well under nutrient-poor conditions relative to

272 copiotrophs) [21,39,40], had the lowest proportions of drought-sensitive taxa that were resilient.

273   In contrast to dominant bacterial communities, dominant fungal communities under more

274 intensive management generally displayed lower resistance and resilience to drought than in

275 extensively managed grasslands. Fungal communities are known to be less sensitive to pH than

276 bacteria [41], and we didn't observe strong pH effects on resistant or resilient dominant fungal taxa

277 in this study (Fig. S4), suggesting that alleviation of pH-related stress was not as relevant a

278 mechanism for fungi in this case. Instead, other local-scale impacts of management such as

279 increased plant biomass and available nutrients (Fig. 4) were the likely drivers of fungal

280 responses, as suggested by the fact that the management variable in our SEMs generally affected

281 dominant fungal groups more strongly than pH or prevailing soil conditions (Fig. 2). Fungal

282 communities have been shown to respond strongly to fertilisation [21,42] and are often suppressed

283 relative to bacteria under more intensive grassland management [18,43,44], consistent with our

284   observation of lower fungal:bacterial ratios under intensive compared to extensive management

285   across sites (Fig 4). Furthermore, we recently showed in a sub-set of the grassland sites studied

286   here that intensive management reduces the flux of recent photosynthate to soil food webs

287   including arbuscular mycorrhizal fungi, indicating importance of this pathway for driving fungal

288   activity [45]. It is therefore possible that this pathway of reduced energy flux could contribute to

289   the increased sensitivity of dominant fungal communities to drought (which further reduces the

290   flux of recent photosynthate below-ground [46]) in intensively managed grasslands. The opposing

291   responses of dominant bacteria and fungi to grassland management in terms of their resistance

292   and resilience to drought may help to explain widespread observations of decreasing

293   fungal:bacterial biomass ratios with grassland intensification [18,44,47].

294   Overall, the alignment of resistance and resilience in the context of grassland

295   management intensity for both bacteria and fungi was unexpected, as other studies have found

296   trade-offs between resistance and resilience in soil microbial communities [34,48,49]. However, in

297   our study encompassing a relatively broad range of soils, pH was an important driver of both

298   resistance and resilience in dominant bacterial communities, while fertilisation may have driven

299   both resistance and resilience of dominant fungal communities, which would help to explain the

300   alignment in both responses with management. While consistencies in taxon-level responses to

301   separate drought and nitrogen addition treatments has been observed previously [50], the sets of

302   traits determining responses to soil water availability versus nutrient availability or pH may not

303   always align and a multi-dimensional framework may be necessary for considering microbial life

304   history strategies [51] and predicting microbial responses to climate extremes.

305   We observed contrasting phylum-level responses to drought in soil dominant bacterial

306   and fungal communities, suggesting that certain phyla may be inherently more resistant and

307   resilient to drought than others. *Actinobacteria* contained a high proportion of resistant and

308   opportunistic taxa, with only one taxon identified as sensitive, consistent with previous

309   observations that *Actinobacteria* are prevalent in dry environments [52] and are highly resistant or

310   increase in response to drought [4,51]. Members of *Firmicutes* and *Bacteroidetes* were generally

311   more sensitive to the drought treatment, and while members of *Bacteroidetes* have been shown

312   to decrease in relative abundance in drier soils, members of *Firmicutes* have previously shown

313   the opposite response [53]. It is possible that these previous observations may have been driven

314   primarily by one or a few taxa, which may not have been present (or defined as dominant) here.

315   Context-dependent drought responses have been previously observed for other phyla including

316   *Proteobacteria* and *Planctomycetes* [53], and we also observed relatively high numbers of taxa

317   with different drought-response strategies in those phyla.

318   Dominant members of *Ascomycota* were particularly opportunistic under drought, which

319   agrees with findings that *Ascomycota* are dominant globally and are generalists that are adapted

320   to a wide range of conditions [6,52]. Within *Glomeromycota,* dominant taxa that responded to our

321   drought treatment were sensitive, in agreement previous findings that both community

322   composition [4] and functionality [54,55] of this group of fungi respond to drought in other systems.

323   However, the majority of dominant *Glomeromycota* in this study were found to be resistant to

324   the drought, suggesting that the results from these other studies my largely be driven by only a

325   few dominant members of *Glomeromycota*, or by taxa that were not defined as dominant here.

326   Two members of *Basidiomycota* indicated sensitivity to drought, and one taxon did not recover

327   after the 60-day post-drought period. Given that *Basidiomycota* are important decomposers and

328   ectomycorrhizal symbionts in forests [56], microbial communities in forested systems (or under

329   forest expansion) may be sensitive to drought with potential implications for forest growth and

330   ecosystem functioning [57], which deserves further study.

331   Overall, our findings from a broad range of grassland sites across the UK indicate that

332   most of the dominant soil microbial taxa are highly resistant to drought, which may explain their

333   prevalence across a diverse range of grassland soils. We further show that grassland

334   management, along with climate and soil properties, shapes the relative abundances of dominant

335   soil microbial taxa with differing drought-response strategies. More intensive grassland

336   management, which creates more optimal pH and higher nitrogen availability compared to

337   extensive management, promotes opportunistic and resilient bacterial taxa that may employ

338   copiotrophic or fast-response strategies and are able to take advantage of changing conditions.

339   However, it has the opposite effect on dominant fungal taxa which may help to explain increases

340   in bacterial prevalence over fungi with grassland intensification [18,44,47,58]. Our results suggest the

341   pattern of bacterial prevalence over fungi under intensive management may be reinforced or

342   exacerbated as droughts become more frequent and intense with climate change, and potentially

343   contribute to less efficient carbon and nitrogen cycling in these systems[26,27].

344   By demonstrating that land management shapes the drought-response strategies of

345   dominant microbial taxa across grasslands, our findings improve our understanding of how soil

346 microbial communities respond to drought. Moreover, by identifying consistent management-
347 and drought-induced responses of dominant microbial taxa, our findings pave the way for future
348 studies that interrogate their functional attributes and links to key ecosystem functions [59]. Given
349 the enormous complexity of soil microbial communities and their dynamics in space and time,
350 our approach of focusing on the drought response strategies of dominant taxa is one way to make
351 this task more feasible in the future.
352
353 **METHODS**
354 **Field sites**
355 The field experiment was carried out between May and September of 2016 across a series of
356 mesotrophic grasslands in the United Kingdom, concentrated in three regions: Devon in
357 southwest England, North Yorkshire in northern England, and Aberdeenshire in northeast
358 Scotland (Fig. S1, Table S1). Prior to the start of the experiment, we identified 15 pairs of fields
359 on working farms with contrasting management and classified them as either intensively or
360 extensively managed based on observations of plant communities and interviews with farmers
361 and land managers. Extensively managed fields received very low or no synthetic fertiliser and
362 lime, had more diverse plant communities, were generally not cut for hay or silage, and were
363 grazed at low stocking densities by sheep or cattle. Intensively managed fields received regular
364 applications of fertiliser and lime (as deemed necessary by the farmer), had less diverse plant
365 species mixtures, were cut for hay or silage, and were grazed at higher stocking densities.
366 Differences in management had been maintained for at least 10 years, and typically longer
367 (Table S1). Wherever possible, we identified paired intensive and extensive fields that were
368 adjacent, to minimize differences in intrinsic environmental variables such as topography,
369 weather patterns, and soil type. If fields were not immediately adjacent, we chose fields no more
370 than 0.5 km apart and used farmer and land manager interviews to ensure minimal differences
371 between paired fields aside from management.
372
373 **Experimental design**
374 This study employed a randomized complete block design with subsampling. In each region, 5
375 sites were identified that each had two differently managed fields within 0.5 km for a total of 15
376 sites and 30 paired fields. In each of the 30 fields, three pairs of drought and ambient control
377 plots were established and enclosed in fencing for protection from large mammals and
378 machinery. A field drought was simulated by placing a transparent roof (1.5 m * 1.3 m) on each
379 drought plot alongside its paired delimited control plot for 60 days between May and July of
380 2016, which equates to a greater than 100-year drought for these sites [60]. In total, there were 90
381 pairs of droughted and ambient control plots, and the three within-field replicates of each were
382 treated appropriately in all statistical models by either including site and field as random effects
383 or by aggregating the data at the field scale where random effects could not be modelled. At the
384 end of the drought period, drought shelters were removed and an initial ("day 0") sampling and

385 measurement of soil functions (in both drought and control plots) was carried out to assess the
386 impact of the drought relative to the ambient control conditions. Sampling and measurement
387 were done in the centre of the plots, leaving a 15 cm buffer to minimize edge effects.
388 Immediately following this sampling event, droughted plots were watered (amounts were based
389 on average July rain events from 2007-2011 for the nearest Met Office from each region [61]) to
390 stimulate the start of the post-drought period. Sampling of drought and ambient control plots was
391 repeated 60 days after the removal of the shelters to capture recovery during the post-drought
392 period (resilience).
393
394 **Soil sampling**
395 At all timepoints, multiple soil samples were collected to 10 cm depth and composited for
396 measurements of soil nematode communities (6 * 1.3-cm diameter cores) soil microarthropod
397 communities (4 * 2.5-cm diameter cores), and soil microbiota and chemical analysis (3 * 2.5-cm
398 diameter cores). Soil samples were immediately composited in plastic sample bags and
399 transferred to coolers for transport to laboratories within 24-48 hours. Samples intended for soil
400 fauna analysis were kept open to allow for gas exchange. At each sampling event, soil moisture
401 and temperature were measured using Wet Sensor probes (WET-2, Delta-T Devices, Cambridge,
402 UK). Bulk density was measured using the core technique at the time of the drought treatment
403 establishment, using one core per plot for a total of 6 cores per field, and the average value for
404 each field was used throughout the study.
405
406 **Soil biogeochemical analysis**
407 Samples for analysis of microbial communities, texture, and C and N analyses were transported
408 to the University of Manchester and stored at 4°C for a maximum of 3 days until further
409 processing and analysis. All samples were sieved to 4 mm for homogenization and removal of
410 visible plant material and rocks, after which samples were divided for further analyses. One
411 subsample was immediately frozen at -80°C awaiting microbial DNA sequencing. A second
412 subsample was weighed, placed in a paper bag, and dried to constant weight at 40°C to calculate
413 soil moisture. This subsample was used for further analyses of total C and N concentrations
414 using a Vario Cube (Elementar Americas Inc., Ronkonkoma, NY, USA), and soil texture
415 analysis by laser granulometry using a Malvern Mastersizer 2000 (Malvern Instruments Ltd,
416 Malvern, Worcestershire, UK) following removal of organic matter with H_2O_2 at 50 °C
417 overnight. Soil pH was measured on field moist subsamples in slurries of 1:2.5 soil:deionized
418 water using a pH meter (Seven2GO Mettler Toledo, Columbus, Ohio, USA). Further analyses
419 are described in Supplemental Methods.
420
421 **16S and ITS amplicon sequencing and data analysis**
422 Amplicon sequencing and bioinformatic and statistical analyses of sequencing data were done
423 following the methods of De Vries et al.[9]. DNA was extracted from 0.16 g of soil using the
424 MoBIO PowerSoil-htp 96-Well DNA Isolation kit (Carlsbad, CA, USA) according to the

425 manufacturer's protocols and the DNA quality was checked by agarose gel electrophoresis.
426 Bacterial 16S rRNA sequencing followed the dual indexing protocol of Kozich et al. (2013) for
427 the MiSeq plaform (Illumina, San Diego, CA, USA). Each primer consisted of the appropriate
428 Illumina adapter, 8-nt index sequence, a 10-nt pad sequence, a 2-nt linker, and the amplicon
429 specific primer. The V3–V4 hypervariable regions of the bacterial 16S rRNA gene were
430 amplified using primers 341F [63] and 806R [64], CCTACGGGAGGCAGCAG, and
431 GCTATTGGAGCTGGAATTAC, respectively. Amplicons were generated using high-fidelity
432 DNA polymerase Q5 Taq (M0491L, New England Biolabs, Ipswich, USA), premixed dNTPs
433 (BIO-39053, Meridian Bioscience, Ohio, US), and using Eppedorf Mastercycler Nexus PCR
434 machines (Hamburg, Germany). After an initial denaturation at 95 °C for 2 minutes, PCR
435 conditions were: denaturation at 95 °C for 15 seconds, annealing at 55 °C for 30 seconds with
436 extension at 72 °C for 30 seconds, repeated for 30 cycles, followed by a final extension of 10
437 minutes at 72 °C.
438   Fungal internal transcribed spacer (ITS) amplicon sequences were generated using a 2-
439 step amplification approach. Primers GTGARTCATCGAATCTTTG and
440 TCCTCCGCTTATTGATATGC [65] were each modified at the 5' end with the addition of
441 Illumina pre-adapter and Nextera sequencing primer sequences. After an initial denaturation at
442 95°C for 2 minutes, PCR conditions were: denaturation at 95°C for 15 seconds, annealing at
443 52°C for 30 seconds with extension at 72°C for 30 seconds, repeated for 25 cycles, with a final
444 extension of 10 minutes at 72°C included. PCR products were cleaned using a DNA Clean-up
445 Kit (ZR-96, Zymo Research Inc., Irvine, US) following manufacturer's instructions. MiSeq
446 adapters AATGATACGGCGACCACCGAGATCTACAC and 8nt dual-indexing barcode
447 sequences were added during a second step of PCR amplification. After an initial denaturation
448 95°C for 2 minutes, PCR conditions were: denaturation at 95°C for 15 seconds; annealing at
449 55°C for 30 seconds with extension at 72°C for 30 seconds; repeated for 8 cycles with a final
450 extension of 10 minutes at 72°C.
451   Amplicon concentrations were normalized using SequalPrep Normalization Plate Kit
452 (A10510-01, Thermo Fisher Scientific, Waltham, US) and amplicon sizes determined using an
453 2200 TapeStation (Agilent, Santa Clara, US) prior to sequencing each amplicon library
454 separately using MiSeq (Illumina, San Diego, US) with V3 600 cycle reagents (MS-102-3003,
455 Illumina, San Diego, US) at concentrations of 14 and 7 pM (16S and ITS respectively) with a 5%
456 PhiX control v3 (FC-110-3001, Illumina, San Diego, US) library.
457   Sequenced paired-end reads were joined using PEAR [66], quality filtered using FASTX
458 tools (hannonlab.cshl.edu), and length-filtered to a minimum length of 300 bp. The presence of
459 PhiX and adaptors were checked for and removed with BBTools (jgi.doe.gov/data-and-
460 tools/bbtools/), and chimeras were identified and removed with VSEARCH_UCHIME_REF [67]
461 using Greengenes Release 13_5 (at 97%). Singletons were removed and the resulting sequences
462 were clustered into operational taxonomic units (OTUs) with VSEARCH_CLUSTER [67] at 97%
463 sequence identity. Representative sequences for each OTU were taxonomically assigned by RDP
464 Classifier with the bootstrap threshold of 0.8 or greater using the Greengenes Release 13_5 (full)

465   as the reference. Unless stated otherwise, default parameters were used for all steps listed. The
466   fungal ITS sequences were analysed using PIPITS [68] with default parameters. Briefly, this
467   involved quality filtering and 97% clustering of the ITS2 region as indicated above for the 16S
468   processing, using the UNITE database for chimera removal and taxonomic identification of
469   representative OTUs. Both bacterial and fungal OTU abundance tables were rarified to a
470   minimum of 9000 reads per sample, and samples with zero reads were removed prior to further
471   analyses.
472   Plots showing circular representations of the taxonomic trees were created using the
473   GraPhlAn software tool (https://huttenhower.sph.harvard.edu/graphlan/).
474
475   **Statistical analysis**
476   All analyses were done separately for bacterial and fungal taxa in R version 4.0.2 [69]. We defined
477   dominant taxa as those which were present across all 15 sites (management pairs) and
478   represented the top 10% of taxa when ranked by relative abundance (rRNA reads). The response
479   of each of these dominant taxa to drought treatment was identified using a generalized linear
480   mixed model across all experimental plot pairs with drought treatment as a fixed effect, and
481   region/site/field as nested random effects (R package glmmTMB version 1.1.5 [70]). For each
482   individual model, the appropriate distribution (poisson, negative binomial, or binomial) was
483   assumed based on diagnostics of model residuals, which were assessed using R package
484   DHARMa version 0.4.6 [71]. The drought-response strategy for each taxon was identified as
485   resistant (no significant response to drought detected), sensitive (negative response), or
486   opportunistic (positive response) using a significance level (α) of 0.05. Further statistical
487   analysis (linear mixed effects models using R package nlme version 3.1-148 [72]) was performed at
488   the drought-response group level (i.e., resistant, opportunistic, sensitive, resilient, not resilient).
489   Group-level indices were calculated as follows: for each OTU in a given group, its relative
490   abundance in a given sample was standardized relative to its abundance across all samples; these
491   standardized abundances were then summed across all OTUs in a given group resulting in one
492   value (index) per group per sample.
493   Structural equation modelling was used to investigate effects of historical management,
494   drought, and soil properties on relative abundances of opportunistic, sensitive, and resistant taxa
495   at the two sampling timepoints. Within-field reps were averaged prior to analysis (n = 180
496   experimental plots/3 field replicates = 60 values per timepoint). We constructed an *a priori*
497   model based on current knowledge of plant-soil-microbe-functioning interactions (see Fig. S5
498   and Supplemental Note 1) and tested whether the data fit these models using the standard
499   modelling approach in the lavaan R package, version 0.6-12 [73]. We created a proxy for soil
500   properties using axis 1 scores from a non-metric multidimensional scaling plot that included total
501   soil carbon, total nitrogen, and soil temperature (see Supplemental Note 1). We used multiple
502   parameters including root mean square error of approximation (RMSEA), comparative fit index
503   (CFI), and Standardized Root Mean Squared Residual (SRMR) to assess model fit.
504

Data availability

The sequence data generated in this study have been deposited in the EMBL Nucleotide Sequence Database (ENA) under accession code PRJEB63076 [https://www.ebi.ac.uk/ena/browser/search]. All other data generated in this study have been deposited on GitHub [DOI: 10.5281/zenodo.10121576].

CODE AVAILABILITY

All code is available from GitHub [DOI: 10.5281/zenodo.10121576].

REFERENCES

1. Wagg, C., Bender, S. F., Widmer, F. & van der Heijden, M. G. A. Soil biodiversity and soil community composition determine ecosystem multifunctionality. *Proc. Natl. Acad. Sci. U. S. A.* **111**, 5266–5270 (2014).

2. Bardgett, R. D. & van der Putten, W. H. Belowground biodiversity and ecosystem functioning. *Nature* **515**, 505–511 (2014).

3. Delgado-Baquerizo, M. *et al.* Microbial diversity drives multifunctionality in terrestrial ecosystems. *Nat. Commun.* **7**, 10541 (2016).

4. Ochoa-Hueso, R. *et al.* Drought consistently alters the composition of soil fungal and bacterial communities in grasslands from two continents. *Glob. Chang. Biol.* **24**, 2818–2827 (2018).

5. Oliverio, A. M., Bradford, M. A. & Fierer, N. Identifying the microbial taxa that consistently respond to soil warming across time and space. *Glob. Chang. Biol.* **23**, 2117–2129 (2017).

6. Egidi, E. *et al.* A few Ascomycota taxa dominate soil fungal communities worldwide. *Nat. Commun.* **10**, 2369 (2019).

7. Delgado-Baquerizo, M. *et al.* A global atlas of the dominant bacteria found in soil. *Science (80-.).* **359**, 320–325 (2018).

8. Grime, J. P. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J. Ecol.* **86**, 902–910 (1998).

9. de Vries, F. T. *et al.* Soil bacterial networks are less stable under drought than fungal networks. *Nat. Commun.* **9**, 912–913 (2018).

10. Hoover, D. L., Knapp, A. K. & Smith, M. D. Resistance and resilience of a grassland ecosystem to climate extremes. *Ecology* **95**, 2646–2656 (2014).

11. Smith, M. D. *et al.* Mass ratio effects underlie ecosystem responses to environmental change. *J. Ecol.* **108**, 855–864 (2020).

12. Bardgett, R. D. & Caruso, T. Soil microbial community responses to climate extremes: Resistance, resilience and transitions to alternative states. *Philos. Trans. R. Soc. B Biol. Sci.* **375**, (2020).

13. Griffiths, B. S. & Philippot, L. Insights into the resistance and resilience of the soil microbial community. *FEMS Microbiol. Rev.* **37**, 112–129 (2013).

14. Evans, S. E. & Wallenstein, M. D. Climate change alters ecological strategies of soil bacteria. *Ecol. Lett.* **17**, 155–164 (2014).

15. Malik, A. A. *et al.* Defining trait-based microbial strategies with consequences for soil carbon cycling under climate change. *ISME J.* **14**, 1–9 (2020).

550   16.   Wallenstein, M. D. & Hall, E. K. A trait-based framework for predicting when and where
551   microbial adaptation to climate change will affect ecosystem functioning.
552   *Biogeochemistry* **109**, 35–47 (2012).
553   17.   Donnison, L. M., Griffith, G. S., Hedger, J., Hobbs, P. J. & Bardgett, R. D. Management
554   influences on soil microbial communities and their function in botanically diverse
555   haymeadows of northern England and Wales. *Soil Biol. Biochem.* **32**, 253–263 (2000).
556   18.   Grayston, S. J. *et al.* Assessing shifts in microbial community structure across a range of
557   grasslands of differing management intensity using CLPP, PLFA and community DNA
558   techniques. *Appl. Soil Ecol.* **25**, 63–84 (2004).
559   19.   Boeddinghaus, R. S. *et al.* Plant functional trait shifts explain concurrent changes in the
560   structure and function of grassland soil microbial communities. *J. Ecol.* **107**, 2197–2210
561   (2019).
562   20.   de Vries, F. T. *et al.* Abiotic drivers and plant traits explain landscape-scale patterns in
563   soil microbial communities. *Ecol. Lett.* **15**, 1230–1239 (2012).
564   21.   Leff, J. W. *et al.* Consistent responses of soil microbial communities to elevated nutrient
565   inputs in grasslands across the globe. *Proc. Natl. Acad. Sci. U. S. A.* **112**, 10967–10972
566   (2015).
567   22.   Lekberg, Y. *et al.* Nitrogen and phosphorus fertilization consistently favor pathogenic
568   over mutualistic fungi in grassland soils. *Nat. Commun.* **12**, 3484 (2021).
569   23.   Vilonen, L., Ross, M. & Smith, M. D. What happens after drought ends: synthesizing
570   terms and definitions. *New Phytol.* **235**, 420–431 (2022).
571   24.   Shade, A., Peter, H., Allison, S. D. & Baho, D. L. Fundamentals of microbial community
572   resistance and resilience. *Front. Microbiol.* **3**, (2012).
573   25.   Nimmo, D. G., Mac Nally, R., Cunningham, S. C., Haslem, A. & Bennett, A. F. Vive la
574   résistance: Reviving resistance for 21st century conservation. *Trends Ecol. Evol.* **30**, 516–
575   523 (2015).
576   26.   Malik, A. A. *et al.* Soil Fungal:Bacterial Ratios Are Linked to Altered Carbon Cycling.
577   *Front. Microbiol.* **7**, 11511–11512 (2016).
578   27.   de Vries, F. T. *et al.* Extensive Management Promotes Plant and Microbial Nitrogen
579   Retention in Temperate Grassland. *PLoS One* **7**, e51201 (2012).
580   28.   Slette, I. J. *et al.* How ecologists define drought, and why we should do better. *Glob.*
581   *Chang. Biol.* 3193–3200 (2019) doi:10.1111/gcb.14747.
582   29.   Pot, V. *et al.* Three-dimensional distribution of water and air in soil pores: Comparison of
583   two-phase two-relaxation-times lattice-Boltzmann and morphological model outputs with
584   synchrotron X-ray computed tomography data. *Adv. Water Resour.* **84**, 87–102 (2015).
585   30.   Jiao, S., Wang, J., Wei, G., Chen, W. & Lu, Y. Dominant role of abundant rather than rare
586   bacterial taxa in maintaining agro-soil microbiomes under environmental disturbances.
587   *Chemosphere* **235**, 248–259 (2019).
588   31.   Jiao, S. & Lu, Y. Abundant fungi adapt to broader environmental gradients than rare fungi
589   in agricultural fields. *Glob. Chang. Biol.* **26**, 4506–4520 (2020).
590   32.   Wan, W. *et al.* Environmental adaptation is stronger for abundant rather than rare
591   microorganisms in wetland soils from the Qinghai-Tibet Plateau. *Mol. Ecol.* **30**, 2390–
592   2403 (2021).
593   33.   Yi, C. & Jackson, N. A review of measuring ecosystem resilience to disturbance. *Environ.*
594   *Res. Lett.* **16**, (2021).
595   34.   Orwin, K. H., Wardle, D. A. & Greenfield, L. G. Context-dependent changes in the

596   resistance and resilience of soil microbes to an experimental disturbance for three primary
597   plant chronosequences. *Oikos* **112**, 196–208 (2006).

598   35.   Malik, A. A., Puissant, J., Goodall, T., Allison, S. D. & Griffiths, R. I. Soil microbial
599   communities with greater investment in resource acquisition have lower growth yield. *Soil*
600   *Biol. Biochem.* **132**, 36–39 (2019).

601   36.   Malik, A. A. *et al.* Land use driven change in soil pH affects microbial carbon cycling
602   processes. *Nat. Commun.* **9**, 3591 (2018).

603   37.   Fierer, N. *et al.* Comparative metagenomic, phylogenetic and physiological analyses of
604   soil microbial communities across nitrogen gradients. *ISME J.* **6**, 1007–1017 (2012).

605   38.   Leff, J. W. *et al.* Consistent responses of soil microbial communities to elevated nutrient
606   inputs in grasslands across the globe. *Proc. Natl. Acad. Sci. U. S. A.* **112**, 10967–10972
607   (2015).

608   39.   Ramirez, K. S., Craine, J. M. & Fierer, N. Consistent effects of nitrogen amendments on
609   soil microbial communities and processes across biomes. *Glob. Chang. Biol.* **18**, 1918–
610   1927 (2012).

611   40.   Fierer, N., Bradford, M. A. & Jackson, R. B. Toward an ecological classification of soil
612   bacteria. *Ecology* **88**, 1354–1364 (2007).

613   41.   Rousk, J. *et al.* Soil bacterial and fungal communities across a pH gradient in an arable
614   soil. *ISME J.* **4**, 1340–1351 (2010).

615   42.   Treseder, K. K. A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and
616   atmospheric CO2 in field studies. *New Phytol.* **164**, 347–355 (2004).

617   43.   de Vries, F. T., Bloem, J., van Eekeren, N., Brusaard, L. & Hoffland, E. Fungal biomass in
618   pastures increases with age and reduced N input. *Soil Biol. Biochem.* **39**, 1620–1630
619   (2007).

620   44.   Bardgett, R. D. & McAlister, E. The measurement of soil fungal:bacterial biomass ratios
621   as an indicator of ecosystem self-regulation in temperate meadow grasslands. *Biol. Fertil.*
622   *Soils* **29**, 282–290 (1999).

623   45.   Chomel, M. *et al.* Intensive grassland management disrupts below-ground multi-trophic
624   resource transfer in response to drought. *Nat. Commun.* **13**, 6991 (2022).

625   46.   Chomel, M. *et al.* Drought decreases incorporation of recent plant photosynthate into soil
626   food webs regardless of their trophic complexity. *Glob. Chang. Biol.* **25**, 3549–3561
627   (2019).

628   47.   de Vries, F. T., Hoffland, E., van Eekeren, N., Brussaard, L. & Bloem, J. Fungal/bacterial
629   ratios in grasslands with contrasting nitrogen management. *Soil Biol. Biochem.* **38**, 2092–
630   2103 (2006).

631   48.   de Vries, F. T. *et al.* Land use alters the resistance and resilience of soil food webs to
632   drought. *Nat. Clim. Chang.* **2**, 276–280 (2012).

633   49.   Piton, G. *et al.* Resistance–recovery trade-off of soil microbial communities under altered
634   rain regimes: An experimental test across European agroecosystems. *J. Appl. Ecol.* **58**,
635   406–418 (2021).

636   50.   Amend, A. S. *et al.* Microbial response to simulated global change is phylogenetically
637   conserved and linked with functional potential. *ISME J.* **10**, 109–118 (2016).

638   51.   Barnard, R. L., Osborne, C. A. & Firestone, M. K. Responses of soil bacterial and fungal
639   communities to extreme desiccation and rewetting. *ISME J.* **7**, 2229–2241 (2013).

640   52.   Maestre, F. T. *et al.* Increasing aridity reduces soil microbial diversity and abundance in
641   global drylands. *Proc. Natl. Acad. Sci. U. S. A.* **112**, 15684–15689 (2015).

642   53.   Naylor, D. & Coleman-Derr, D. Drought stress and root-associated bacterial communities.
643   *Front. Plant Sci.* **8**, (2018).
644   54.   Jia, Y., van der Heijden, M. G. A., Wagg, C., Feng, G. & Walder, F. Symbiotic soil fungi
645   enhance resistance and resilience of an experimental grassland to drought and nitrogen
646   deposition. *J. Ecol.* **109**, 3171–3181 (2021).
647   55.   Worchel, E. R., Giauque, H. E. & Kivlin, S. N. Fungal Symbionts Alter Plant Drought
648   Response. *Microb. Ecol.* **65**, 671–678 (2013).
649   56.   Watkinson, S. C. Basidiomycota. *Encyclopedia of Life Sciences (ELS)* (2008)
650   doi:10.1002/9780470015902.a0000347.pub2.
651   57.   Anthony, M. A. *et al.* Forest tree growth is linked to mycorrhizal fungal composition and
652   function across Europe. *ISME J.* **16**, 1327–1336 (2022).
653   58.   Bardgett, R. D., Hobbs, P. J. & Frostegård, Å. Changes in soil fungal:bacterial biomass
654   ratios following reductions in the intensity of management of an upland grassland. *Biol.*
655   *Fertil. Soils* **22**, 261–264 (1996).
656   59.   Torsvik, V. & Øvreås, L. Microbial diversity and function in soil: from genes to
657   ecosystems. *Curr. Opin. Microbiol.* **5**, 240–245 (2002).
658   60.   Bloor, J. M. G. & Bardgett, R. D. Stability of above-ground and below-ground processes
659   to extreme drought in model grassland ecosystems: Interactions with plant species
660   diversity and soil nitrogen availability. *Perspect. Plant Ecol. Evol. Syst.* **14**, 193–204
661   (2012).
662   61.   Met Office (2016): Met Office MIDAS Open: UK Land Surface Stations Data (1853-
663   current). *Centre for Environmental Data Analysis*
664   http://catalogue.ceda.ac.uk/uuid/dbd451271eb04662beade68da43546e1.
665   62.   Kozich, J. J., Westcott, S. L., Baxter, N. T., Highlander, S. K. & Schloss, P. D.
666   Development of a dual-index sequencing strategy and curation pipeline for analyzing
667   amplicon sequence data on the miseq illumina sequencing platform. *Appl. Environ.*
668   *Microbiol.* **79**, 5112–5120 (2013).
669   63.   Muyzer, G., de Waal, E. C. & Uitterlinden, A. G. Profiling of complex microbial
670   populations by denaturing gradient gel electrophoresis analysis of polymerase chain
671   reaction-amplified genes coding for 16S rRNA. *Appl. Environ. Microbiol.* **59**, 695–700
672   (1993).
673   64.   Yu, Y., Lee, C., Kim, J. & Hwang, S. Group-specific primer and probe sets to detect
674   methanogenic communities using quantitative real-time polymerase chain reaction.
675   *Biotechnol. Bioeng.* **89**, 670–679 (2005).
676   65.   Ihrmark, K. *et al.* New primers to amplify the fungal ITS2 region - evaluation by 454-
677   sequencing of artificial and natural communities. *FEMS Microbiol. Ecol.* **82**, 666–677
678   (2012).
679   66.   Zhang, J., Kobert, K., Flouri, T. & Stamatakis, A. PEAR: A fast and accurate Illumina
680   Paired-End reAd mergeR. *Bioinformatics* **30**, 614–620 (2014).
681   67.   Rognes, T., Flouri, T., Nichols, B., Quince, C. & Mahé, F. VSEARCH: A versatile open
682   source tool for metagenomics. *PeerJ* **4**, e2584 (2016).
683   68.   Gweon, H. S. *et al.* PIPITS: An automated pipeline for analyses of fungal internal
684   transcribed spacer sequences from the Illumina sequencing platform. *Methods Ecol. Evol.*
685   **6**, 973–980 (2015).
686   69.   R Core Team. R: A language and environment for statistical computing. at http://www.r-
687   project.org/ (2020).

688 70. Mollie E. Brooks *et al.* glmmTMB Balances Speed and Flexibility Among Packages for
689   Zero-inflated Generalized Linear Mixed Modeling. *R J.* **9**, 378–400 (2017).
690 71. Hartig, F. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed)
691   Regression Models. at https://cran.r-project.org/package=DHARMa (2022).
692 72. Pinheiro, J., Bates, D. & R Core Team. nlme: Linear and Nonlinear Mixed Effects
693   Models. at (2023).
694 73. Rosseel, Y. lavaan: An R Package for Structural Equation Modeling. *J. Stat. Softw.* **48**, 1–
695   36 (2012).
696 74. Lavallee, J. M. *et al.* Code for Lavallee et al. (2023) Land management shapes drought
697   responses of dominant soil microbial taxa across grasslands, soilnerd/lavallee-dom-
698   micro-drought, DOI: 10.5281/zenodo.10121576, 2023.
699
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701
712
713 **AUTHOR CONTRIBUTIONS STATEMENT**
714 R.D.B. initiated and gained funding for the project with D.J., M.E., T.C., F.d.V., and E.M.B..
715 J.L. M.C., F.d.C., R.D.B., D.J., M.E., T.C., F.d.V. and E.M.B. conceived and designed the
716 experiment. J.L., M.C., J.R., F.d.C., N.A., and M.M. set up the experiment and performed
717 sampling and field measurements. T.G. performed amplicon sequencing and analysis. J.L., J.R.,
718 M.C., N.A., performed all other laboratory analyses. J.L. and M.D.B. statistically analysed the
719 data and led writing the manuscript in close consultation with R.D.B., T.C., D.J., and R.I.G. and
720 with discussions and contributions from all authors.
721
722 **COMPETING INTERESTS STATEMENT**
723 The authors declare no competing interests.
724
725 **FIGURE LEGENDS**
726
727 Figure 1. Taxonomic tree showing drought responses of dominant soil microbial taxa. Dominant
728 bacterial (a) and fungal (b) community responses to drought immediately following the drought
729 treatment ("resistance") and after the 60-day post-drought period ("resilience"), limited to the top
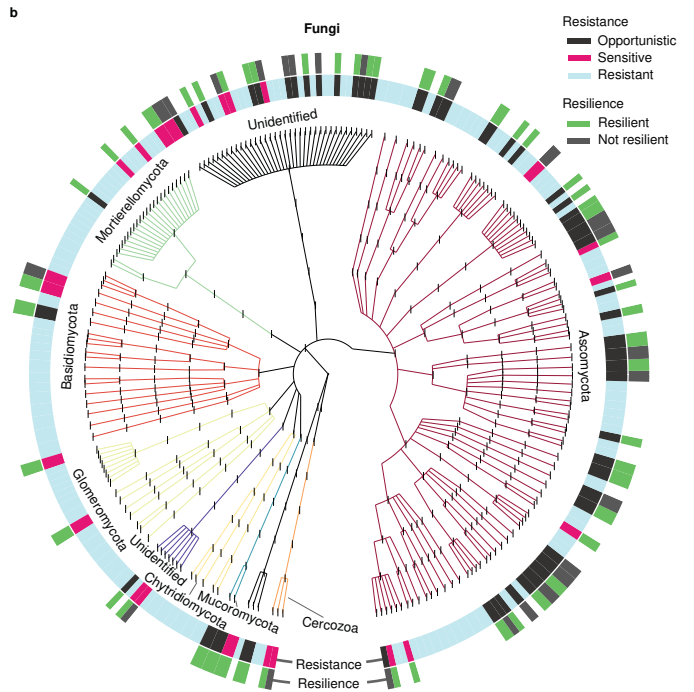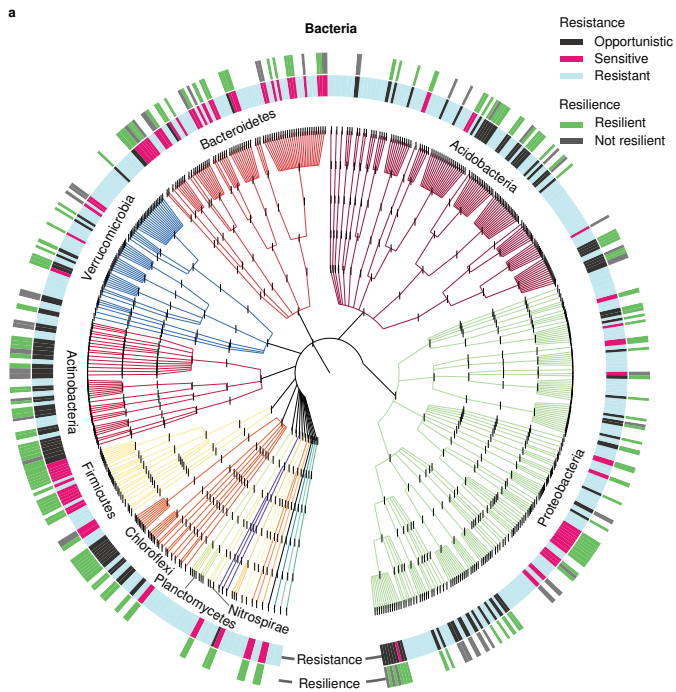
730 500 most abundant taxa across all samples for readability. The inner ring shows the taxonomic
731 tree, coloured by phylum. The middle ring displays responses of each out immediately following
732 drought (light blue = resistant, black = opportunistic, pink = sensitive). The outer ring displays
733 responses after the 60-day post drought period (green = resilient taxa that recovered to control
734 levels, dark grey = not resilient). Taxa defined as resistant to drought (light blue, inner ring) were
735 not tested for resilience. For further information on the identities of all OTUs, see Supplemental
736 Note 2. Source data are provided on GitHub[74].
737
738 Figure 2. Potential mechanisms potential mechanisms affecting dominant soil microbial taxa
739 across sites. Structural equation models (SEMs) of dominant bacteria and fungi at the two time
740 points in this study: immediately following the drought treatment (day 0), and after the 60-day
741 post-drought recovery period. The "soil" variable is a composite representation of soil C, N,
742 texture, and temperature. SWC is soil water content by volume. The drought-response strategy
743 (opportunistic, sensitive, resistant) of each OTU was determined by the drought treatment effect
744 using linear mixed models. Arrow (path) thickness corresponds to the standardized coefficients,
745 also written next to their respective paths. Paths of less interest are shaded grey to improve overall
746 readability. Wald tests were used to evaluate the null hypothesis that individual path coefficients
747 were equal to zero. Solid arrows indicate individual path coefficients with P values < 0.05; path
748 coefficients with P values > 0.05 are not shown. Overall model fit for each model was assessed
749 using Chi-squared test (χ^2) with associated P value and degrees of freedom (DF), Comparative Fit
750 Index (CFI), and root mean square error of approximation (RMSEA). See Fig. S5 and
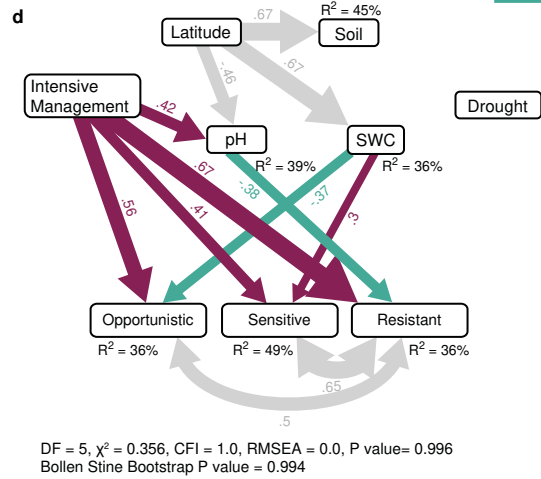751 Supplemental Note 1 for more detail. Source data are provided on GitHub[74].
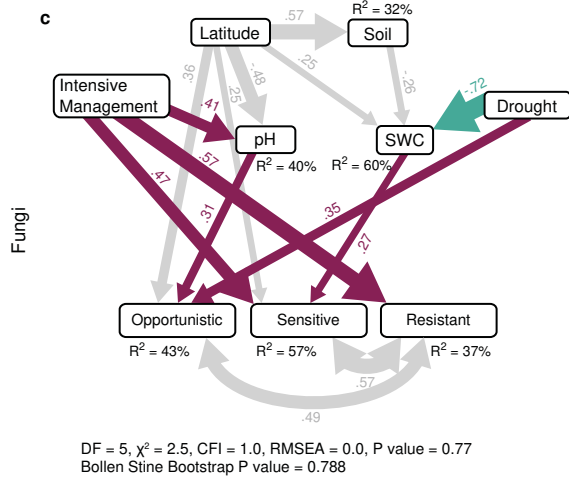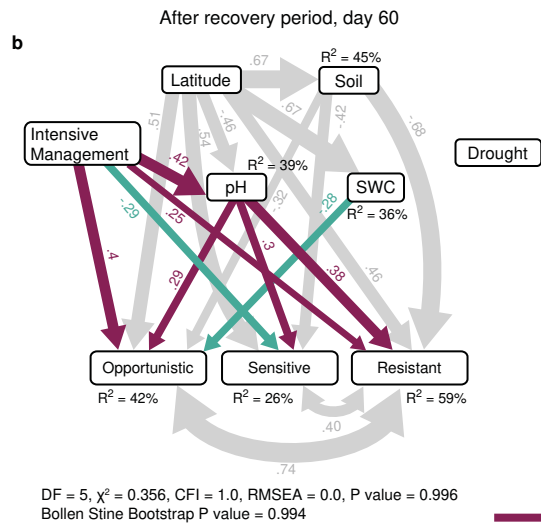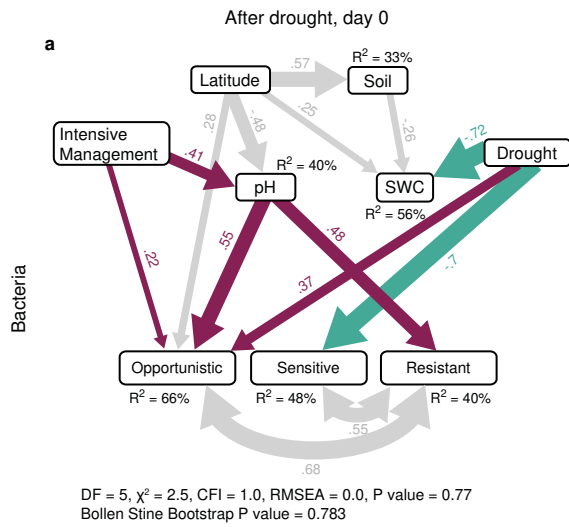752
753 Figure 3. Grassland management effects on dominant soil microbial taxa. Ratios of the
754 standardized relative abundances of opportunistic:sensitive dominant taxa (a) and resilient:not
755 resilient dominant taxa (b) by grassland management, with bacteria on left and fungi on right.
756 Boxplots show the median (centre line), first and third quartiles (box limits), and smallest and
757 largest values within 1.5x interquartile range (whiskers), and all datapoints are shown (n = 90
758 experimental plots for all boxplots). Resilient taxa were defined as having similar relative
759 abundances to those in control plots after the 60-day post-drought recovery period. Ratios were
760 higher for bacteria but lower for fungi in intensively managed grasslands based on linear mixed
761 models using data from control plots across both timepoints (P value < 0.05 indicated by *).
762 Output of linear mixed models of effects of intensive versus extensive management for each
763 response variable: panel a, left: t(14) = 5.61, P = 0.0001, effect size = 0.277, 95 % Confidence
764 Intervals = 0.267, 0.287; panel a, right: t(14)= -4.58, P = 0.0004, effect size = -0.382, 95 %
765 Confidence Intervals = -0.542, -0.222; panel b, left: t(14) = 3.48, P = 0.0036, effect size = 0.134,
766 95 % Confidence Intervals = 0.058, 0.21; panel b, right: t(14) = -2.20, P = 0.045, effect size = -
767 0.377, 95 % Confidence Intervals = -0.717, -0.037. Source data are provided on GitHub[74].
768

769   Figure 4. Grassland management affects a range of environmental variables. Log response ratio
770   of key variables related to grassland intensification (C is carbon, N is nitrogen). Log response
771   ratio is calculated as the natural log of the ratio of the value of a given variable in an intensively
772   managed field to the corresponding value in the paired extensively managed field. Fifteen pairs
773   of intensive and extensive grasslands, 5 per region, are shown here with each point representing
774   the log ratio of within-field means for one pair (site). Boxplots show the median (centre line),
775   first and third quartiles (box limits), and smallest and largest values within 1.5x interquartile
776   range (whiskers), and all datapoints are shown. Source data are provided on GitHub[74].
777

a **Bacteria**

Resistance
- Opportunistic
- Sensitive
- Resistant

Resilience
- Resilient
- Not resilient

Bacteroidetes
Acidobacteria
Verrucomicrobia
Actinobacteria
Firmicutes
Chloroflexi
Planctomycetes
Nitrospirae
Proteobacteria

Resistance
Resilience

b **Fungi**

Resistance
- Opportunistic
- Sensitive
- Resistant

Resilience
- Resilient
- Not resilient

Unidentified
Mortierellomycota
Basidiomycota
Glomeromycota
Unidentified
Chytridiomycota
Mucoromycota
Cercozoa
Ascomycota

Resistance
Resilience

After drought, day 0

a

Latitude — .57 → Soil   R² = 33%

.28 .48 .25 .26

Intensive Management — .41 → pH   R² = 40%

.72 → SWC   R² = 56%   ← Drought

.22   .55   .48   .37   .7

Opportunistic   R² = 66%   Sensitive   R² = 48%   Resistant   R² = 40%

.55   .68

DF = 5, χ² = 2.5, CFI = 1.0, RMSEA = 0.0, P value = 0.77
Bollen Stine Bootstrap P value = 0.783

After recovery period, day 60

b

Latitude — .67 → Soil   R² = 45%

.51 .54 .46 .67 .42 .68

Intensive Management — .42 → pH   R² = 39%   SWC   R² = 36%   Drought

.29 .25 .32 .28 .4 .29 .3 .38 .46

Opportunistic   R² = 42%   Sensitive   R² = 26%   Resistant   R² = 59%

.40   .74

DF = 5, χ² = 0.356, CFI = 1.0, RMSEA = 0.0, P value = 0.996
Bollen Stine Bootstrap P value = 0.994

Bacteria

c

Latitude — .57 → Soil   R² = 32%

.36 .25 .48 .25 .26

Intensive Management — .41 → pH   R² = 40%

.72 → SWC   R² = 60%   ← Drought

.57 .47 .31 .35 .27

Opportunistic   R² = 43%   Sensitive   R² = 57%   Resistant   R² = 37%

.57   .49

DF = 5, χ² = 2.5, CFI = 1.0, RMSEA = 0.0, P value = 0.77
Bollen Stine Bootstrap P value = 0.788

d

Latitude — .67 → Soil   R² = 45%

.46 .67

Intensive Management — .42 → pH   R² = 39%   SWC   R² = 36%   Drought

.67 .38 .37 .56 .41 .3

Opportunistic   R² = 36%   Sensitive   R² = 49%   Resistant   R² = 36%

.65   .5
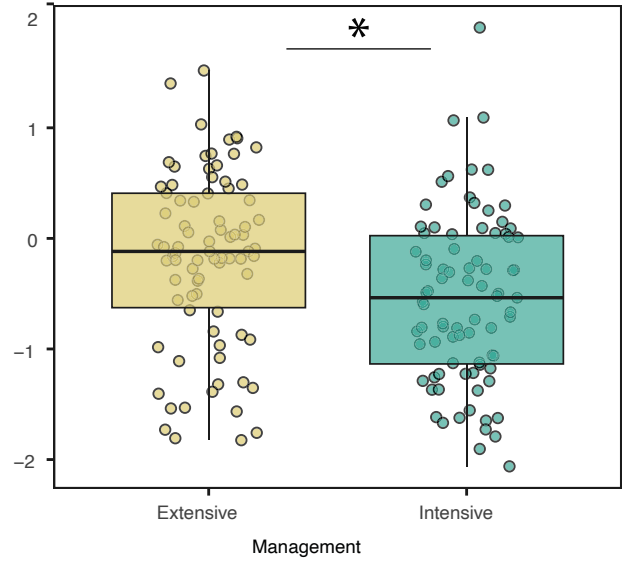
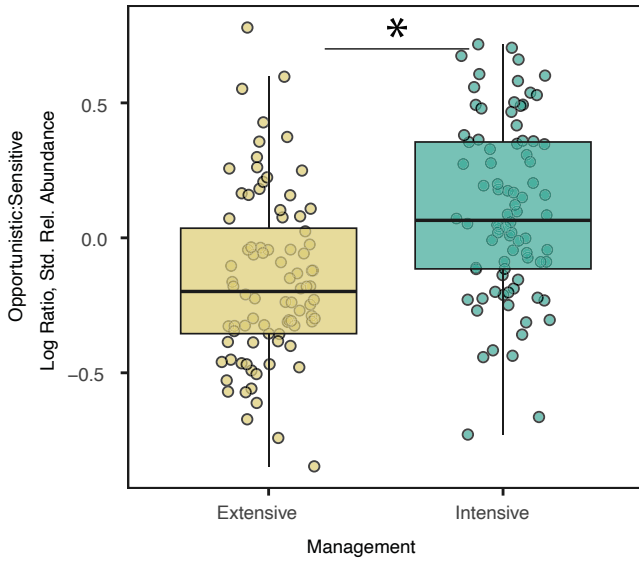DF = 5, χ² = 0.356, CFI = 1.0, RMSEA = 0.0, P value= 0.996
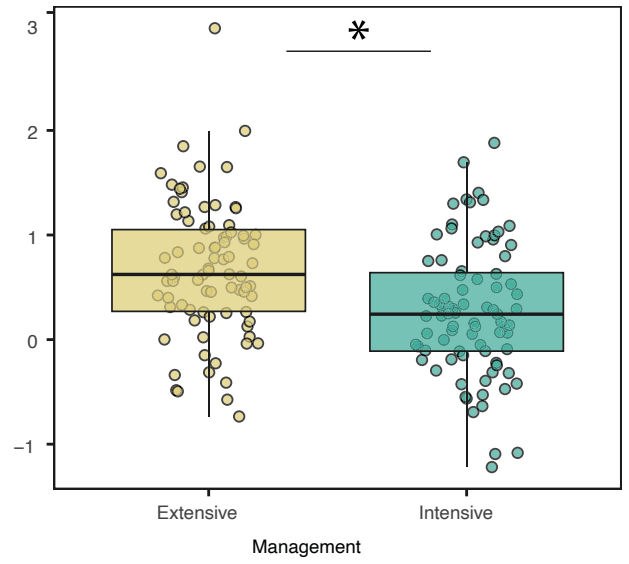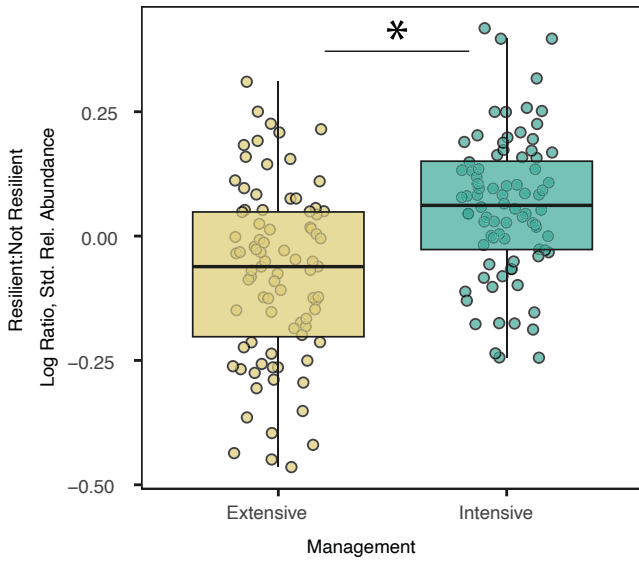Bollen Stine Bootstrap P value = 0.994

Fungi

→ Positive

→ Negative

Bacteria
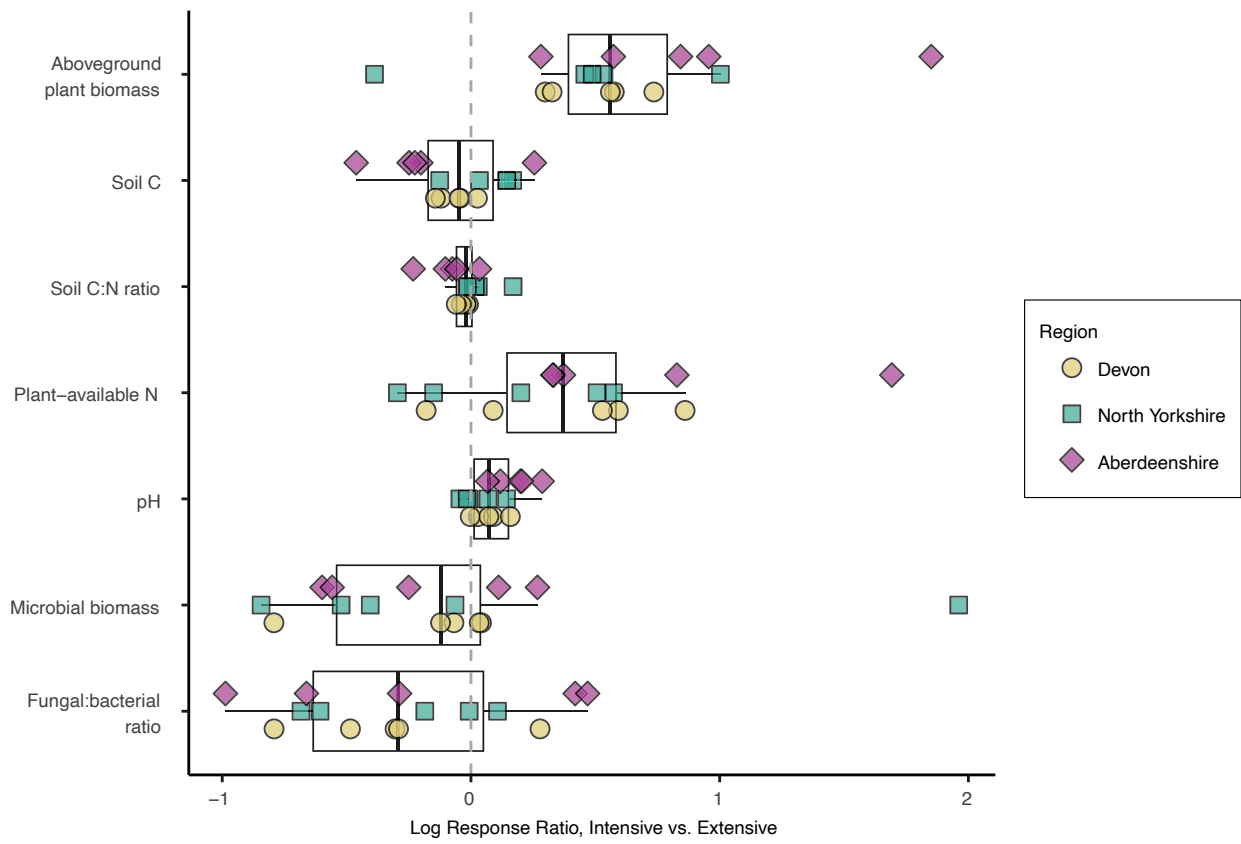
Fungi

a

b

Soil microbial communities are affected by climate extremes. Here, the authors impose experimental drought across 30 UK grasslands showing that bacteria and fungi exhibit drought resistance but that intensive management has a negative impact on fungi drought resilience.