



# Plant and soil communities are associated with the response of soil water repellency to environmental stress

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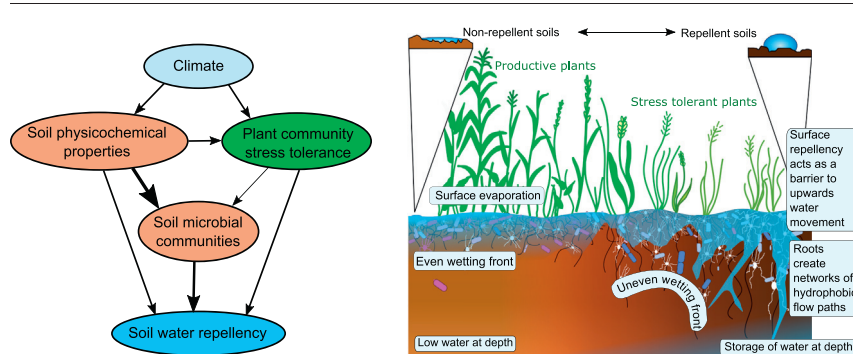
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## HIGHLIGHTS

- We measured repellency, soil and biotic variables in 1300 heterogeneous sites.
- Surface soil water repellency was found to affect 92% of soils at a national scale.
- Plant and soil microbial community composition strongly influenced repellency.
- Biota mediated the association between repellency and many physicochemical stresses.

## GRAPHICAL ABSTRACT



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## ABSTRACT

A warming climate and expected changes in average and extreme rainfall emphasise the importance of understanding how the land surface routes and stores surface water. The availability and movement of water within an ecosystem is a fundamental control on biological and geophysical activity, and influences many climatic feedbacks. A key phenomenon influencing water infiltration into the land surface is soil hydrophobicity, or water repellency. Despite repellency dictating the speed, volume and pattern of water infiltration, there is still major uncertainty over whether this critical hydrological process is biologically or physicochemically controlled. Here we show that soil water repellency is likely driven by changes in the plant and soil microbial communities in response to environmental stressors. We carried out a field survey in the summers of 2013 to 2016 in a variety of temperate habitats ranging across arable, grassland, forest and bog sites. We found that moderate to extreme repellency occurs in 68% of soils at a national scale in temperate ecosystems, with 92% showing some repellency. Taking a systems approach, we show that a wetter climate and low nutrient availability alter plant, bacterial and fungal community structure, which in turn are associated with increased soil water repellency across a large-scale gradient of soil, vegetation and land-use. The stress tolerance of the plant community and associated changes in soil microbial communities were more closely linked to changes in repellency than soil physicochemical properties. Our results indicate that there are consistent responses to diverse ecosystem stresses that will impact plant and microbial community composition, soil properties, and hydrological behaviour. We suggest that the ability of a biological community to induce such hydrological responses will influence the resilience of the

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whole ecosystem to environmental stress. This highlights the crucial role of above-belowground interactions in mediating climatic feedbacks and dictating ecosystem health.

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## 1. Introduction

The frequency and intensity of extreme climatic events is predicted to increase over the next century and beyond (IPCC, 2014). Soil moisture has been shown to have major implications for carbon storage and related climatic feedbacks (Green et al., 2019), therefore it is more important than ever to understand how the flow of water interacts with ecosystem health and the mechanisms controlling water fluxes at the land-atmosphere interface. There are still many uncertainties surrounding how water, soil, and vegetation will respond to the escalation of climatic stress in addition to prevailing land use stresses. Resilience to change varies between ecosystems, yet in most cases resilience and recovery only occur within limits and are less likely under multiple stressors (Côté et al., 2016). Biological communities shift in response to stress, and soil physicochemical properties change in tandem, creating an overall ecosystem response (van der Putten et al., 2013). Further, the ecosystem response to one stressor, such as drought, may change the response to another, such as flood. Many habitat stressor responses and feedbacks are as yet unknown but are globally important if we are to model and predict impacts helping to mitigate ecosystem damage (Robinson et al., 2019).

Soil water repellency fundamentally changes the way water infiltrates and moves through the soil. A water repellent (hydrophobic) soil is defined by the behaviour of liquid on the soil surface, with repellent soils causing water drops to bead and resist capillary absorption. Previous seminal work on water repellency has emphasised its impact on hydrological processes through increasing surface runoff and soil erodibility, predominantly in fire driven systems (Doerr et al., 2000; Goebel et al., 2011). To date, it is often negative impacts of repellency associated with crop production, flood risk, water quality and biogeochemical cycling that have been the focus of the literature (Dekker and Ritsema, 1994; Doerr et al., 2000). However, an emerging body of work provides evidence for the ecological role of repellency in promoting the resilience of plant communities and soil carbon stock to wildfire and drought stress in various ecosystems (Kettridge et al., 2014; Robinson et al., 2010; Zeppenfeld et al., 2017). Water repellency has been shown to induce unsaturated preferential flow of water into the soil rather than piston flow in many soils (Dekker and Ritsema, 1994; Rye and Smettem, 2017). Of the 17 ecosystem service categories identified by Costanza et al. (1997), twelve benefit from preferential flow and three are affected detrimentally (Clothier et al., 2008).

Water repellency induces increased runoff if the soil has no macropores and unsaturated preferential flow of water into the soil, rather than piston flow, in the presence of macropores (Dekker and Ritsema, 1994). The partitioning between preferential flow and surface run-off will depend on a number of factors in addition to the degree of repellency, e.g. texture, macropore density, the topography of the area, and the spatial pattern of repellency, which is often highly spatially heterogeneous (Bodí et al., 2013; Doerr et al., 2000). With preferential flow, water penetrates deeper into the soil profile by following roots or other macropores generating fingered flow, while with piston flow it penetrates evenly down the soil profile (Bogner et al., 2010). In an ecosystem where the spatial pattern of plants can adjust to the heterogeneity of infiltration due to repellency, preferential flow can be an advantage. For example, preferential flow can result in greater storage of water at depth (Rye and Smettem, 2018) which can increase a plant's resilience to drought stress and give an advantage to deep-rooting plants over shallow-rooting plants in drought stressed environments (De Boeck and Verbeeck, 2011; Zeppenfeld et al., 2017). Whereas, in agricultural production systems where the pattern of plants is predetermined and there are

limited macropores for the development of preferential flow paths soil moisture spatial heterogeneity and dry spots results in yield loss.

Water repellency is considered to be created by the amount, nature and configuration of soil organic material (Doerr et al., 2000; Mao et al., 2019), yet there is still uncertainty over the origins of the hydrophobic compounds in global soils (Mao et al., 2016; Schaumann et al., 2007; Spohn and Rillig, 2012). Until now, potential mechanisms for inducing water repellency have not been tested at realistic scales, hampering the emergence of a coherent theory across habitat types for the development and persistence of water repellency. In this work we analysed soil repellency across a wide range of habitats (Fig. 1) within a temperate oceanic climate. This wide range of biota within a limited climatic range enabled us to evaluate the relative role of biotic influence on repellency versus soil physicochemical influences, without confounding effects of climate. We characterised the plant community and soil physicochemical properties within 1326 sites, including 425 sites in which the belowground communities were measured, allowing an in-depth look at how the whole ecosystem shifts in tandem with soil hydrological shifts. Given the emerging evidence discussed we hypothesise that:

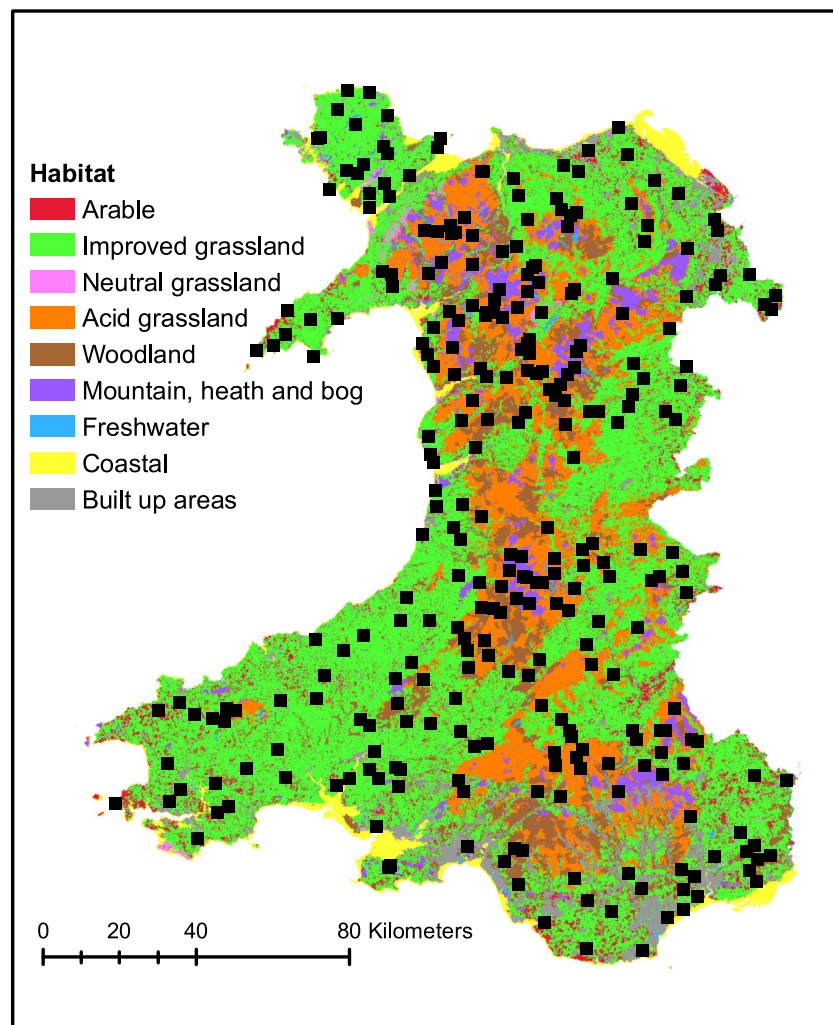
- 1) Soil water repellency depends on habitat, particularly showing greater persistence in those habitats that experience environmental stress such as drought and high acidity.
- 2) Persistence of repellency depends on the microbial community composition, as microbes can adapt to water stress by either becoming repellent or producing repellent compounds to aid water conservation.

We test these hypotheses through the following objectives: (i) measure repellency across habitat types and determine its prevalence; (ii) test the relationship between soil, plant and microbial communities and the persistence of soil repellency; and (iii) explore whether our pre-identified physicochemical and biological variables predict the changes in repellency across land use.

## 2. Methods

### 2.1. Field sampling design

We used data collected as part of the Glastir Monitoring and Evaluation Programme (GMEP) field measurement program in Wales, a sampling domain of ~2,000,000 ha comprising varied land use and topography and situated on the oceanic Atlantic seaboard of NW Europe (Emmett and the GMEP team, 2017). There were 300 individual 1 km squares randomly selected from within land classification strata and each included 5 vegetation plots (Fig. 1, Fig. S1). The sites were selected to be representative of the range of habitat types across Wales; consequently, different grassland habitats were sampled extensively, complemented by substantial numbers of woodland and wetland sites (Table S1). Sampling occurred over a five month period across each of the summers of 2013 to 2016, each square was only surveyed once over the four years with different squares being surveyed each year. Every plot had a vegetation survey performed for a 200 m<sup>2</sup> square and where possible soil samples taken at the south corner of an inner 2 m square (Fig. S1). A soil core for physicochemical analysis was taken with a plastic corer of 5 cm diameter down to 15 cm depth. The squares from the first two years of the survey had soil samples for microbiology taken from three randomly selected plots within the square. Soil samples for microbiology were taken using a gouge auger at 5 points around the physicochemical soil core location down to 15 cm, and then bulking



**Fig. 1.** A map of the survey square locations and the range of habitats included in the survey. The white circles represent approximate survey square locations. The habitats shown are aggregated from the categories within the Land Cover Map 2015. These aggregated habitat classes were not obtained using the same methods as the field survey assignment so care must be taken in linking the results.

together the samples. The surveyors assigned each plot to a habitat according to the Joint Nature Conservation Committee criteria (Jackson, 2000). The main habitats included in this study were: arable; improved grassland; neutral grassland; acid grassland; broadleaved woodland; coniferous woodland; dwarf shrub heath; fen, marsh and swamp; bog; and bracken.

Elevation data was taken from NEXTmap based on the GPS coordinates of the plots. Precipitation is the Standardised Annual Average Rainfall for 1961–1990 calculated on a 1 km grid. Drought is a measure of the annual average number of dry spell events, defined as 14 day events with <2 mm rainfall per day, over the previous 30 years to sample collection and calculated on 5 km grid square basis. All precipitation and drought data came from the Met Office © Crown copyright 2017. The Land Cover Map 2015 was used to represent the range of habitats across Wales (Rowland et al., 2017).

## 2.2. Soil physicochemical laboratory analyses

Analysis of soil variables was undertaken using the methods of the Countryside Survey (Emmett et al., 2008). Soil pH was measured by suspending 10 g of fresh soil in 0.01 M CaCl<sub>2</sub> in a 1:2.5 (weight/volume) soil suspension (Avery and Bascomb, 1974). The pH used was measured in CaCl<sub>2</sub> instead of deionised water as the CaCl<sub>2</sub> solution has similar ionic strength to the soil solution in fertilised temperate soils and thus

the pH is more representative of field conditions (Schofield and Taylor, 1955).

The surface 2 cm of the air-dry core was removed intact for water repellency measurement using the water drop penetration time method on the soil surface (Doerr, 1998) in the laboratory between 50 and 60% relative humidity. Six 1 ml droplets of deionised water were dropped on top of the soil surface from a height of 1 cm using a pipette. The absorption of the water droplets was recorded using video recording equipment, enabling measurement of the WDPT at a precision of 1 s. This surface section of the soil was recombined with the rest of the core for further processing. The complete soil samples had particles >2 mm size removed and the remaining fine earth fraction ground by a deagglomerator (Pulverisette 8). Soil carbon of the fine earth fraction of the soil was measured by oxidative combustion followed by thermal conductivity detection using an Elementar Vario EL analyser. The soil water content was calculated as the volumetric percentage of the fine earth fraction of the soil, taking into account the volume of particles >2 mm removed.

## 2.3. Biological community data

### 2.3.1. Plant community analysis

Multiple indices of plant community properties were calculated, including both those based on Ellenberg indicator values (Hill et al., 2004) and those based on Grime's CSR theory. Grime's CSR theory states that



species can be categorised into competitors, stress tolerators and ruderals (Grime, 1977; Hodgson et al., 1995). For these indices the score assigned to each plant species was taken and then a mean score per plot calculated based on species identity. Within this analysis we used Ellenberg fertility and Grime's stress tolerance.

### 2.3.2. Microbial community analysis

DNA was extracted using a mechanical lysis and homogenisation in triplicate from 0.25 g of soil per sample using PowerLyzer PowerSoil DNA Isolation Kits (MO-BIO) after pre-treatment with 750 µl of 1 M CaCO<sub>3</sub> (Sagova-Mareckova et al., 2008). Amplicon libraries were created using primers for the 16S (bacteria) and ITS1 (fungi) regions of the rRNA marker gene using a two-round PCR. The primer combinations used for the first round were 515F/806R (V4 16S) for 16S libraries (Caporaso et al., 2011; Walters et al., 2011) and ITS5/5.8S\_fungi (ITS1) for ITS1 libraries (Epp et al., 2012). For a full description of the methods used see George et al. (2019). Amplicon libraries of 2013 samples were constructed at Bangor University. Library preparation for 2014 samples and Illumina sequencing for both years were conducted at the Liverpool Centre for Genome Research. Sequences with limited sample metadata have been uploaded to The European Nucleotide Archive with the following primary accession codes: PRJEB27883 (16S) and PRJEB28028 (ITS1).

All bioinformatics were performed on the Supercomputing Wales system. Illumina adapters were trimmed from sequences using Cutadapt (Martin, 2011). The sequences were then de-multiplexed, filtered, quality-checked, and clustered using a combination of USEARCH v. 7.0 (Edgar, 2010) and VSEARCH v. 2.3.2 (Rognes et al., 2016) programmes. Sequences with a maximum error >1 and > 200 basepairs were removed following the merging of forward and reverse reads for all sequences. Operational taxonomic units (OTUs) were clustered using open reference methodology as described in George et al. (2019). Filtered sequences were matched first against either the GreenGenes v. 13.8 (DeSantis et al., 2006) or UNITE v. 7.2 (Kõljalg et al., 2013) databases. Ten percent of sequences that failed to match were clustered de novo and used as a new reference database for failed sequences. Sequences that failed to match with the de novo database were subsequently clustered de novo. Chimeric sequences were removed. Taxonomy was assigned to OTUs using QIIME (Caporaso et al., 2010) with RDP methodology (Wang et al., 2007) from the GreenGenes database v. 13.8 and UNITE database v. 7.2 for the 16S and ITS1 data, respectively. Singletons and OTUs appearing in only 1 sample were removed from OTU tables following taxonomic assignment. All non-bacterial and non-fungal OTUs were removed from each OTU table.

To account for variation in read depth across samples, fungal data was rarefied to 1750 reads and bacterial data was rarefied to 18,800 reads using the vegan package (Oksanen et al., 2018; Weiss et al., 2017). Rarefaction was repeated 100 times for fungi and 50 times for bacteria and the rounded mean used for all analyses. Fungal OTUs were also assigned to trophic mode using FUNGuild (Nguyen et al., 2016). In total 53.2% of the OTUs were assigned to a trophic mode, 82.9% of those assignments being rated probable or highly probable. The FUNGuild data was rarefied to 1500 read depth 100 times and the mean value across the repetitions used to calculate the proportions of OTUs identified to be solely pathotrophic, symbiotrophic or saprotrophic. Due to the low proportion of solely pathotrophic fungi within our samples only the symbiotrophic and saprotrophic proportions were used in the statistical analysis.

### 2.4. Statistical analysis

All statistical analysis was undertaken in R (R Core Team, 2018), and were performed on the natural logarithm of the median WDPT. The WDPT was categorised into the WDPT ratings of Doerr et al. (2006). Fig. 4 was created using the ggplot2 package (Wickham, 2009). Non-metric multidimensional scaling of the OTUs was performed using the

vegan package (Oksanen et al., 2018) using Sørensen community composition distances.

Structural equation modelling was used to evaluate the factors influencing water repellency in our dataset. This approach involves proposing a causative model, taking into account direct and indirect pathways, then fitting to the data and critically evaluating the proposed causative model. A set of climate, soil and plant variables were selected based on previous work constructing hypothesised relationships consistent with mechanisms that could drive repellency. These variables were built into a piecewise structural equation model (SEM) (Shipley, 2000) using Bayesian multilevel models (Bürkner, 2017; Clough, 2012), and evaluated using Shipley's test of d-separation (Shipley, 2013, 2009). Further details on the SEM approach and parameter selection are contained within the supplementary information.

## 3. Results

### 3.1. Soil water repellency at the national scale

Overall, we found that 92% of the soils showed at least slight water repellency with 32% showing severe to extreme water repellency (Table S1). We found that water repellency was strongly associated with soil carbon, water content and the composition of the plant and soil microbial communities at a site (Fig. 2). Soil carbon had the largest impact upon water repellency in both the model across the full dataset (Fig. 3b, Table S2) and the model with microbial data (Fig. 2b, Table S3).

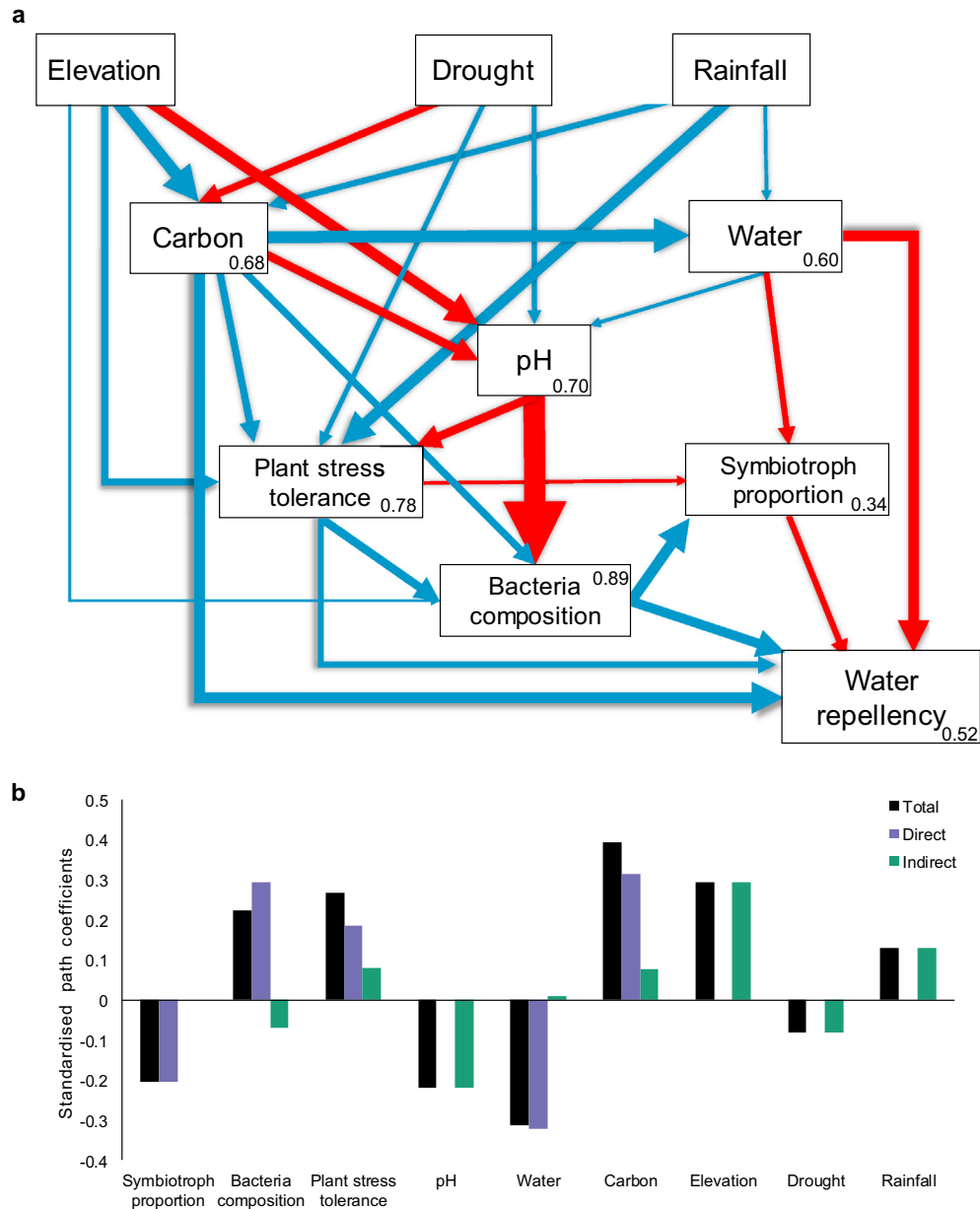
### 3.2. Biological influences on water repellency

Plant stress tolerance strongly impacted water repellency, having a direct impact that was over 50% higher than the effects of soil pH, soil water or climatic variables across the entire dataset (Fig. 3, Table S2). Although precipitation and drought were negatively correlated, both significantly increased the Grime stress tolerance score of a site. The stress score as a representative of the plant community was responsive to multiple forms of climatic stress as well as pH stress. A stress tolerant plant community at a site was associated with more repellent soils. The stress tolerance of the plant community impacts repellency directly and indirectly through differences in the soil microbial communities.

Both bacterial and fungal community composition explained significant residual variance in soil water repellency once changes in soil carbon, pH and water content were accounted for ( $p < 0.001$ ), indicating a direct link between the soil microbial communities and water repellency. Soil water repellency decreased with increasing proportions of symbiotrophic fungi (Fig. 2), the majority of which were ectomycorrhizal in this dataset (61%). Bacterial composition had a particularly high direct impact upon repellency (93% of the impact of soil carbon, the source of hydrophobic material; Fig. 2b, Table S3).

### 3.3. Mediation of climate and pH stress

Within our model the impacts of environmental stressors on repellency were completely mediated by changes in the biological communities at a site. Within the model without microbial data there are direct links between precipitation, drought and repellency (Fig. 3) however these were not present in the model with microbial data (Fig. 2). Water repellency does increase considerably with elevation, and alters with changing rainfall regime, yet this was entirely mediated by changes in soil properties and the biological community (Fig. 2b). We also found no further association between soil pH and water repellency once changes in the soil bacterial community composition were accounted for.



**Fig. 2.** Structural equation modelling reveals soil water repellency is strongly influenced by biological community composition. **a** The width of the arrow joining two boxes is proportional to the strength of the relationship, i.e. the parameter estimate. Positive relationships are represented by a blue arrow, negative by red and endogenous variables feature the proportion of variance within the variable explained by the model, the conditional  $R^2$  value, in the corner of the box. The model fitted the data well ( $C = 20.22$ ,  $p = 0.68$ ,  $n = 425$ ) and all other SEMs tested had a  $\Delta AICc$  score  $> 2$ . The full output from the model is in Supplementary Table 2. **b** The total, direct and indirect effect of each predictor on soil water repellency as estimated from the model parameters. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

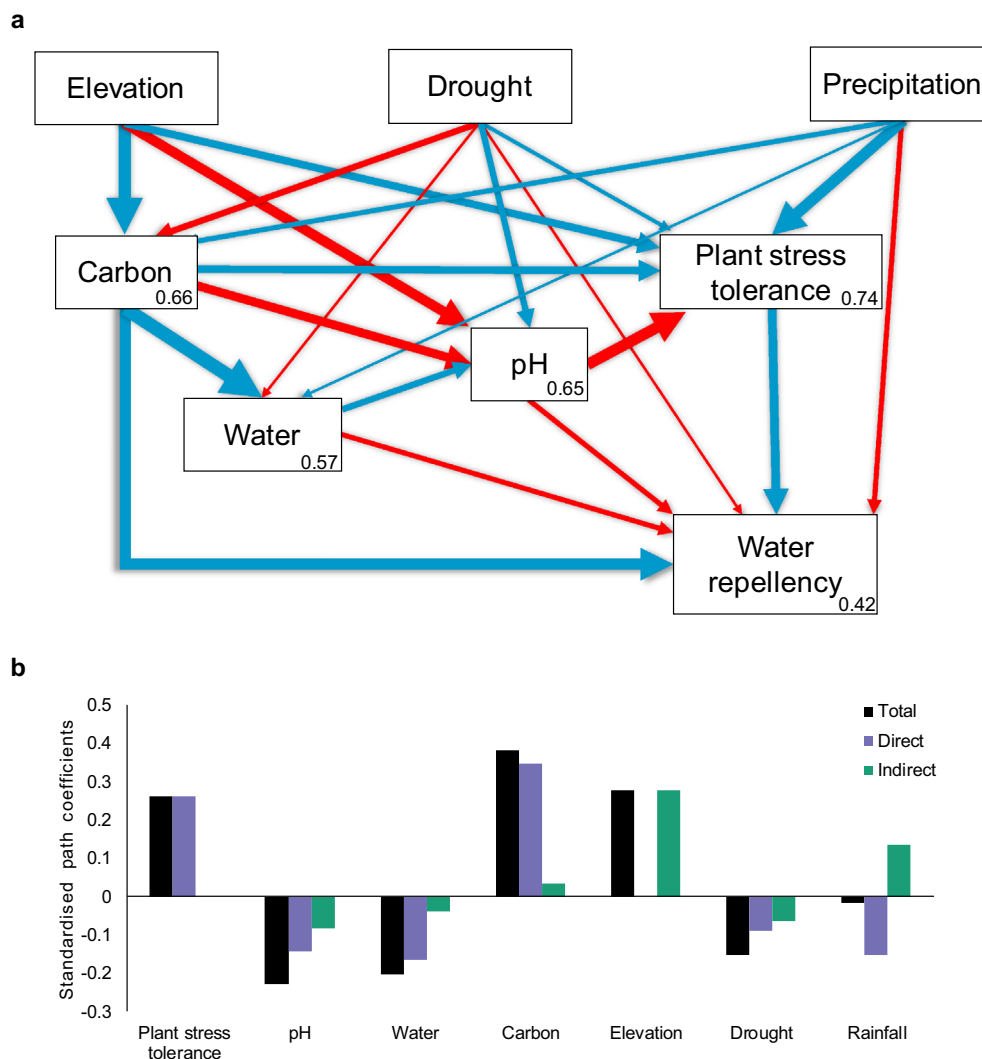
### 3.4. Influence of land use on soil water repellency

Repellency varied across the different habitat types in our study, with higher repellency in low productivity habitats such as acid grassland and bog compared to high productivity habitats such as improved grassland. Repellency was highly variable within most habitat types, particularly in broadleaved woodlands and fens (Fig. 4). Arable systems had significantly lower water repellency than all other habitat types (Fig. 4, Table S1). The low water repellency of arable systems persisted after accounting for their higher pH and lower soil carbon content (ANOVA on impact of habitat on residuals for whole dataset:  $F_{9,1295} = 7.394$ ;  $p < 0.0001$ ; Table S4) and different microbial communities (ANOVA on impact of habitat on residuals:  $F_{2,380} = 2.458$ ;  $p = 0.01$ ; Table S5). Arable habitats were the only habitats that were still different from other habitats after accounting for soil physicochemical and biotic variables (Table S5).

## 4. Discussion

### 4.1. Biological influences on soil water repellency

We found that repellency is higher in ecosystems with greater soil carbon, higher plant stress tolerance and associated changes in soil pH and microbial communities (Fig. 5). The strong influence of soil carbon on water repellency is consistent with previous work (Hermansen et al., 2019; Mao et al., 2019; Wang et al., 2016), but the association between plant community stress tolerance, microbial composition and repellency is novel. Our results provide evidence supporting literature conjecture that the ability to induce water repellency could confer a competitive advantage to plants within stressful environments (Robinson et al., 2010; Verboom and Pate, 2006). Multiple types of environmental stressors, including both climatic and acidity related



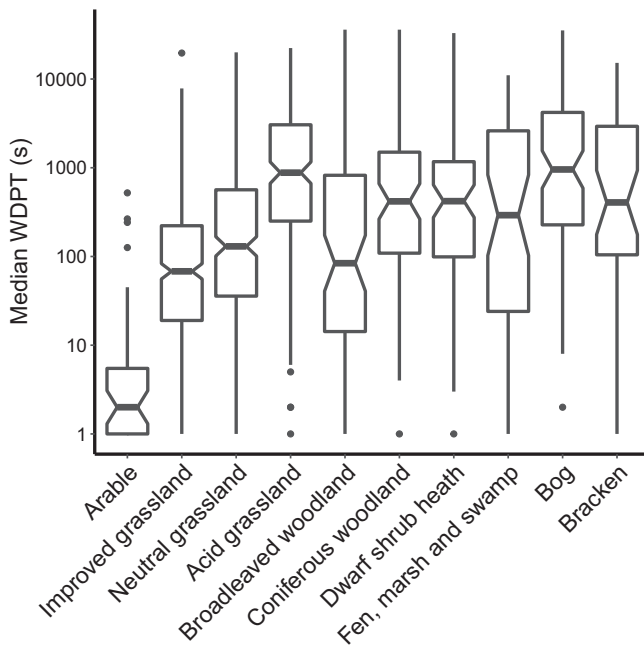
**Fig. 3.** Structural equation modelling reveals the drivers of soil water repellency across the entire dataset. **a** The width of the arrow joining two boxes is proportional to the strength of the relationship, i.e. the parameter estimate. Positive relationships are represented by a blue arrow, negative by red and endogenous variables feature the proportion of variance within the variable explained by the model, the conditional  $R^2$  value, in the corner of the box. The model fitted the data well ( $C = 8.40$ ,  $p = 0.40$ ,  $n = 1326$ ), and all other SEMs tested had  $\Delta AICc > 2$ . The full output from the model is in Supplementary Table 3. **b** The total, direct and indirect effect of each predictor on soil water repellency is depicted as estimated from the model parameters. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

stressors, have been found to be related to repellency. Surface water repellency can divert water deeper into the soil profile through inducing preferential flow of water and preventing water movement upwards by creating an evaporative barrier layer at the soil surface providing dual protection from evaporation (Doerr et al., 2006; Rye and Smettem, 2017). In semi-arid ecosystems the pattern of soil moisture in relation to trees suggests that the trees respond to drought by inducing water repellency to promote water flux down their root systems into deeper soil layers (Robinson et al., 2010; Verboom and Pate, 2006). Rhizosphere hydrophobicity has been found in modelling exercises to give a competitive advantage for plant growth due to greater acquisition of water and mitigating the impacts of drought stress (Kroener et al., 2016; Zeppenfeld et al., 2017).

We know from different parts of the literature that plant exudates (Svenningsson et al., 1990), fungal mats (Spohn and Rillig, 2012), and bacterial communities (Achtenhagen et al., 2015) can all respond to stress by producing water repellent compounds. For the microbial community the production of water repellent compounds can be an important survival mechanism both in dry and saturated systems. For example, Unestam (1991) argued that the lipid, hydrophobic fungal surface protected both the fungus and tree roots against desiccation

during drought periods. Furthermore, he observed that the mycorrhizal roots withstood a drier soil environment in rhizoscopes than did the hydrophilic non-mycorrhizal roots. Another advantage is that hydrophobic mycorrhizal hyphae may translocate water more efficiently, being less susceptible to water loss (Duddridge et al., 1980; Read et al., 1985). In saturated conditions, Unestam (1991) argued that the fungal mats, particularly the complex hydrophobic structures, such as the mantle, cords, and patches, could produce air pockets. As obligate aerobes, saturation for extended periods would cause death, so the air pockets could provide a lifeline.

Bacteria have been found to produce extremely water repellent biofilms (Epstein et al., 2011) (Epstein et al., 2011). One aspect of this repellency is that it prevents the penetration of antimicrobials into the biofilm. This has been exploited in crop protection where the biofilm development can shield roots from waterborne pathogens. Moreover, it has been argued that both hydrophobic bacterial cell walls and bacterial biofilms protect bacteria from desiccation or bursting in response to cycles of drying and rapid rewetting (Achtenhagen et al., 2015). Water stress was shown to activate a number of processes in microorganisms, (Morales et al., 2010; Schimel et al., 2007). Hence our proposal that the development of water repellency is an ecosystem response to a stressful

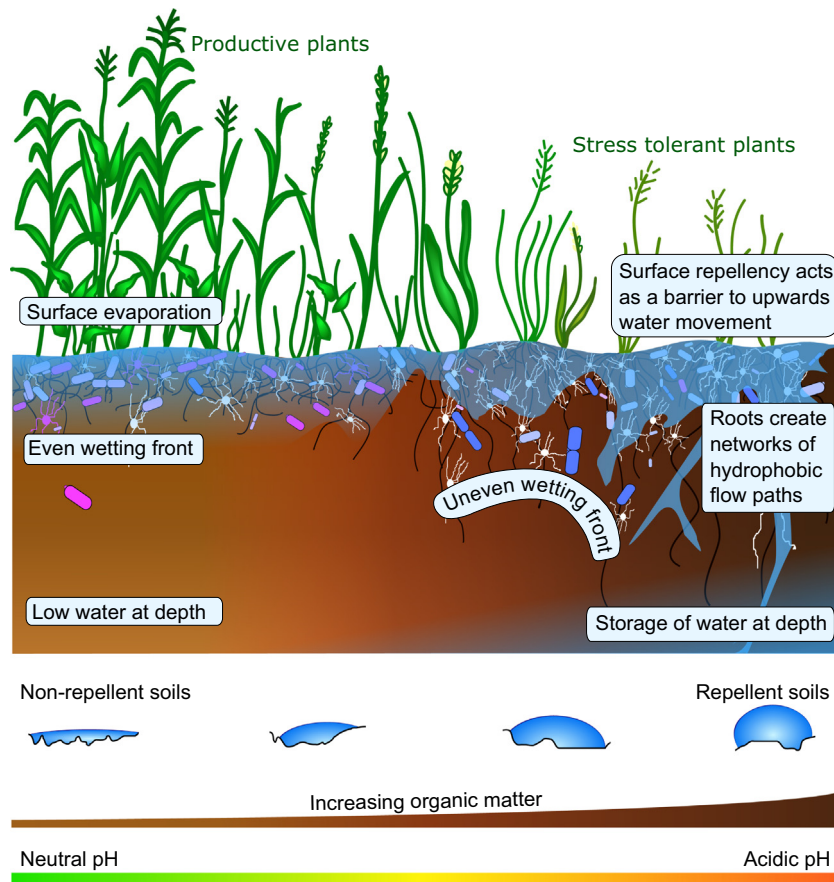


**Fig. 4.** Arable systems show lower water repellency than all other habitat types. Water repellency increases with decreasing fertility of grassland (improved to neutral to acid grassland). The non-overlap of notches indicates that their medians are approximately significantly different at a 95% confidence level. Other habitats had lower sample sizes, overlapping notches and it is more difficult to draw strong conclusions.

environment, as a means of protection for microbes and better resource allocation with plants. Our results, covering climatic stress, soil physico-chemical properties, plant and soil microbial communities together, support the development of such an ecological theory.

#### 4.2. Persistence of repellency

Microbial communities are quicker to respond to change than plants and our results indicate that repellency could be induced by microbes on short timescales in response to environmental stressors. There is still much uncertainty over the persistence of repellency over time and space (Bodí et al., 2013; Leighton-Boyce et al., 2007; Müller et al., 2014; Rye and Smettem, 2015). Our study analysed the air-dry repellency of the soil, which can be interpreted as the ability of the sample to become repellent upon drying and thus would be less variable over time than repellency of the fresh soil surface. The different ways in which repellency is created and maintained may be a critical factor in determining how long repellency will persist. Some studies have found that hydrophobicity can originate from plant material, both litter and root exudates, which clearly indicates a potential for long term maintenance of repellency by plants (Cesarano et al., 2016; Hallett et al., 2009; Mao et al., 2016; Naveed et al., 2018). Microbial communities are more changeable than plants yet could still result in the long term ability to induce repellency. Microbes both create and destroy repellent compounds, and changes in the composition of the community help determine water repellency.



**Fig. 5.** A representation of the change in repellency across an environmental stress gradient and its impact upon water fluxes in the soil when dry. Upon the left of the diagram we have a plant community that is adapted to be competitive in low-stress environments, highly productive with a non-repellent soil. Water infiltrates the soil in a piston flow manner. On the right we have a stress tolerant plant community with a repellent soil that alters water infiltration to follow preferential flow paths. This results in greater water next to plant roots and stored at depth within the soil.



#### 4.3. Evaluating the directionality of links and mediation in SEM

Within our analysis we assumed that soil repellency was caused by changes in the microbial community, rather than the reverse. We consider that repellency is caused by hydrophobic compounds within the soil (Hermansen et al., 2019; Mainwaring et al., 2013; Mao et al., 2019), however, it is feasible that the physical configuration of soil components could play some role, which remains largely unexplored (Benard et al., 2018). It is these hydrophobic factors that we consider to be altered by biotic communities. It is possible that the hydrophobic compounds within the soil could be altering the microbial communities through changing the suitability of the environment (Barnard et al., 2013; Or et al., 2007; Wang and Or, 2013). However microbial communities are both the source of, and mediator of, the breakdown of hydrophobic compounds (Achtenhagen et al., 2015; Chau et al., 2012; Li et al., 2018; Schaumann et al., 2007). There is likely a feedback mechanism whereby, as the physical environment is altered by the production or degradation of hydrophobic compounds, this then forces changes in microbial communities which are adapted to different situations. We believe that the shorter feedback is in the direction of microbes to repellency, and it is this we have included in our model.

We have found complete mediation of climatic and some physicochemical stressors on repellency. Thus once we know the biotic community composition we do not need to know the wider environmental conditions to be able to predict repellency. In particular, the complete mediation of pH related influences on repellency by the microbial community is of interest. This suggests that the change in water repellency with pH found in many observational studies (Lebron et al., 2012; Mirbabaei et al., 2013; Zavala et al., 2014) is not likely to be due to chemical modification of particles, which has been found to alter water repellency in pH modification experiments (Amer et al., 2017; Diehl, 2013). The complete mediation of climatic stressors upon repellency suggests that the influence of climate on soil surface water content will be strongly impacted by the biological community at a site, with implications for earth system modelling (Goebel et al., 2011; Green et al., 2019). The infiltration of water into the soil in these systems is driven by biological factors, not physicochemical, and will therefore change as biological communities are placed under increasing stress.

#### 4.4. Influence of land use on soil water repellency

The differing land uses within our study had differing repellency, however the impact of land use on repellency was in most cases explained by the variation in carbon, pH and biotic communities across the land use types. This supports the findings of Doerr et al. (2006), who also found a land cover dependency for soil water repellency in the United Kingdom. Repellency is known to have a strong role in the function of some land use types. For example, within some peatland systems extreme water repellency was created after fire, which lowered evaporation, allowed the maintenance of a high water table, and increased speed of ecosystem recovery compared to systems that did not become repellent after fire (Kettridge et al., 2014). With regard to stress it has been found that, in pasture systems a negative relationship between productivity and repellency has been found (Müller et al., 2014). This suggests that the competitive advantage found by the aforementioned modelling studies (Kroener et al., 2016; Zeppenfeld et al., 2017) are limited to locations that are undergoing stress and are potentially therefore less productive. Our results are consistent with this as stress resilient plant species are found in less productive sites.

There is however one habitat in which knowing the carbon, water and biotic community does not mean that you can predict repellency: arable. Arable systems have lower than predicted repellency even after taking into account soil physicochemical, above and belowground community composition. There is something qualitatively different about arable systems which results in lower repellency, perhaps due

to the mechanical disturbance of the soil through tillage, which has been found to reduce water repellency and infiltration (Müller et al., 2016; Roper et al., 2013). Water repellency is likely to be related to soil biophysical structure, the networks of roots, fungal hyphae and microbial biofilms that permeate the soil and follow, create and maintain preferential flow paths for water infiltration.

#### 4.5. Water repellency and biological community response to stress

The concept of water repellency as an adaptive stress response suggests that the ability to induce water repellency promotes ecosystem resilience to drought and other stressors. Access to water stores has been shown to be crucial in determining carbon loss and plant resilience during drought (De Boeck and Verbeeck, 2011). We propose that water repellency indicates a healthy ecosystem response to stress, and the inability of tilled land to induce water repellency can be interpreted as an unhealthy lack of resilience. We have found that multiple different natural stressors: drought; high precipitation and low nutrient status acidic soils had a consistent relationship with our realistic large-scale gradient of soil water repellency. It is the biological communities which are more closely related to soil repellency than physicochemical factors, showing the importance of ecology in modifying hydrological processes through feedbacks that will help conserve water. The homogeneity of response indicates there are consistent mechanisms induced by biological communities across ecosystem types to increase resilience. These mechanisms are those we should be interested in monitoring and influencing to understand, predict and mitigate ecosystem shifts in response to increasing stress from land use and climate change.

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#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2019.06.052>.

#### References

- Achtenhagen, J., Goebel, M.O., Miltner, A., Woche, S.K., Kästner, M., 2015. Bacterial impact on the wetting properties of soil minerals. *Biogeochemistry* 122, 269–280. <https://doi.org/10.1007/s10533-014-0040-9>.
- Amer, A., Schaumann, G.E., Diehl, D., 2017. The effect of pH modification on wetting kinetics of a naturally water-repellent coniferous forest soil. *Eur. J. Soil Sci.* 68, 317–326. <https://doi.org/10.1111/ejss.12419>.
- Avery, B.W., Bascomb, C.L., 1974. *Soil Survey Laboratory Methods. Soil Survey Technical Monograph No. 6* (Harpenden).
- Barnard, R.L., Osborne, C.A., Firestone, M.K., 2013. Responses of soil bacterial and fungal communities to extreme desiccation and rewetting. *ISME J* 7, 2229–2241. <https://doi.org/10.1038/ismej.2013.104>.
- Benard, P., Zarebanadkouki, M., Hedwig, C., Holz, M., Ahmed, M.A., Carminati, A., 2018. Pore-scale distribution of mucilage affecting water repellency in the rhizosphere. *Vadose Zo. J.* 17, 0. <https://doi.org/10.2136/vzj2017.01.0013>.



- Bodí, M.B., Muñoz-Santa, I., Armero, C., Doerr, S.H., Mataix-Solera, J., Cerdà, A., 2013. Spatial and temporal variations of water repellency and probability of its occurrence in calcareous Mediterranean rangeland soils affected by fires. *Catena* 108, 14–25. <https://doi.org/10.1016/j.catena.2012.04.002>.
- Bogner, C., Gaul, D., Kolb, A., Schmiedinger, I., Huwe, B., 2010. Investigating flow mechanisms in a forest soil by mixed-effects modelling. *Eur. J. Soil Sci.* 61, 1079–1090. <https://doi.org/10.1111/j.1365-2389.2010.01300.x>.
- Bürkner, P.-C., 2017. brms: an R package for Bayesian multilevel models using Stan. *J. Stat. Softw.* 80, 1–28. <https://doi.org/10.18637/jss.v080.i01>.
- Caporaso, J.G., Kuczynski, J., Stombaugh, J., Bittinger, K., Bushman, F.D., Costello, E.K., Fierer, N., Peña, A.G., Goodrich, J.K., Gordon, J.L., Huttley, G.A., Kelley, S.T., Knights, D., Koenig, J.E., Ley, R.E., Lozupone, C.A., McDonald, D., Muegge, B.D., Pirrung, M., Reeder, J., Sevinsky, J.R., Turnbaugh, P.J., Walters, W.A., Widmann, J., Yatsunenko, T., Zaneveld, J., Knight, R., 2010. QIIME allows analysis of high-throughput community sequencing data. *Nat. Methods* 7, 335–336. <https://doi.org/10.1038/nmeth.f303>.
- Caporaso, J.G., Lauber, C.L., Walters, W.A., Berg-lyons, D., Lozupone, C.A., Turnbaugh, P.J., Fierer, N., Knight, R., 2011. Global patterns of 16S rRNA diversity at a depth of millions of sequences per sample. *Proc. Natl. Acad. Sci.* 108, 4516–4522. <https://doi.org/10.1073/pnas.1000801107>.
- Cesarano, G., Incerti, G., Bonanomi, G., 2016. The influence of plant litter on soil water repellency: insight from <sup>13</sup>C NMR spectroscopy. *PLoS One* 11, e0152565. <https://doi.org/10.1371/journal.pone.0152565>.
- Chau, H.W., Goh, Y.K., Vujanovic, V., Si, B.C., 2012. Wetting properties of fungi mycelium alter soil infiltration and soil water repellency in a γ-sterilized wettable and repellent soil. *Fungal Biol* 116, 1212–1218. <https://doi.org/10.1016/j.funbio.2012.10.004>.
- Clothier, B.E., Green, S.R., Deurer, M., 2008. Preferential flow and transport in soil: progress and prognosis. *Eur. J. Soil Sci.* 59, 2–13. <https://doi.org/10.1111/j.1365-2389.2007.00991.x>.
- Clough, Y., 2012. A generalized approach to modeling and estimating indirect effects in ecology. *Ecology* 93, 1809–1815. <https://doi.org/10.1890/11-1899.1>.
- Costanza, R., D'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P., van den Belt, M., 1997. The value of the world's ecosystem services and natural capital. *Nature* 387, 253–260. <https://doi.org/10.1038/387253a0>.
- Côté, I.M., Darling, E.S., Brown, C.J., 2016. Interactions among ecosystem stressors and their importance in conservation. *Proc. Biol. Sci.* 283. <https://doi.org/10.1098/rspb.2015.2592>.
- De Boeck, H.J., Verbeeck, H., 2011. Drought-associated changes in climate and their relevance for ecosystem experiments and models. *Biogeosciences* 8, 1121–1130. <https://doi.org/10.5194/bg-8-1121-2011>.
- Dekker, L.W., Ritsema, C.J., 1994. How water moves in a water repellent sandy soil: 1. Potential and actual water repellency. *Water Resour. Res.* 30, 2507–2517. <https://doi.org/10.1029/94WR00749>.
- DeSantis, T.Z., Hugenholtz, P., Larsen, N., Rojas, M., Brodie, E.L., Keller, K., Huber, T., Dalevi, D., Hu, P., Andersen, G.L., 2006. Greengenes, a chimera-checked 16S rRNA gene database and workbench compatible with ARB. *Appl. Environ. Microbiol.* 72, 5069–5072. <https://doi.org/10.1128/AEM.03006-05>.
- Diehl, D., 2013. Soil water repellency: dynamics of heterogeneous surfaces. *Colloids Surf. A Physicochem. Eng. Asp.* 432, 8–18. <https://doi.org/10.1016/j.colsurfa.2013.05.011>.
- Doerr, S.H., 1998. On standardizing the 'water drop penetration time' and the 'molarity of an ethanol droplet' techniques to classify soil hydrophobicity: a case study using medium textured soils. *Earth Surf. Process. Landf.* 23, 663–668. [https://doi.org/10.1002/\(SICI\)1096-9837\(199807\)23:7<663::AID-ESP909>3.0.CO;2-6](https://doi.org/10.1002/(SICI)1096-9837(199807)23:7<663::AID-ESP909>3.0.CO;2-6).
- Doerr, S.H., Shakesby, R.A., Walsh, R.P.D., 2000. Soil water repellency: its causes, characteristics and hydro-geomorphological significance. *Earth Sci. Rev.* 51, 33–65. [https://doi.org/10.1016/S0012-8252\(00\)00011-8](https://doi.org/10.1016/S0012-8252(00)00011-8).
- Doerr, S.H., Shakesby, R.A., Dekker, L.W., Ritsema, C.J., 2006. Occurrence, prediction and hydrological effects of water repellency amongst major soil and land-use types in a humid temperate climate. *Eur. J. Soil Sci.* 57, 741–754. <https://doi.org/10.1111/j.1365-2389.2006.00818.x>.
- Duddridge, J.A., Malibari, A., Read, D.J., 1980. Structure and function of mycorrhizal rhizomorphs with special reference to their role in water transport. *Nature* 287, 834–836. <https://doi.org/10.1038/287834a0>.
- Edgar, R.C., 2010. Search and clustering orders of magnitude faster than BLAST. *Bioinformatics* 26, 2460–2461. <https://doi.org/10.1093/bioinformatics/btq461>.
- Emmett, B.A., the GMEP team, 2017. *Glastir Monitoring & Evaluation Programme. Final Report to Welsh Government*.
- Emmett, B.A., Frogbrook, Z.L., Chamberlain, P.M., Giffiths, R., Pickup, R., Poskitt, J., Reynolds, B., Rowe, E., Spurgeon, D., Rowland, P., Wilson, J., Wood, C.M., 2008. *CS Technical Report No. 3/07: Soils Manual. NERC/Centre for Ecology & Hydrology* (180 pp. (CEH Project Number: C03259)).
- Epp, L.S., Boessenkool, S., Bellemain, E.P., Haile, J., Esposito, A., Riaz, T., Erséus, C., Gusarov, V.I., Edwards, M.E., Johnsen, A., Stenøien, H.K., Hassel, K., Kausarud, H., Yoccoz, N.G., Bråthen, K.A., Willerslev, E., Taberlet, P., Coissac, E., Brochmann, C., 2012. New environmental metabarcodes for analysing soil DNA: potential for studying past and present ecosystems. *Mol. Ecol.* 21, 1821–1833. <https://doi.org/10.1111/j.1365-294X.2012.05537.x>.
- Epstein, A.K., Pokroy, B., Seminara, A., Aizenberg, J., 2011. Bacterial biofilm shows persistent resistance to liquid wetting and gas penetration. *Proc. Natl. Acad. Sci.* 108, 995–1000. <https://doi.org/10.1073/pnas.1011033108>.
- George, P.B.L., Lallias, D., Creer, S., Seaton, F.M., Kenny, J.G., Eccles, R.M., Griffiths, R.I., Lebron, I., Emmett, B.A., Robinson, D.A., Jones, D.L., 2019. Divergent national-scale trends of microbial and animal biodiversity revealed across diverse temperate soil ecosystems. *Nat. Commun.* 10, 1107. <https://doi.org/10.1038/s41467-019-09031-1>.
- Goebel, M., Bachmann, J., Reichstein, M., Janssens, I.A., Guggenberger, G., 2011. Soil water repellency and its implications for organic matter decomposition - is there a link to extreme climatic events? *Glob. Chang. Biol.* 17, 2640–2656. <https://doi.org/10.1111/j.1365-2486.2011.02414.x>.
- Green, J.K., Seneviratne, S.I., Berg, A.M., Findell, K.L., Hagemann, S., Lawrence, D.M., Gentile, P., 2019. Large influence of soil moisture on long-term terrestrial carbon uptake. *Nature* 565, 476–479. <https://doi.org/10.1038/s41586-018-0848-x>.
- Grime, J.P., 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat.* 111, 1169–1194.
- Hallett, P.D., Feeney, D.S., Bengough, A.G., Rillig, M.C., Scrimgeour, C.M., Young, I.M., 2009. Disentangling the impact of AM fungi versus roots on soil structure and water transport. *Plant Soil* <https://doi.org/10.1007/s11104-008-9717-y>.
- Hermansen, C., Moldrup, P., Müller, K., Jensen, P.W., van den Dijk, C., Jeyakumar, P., de Jonge, L.W., 2019. Organic carbon content controls the severity of water repellency and the critical moisture level across New Zealand pasture soils. *Geoderma* 338, 281–290. <https://doi.org/10.1016/j.geoderma.2018.12.007>.
- Hill, M.O., Preston, C.D., Roy, D.B., 2004. *PLANTATT - Attributes of British and Irish Plants: Status, Size, Life History, Geography and Habitats*. Centre for Ecology & Hydrology.
- Hodgson, J.G., Grime, J.P., Hunt, R., Thompson, K., 1995. *The Electronic Comparative Plant Ecology*. Springer.
- IPCC, 2014. In: *Core Writing Team, Pachauri, R.K., Meyer, L.A. (Eds.), Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*.
- Jackson, D.L., 2000. *Guidance on the Interpretation of the Biodiversity Broad Habitat Classification (Terrestrial and Freshwater Types): Definitions and the Relationships with Other Classifications*, JNCC Report 307.
- Kettridge, N., Humphrey, R.E., Smith, J.E., Lukenbach, M.C., Devito, K.J., Petrone, R.M., Waddington, J.M., 2014. Burned and unburned peat water repellency: implications for peatland evaporation following wildfire. *J. Hydrol.* 513, 335–341. <https://doi.org/10.1016/j.jhydrol.2014.03.019>.
- Köljal, U., Nilsson, R.H., Abarenkov, K., Tedersoo, L., Taylor, A.F.S., Bahram, M., Bates, S.T., Bruns, T.D., Bengtsson-Palme, J., Callaghan, T.M., Douglas, B., Drenkhan, T., Eberhardt, U., Dueñas, M., Grebenc, T., Griffith, G.W., Hartmann, M., Kirk, P.M., Kohout, P., Larsson, E., Lindahl, B.D., Lücking, R., Martin, M.P., Matheny, P.B., Nguyen, N.H., Niskanen, T., Oja, J., Peay, K.G., Peintner, U., Peterson, M., Pöhlmaa, K., Saag, L., Saar, I., Schöler, A., Scott, J.A., Senés, C., Smith, M.E., Suija, A., Taylor, D.L., Telleria, M.T., Weiss, M., Larsson, K.-H., 2013. Towards a unified paradigm for sequence-based identification of fungi. *Mol. Ecol.* 22, 5271–5277. <https://doi.org/10.1111/mec.12481>.
- Kroener, E., Zarebanadkouki, M., Bittelli, M., Carminati, A., 2016. Simulation of root water uptake under consideration of nonequilibrium dynamics in the rhizosphere. *Water Resour. Res.* 52, 5755–5770. <https://doi.org/10.1002/2015WR018579>.
- Lebron, I., Robinson, D.A., Oatham, M., Wuddivira, M.N., 2012. Soil water repellency and pH soil change under tropical pine plantations compared with native tropical forest. *J. Hydrol.* 414–415, 194–200. <https://doi.org/10.1016/j.jhydrol.2011.10.031>.
- Leighton-Boyce, G., Doerr, S.H., Shakesby, R.A., Walsh, R.P.D., 2007. Quantifying the impact of soil water repellency on overland flow generation and erosion: a new approach using rainfall simulation and wetting agent on in situ soil. *G. Hydrol. Process.* 21, 2337–2345. <https://doi.org/10.1002/hyp.6744>.
- Li, B., Pales, A.R., Clifford, H.M., Kupis, S., Hennessy, S., Liang, W.-Z., Moysey, S., Powell, B., Finneran, K.T., Darnault, C.J.G., 2018. Preferential flow in the vadose zone and interface dynamics: impact of microbial exudates. *J. Hydrol.* 558, 72–89. <https://doi.org/10.1016/j.jhydrol.2017.12.065>.
- Mainwaring, K., Hallin, I.L., Douglas, P., Doerr, S.H., Morley, C.P., 2013. The role of naturally occurring organic compounds in causing soil water repellency. *Eur. J. Soil Sci.* 64. <https://doi.org/10.1111/ejss.12078>.
- Mao, J., Nierop, K.G.J., Rietkerk, M., Sinnighe Damsté, J.S., Dekker, S.C., 2016. The influence of vegetation on soil water repellency-markers and soil hydrophobicity. *Sci. Total Environ.* 566, 608–620. <https://doi.org/10.1016/j.scitotenv.2016.05.077>.
- Mao, J., Nierop, K.G.J., Dekker, S.C., Dekker, L.W., Chen, B., 2019. Understanding the mechanisms of soil water repellency from nanoscale to ecosystem scale: a review. *J. Soils Sediments* 19, 171–185. <https://doi.org/10.1007/s11368-018-2195-9>.
- Martin, M., 2011. Cutadapt removes adapter sequences from high-throughput sequencing reads. *EMBnet journal* 17, 10. <https://doi.org/10.14806/ej.17.1.200>.
- Mirbabaie, S.M., Shahrestani, M.S., Zolfaghari, A., Abkenar, K.T., 2013. Relationship between soil water repellency and some of soil properties in northern Iran. *Catena* 108, 26–34. <https://doi.org/10.1016/j.catena.2013.02.013>.
- Morales, V.L., Parlange, J.Y., Steenhuis, T.S., 2010. Are preferential flow paths perpetuated by microbial activity in the soil matrix? A review. *J. Hydrol.* 393, 29–36. <https://doi.org/10.1016/j.jhydrol.2009.12.048>.
- Müller, K., Deurer, M., Jeyakumar, P., Mason, K., van den Dijk, C., Green, S., Clothier, B., 2014. Temporal dynamics of soil water repellency and its impact on pasture productivity. *Agric. Water Manag.* 143, 82–92. <https://doi.org/10.1016/j.agwat.2014.06.013>.
- Müller, K., Carrick, S., Meenen, E., Clemens, G., Hunter, D., Rhodes, P., Thomas, S., 2016. Is subcritical water repellency an issue for efficient irrigation in arable soils? *Soil Tillage Res.* 161, 53–62. <https://doi.org/10.1016/j.still.2016.03.010>.
- Naveed, M., Brown, L.K., Raffan, A.C., George, T.S., Bengough, A.G., Roose, T., Sinclair, I., Koebnick, N., Cooper, L., Hallett, P.D., 2018. Rhizosphere-scale quantification of hydraulic and mechanical properties of soil impacted by root and seed exudates. *Vadose Zo. J.* 17, 0. <https://doi.org/10.2136/vzj2017.04.0083>.
- Nguyen, N.H., Song, Z., Bates, S.T., Branco, S., Tedersoo, L., Menke, J., Schilling, J.S., Kennedy, P.G., 2016. FUNGuild: an open annotation tool for parsing fungal community datasets by ecological guild. *Fungal Ecol.* 20, 241–248. <https://doi.org/10.1016/j.funeco.2015.06.006>.
- Oksanen, J., Blanchet, G., Friendly, M., Kindt, R., Legendre, P., McGinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2018. *Vegan: Community Ecology Package*.
- Or, D., Smets, B.F., Wraith, J.M., Dechesne, A., Friedman, S.P., 2007. Physical constraints affecting bacterial habitats and activity in unsaturated porous media - a review. *Adv. Water Resour.* 30, 1505–1527. <https://doi.org/10.1016/j.advwatres.2006.05.025>.
- R Core Team, 2018. *R: A Language and Environment for Statistical Computing*.

- Read, D.J., Francis, R., Finlay, R.D., 1985. Mycorrhizal mycelia and nutrient cycling in plant communities. In: Fitter, A., Atkinson, D., Read, D.J., Usher, M. (Eds.), *Ecological Interactions in Soil*. Blackwell, Oxford, UK, pp. 193–218.
- Robinson, D.A., Lebron, I., Ryel, R.J., Jones, S.B., 2010. Soil water repellency: a method of soil moisture sequestration in pinyon–juniper woodland. *Soil Sci. Soc. Am. J.* 74, 624. <https://doi.org/10.2136/sssaj2009.0208>.
- Robinson, D.A., Hopmans, J.W., Filipovic, V., van der Ploeg, M., Lebron, I., Jones, S.B., Reinsch, S., Jarvis, N., Tuller, M., 2019. Global environmental changes impact soil hydraulic functions through biophysical feedbacks. *Glob. Chang. Biol.* 25, 1895–1904. <https://doi.org/10.1111/gcb.14626>.
- Rognes, T., Flouri, T., Nichols, B., Quince, C., Mahé, F., 2016. VSEARCH: a versatile open source tool for metagenomics. *PeerJ* 4, e2584. <https://doi.org/10.7717/peerj.2584>.
- Roper, M.M., Ward, P.R., Keulen, A.F., Hill, J.R., 2013. Under no-tillage and stubble retention, soil water content and crop growth are poorly related to soil water repellency. *Soil Tillage Res.* 126, 143–150. <https://doi.org/10.1016/j.still.2012.09.006>.
- Rowland, C.S., Morton, R.D., Carrasco, L., McShane, G., O'Neil, A.W., Wood, C.M., 2017. Land Cover Map 2015 (1km Dominant Aggregate Class, GB). <https://doi.org/10.5285/711c8dc1-0f4e-42ad-a703-8b5d19c92247>.
- Rye, C.F., Smettem, K.R.J., 2015. Seasonal and interannual variability of the effective flow cross-sectional area in a water-repellent soil. *Vadose Zo. J.* 14. <https://doi.org/10.2136/vzj2014.10.0141>.
- Rye, C.F., Smettem, K.R.J., 2017. The effect of water repellent soil surface layers on preferential flow and bare soil evaporation. *Geoderma* 289, 142–149. <https://doi.org/10.1016/j.geoderma.2016.11.032>.
- Rye, C.F., Smettem, K.R.J., 2018. Seasonal variation of subsurface flow pathway spread under a water repellent surface layer. *Geoderma* 327, 1–12. <https://doi.org/10.1016/j.geoderma.2018.04.008>.
- Sagova-Mareckova, M., Cermak, L., Novotna, J., Plhachova, K., Forstova, J., Kopecky, J., 2008. Innovative methods for soil DNA purification tested in soils with widely differing characteristics. *Appl. Environ. Microbiol.* 74, 2902–2907. <https://doi.org/10.1128/AEM.02161-07>.
- Schaumann, G.E., Braun, B., Kirchner, D., Rotard, W., Szewzyk, U., Grohmann, E., 2007. Influence of biofilms on the water repellency of urban soil samples. *Hydrol. Process.* 21, 2276–2284. <https://doi.org/10.1002/hyp.6746>.
- Schimel, J., Balser, T.C., Wallenstein, M., 2007. Microbial stress response physiology and its implications for ecosystem function. *Ecology* 88, 1386–1394. <https://doi.org/10.1890/06-0219>.
- Schofield, R.K., Taylor, A.W., 1955. The measurement of soil pH. *Soil Sci. Soc. Am. J.* 19, 164–167. <https://doi.org/10.2136/sssaj1955.03615995001900020013x>.
- Shipley, B., 2000. A new inferential test for path models based on directed acyclic graphs. *Struct. Equ. Model.* 7, 206–218. [https://doi.org/10.1207/S15328007SEM0702\\_4](https://doi.org/10.1207/S15328007SEM0702_4).
- Shipley, B., 2009. Confirmatory path analysis in a generalized multilevel context. *Ecology* 90, 363–368. <https://doi.org/10.1890/08-1034.1>.
- Shipley, B., 2013. The AIC model selection method applied to path analytic models compared using a d-separation test. *Ecology* 94, 560–564. <https://doi.org/10.1890/12-0976.1>.
- Spohn, M., Rillig, M.C., 2012. Temperature- and moisture-dependent soil water repellency induced by the basidiomycete *Agaricus bisporus*. *Pedobiologia* 55, 59–61. <https://doi.org/10.1016/j.pedobi.2011.10.006>.
- Svenningsson, H., Sundin, P., Liljenberg, C., 1990. Lipids, carbohydrates and amino acids exuded from the axenic roots of rape seedlings exposed to water-deficit stress. *Plant Cell Environ.* 13, 155–162. <https://doi.org/10.1111/j.1365-3040.1990.tb01287.x>.
- Unestam, T., 1991. Water repellency, mat formation, and leaf-stimulated growth of some ectomycorrhizal fungi. *Mycorrhiza* 1, 13–20. <https://doi.org/10.1007/BF00205897>.
- van der Putten, W.H., Bardgett, R.D., Bever, J.D., Bezemer, T.M., Casper, B.B., Fukami, T., Kardol, P., Klironomos, J.N., Kulmatiski, A., Schweitzer, J.A., Suding, K.N., Van de Voorde, T.F.J., Wardle, D.A., 2013. Plant-soil feedbacks: the past, the present and future challenges. *J. Ecol.* 101, 265–276. <https://doi.org/10.1111/1365-2745.12054>.
- Verboom, W.H., Pate, J.S., 2006. Bioengineering of soil profiles in semiarid ecosystems: the “phytotarium” concept. A review. *Plant Soil* <https://doi.org/10.1007/s11104-006-9073-8>.
- Walters, W.A., Caporaso, J.G., Lauber, C.L., Berg-Lyons, D., Fierer, N., Knight, R., 2011. PrimerProspector: de novo design and taxonomic analysis of barcoded polymerase chain reaction primers. *Bioinformatics* 27, 1159–1161. <https://doi.org/10.1093/bioinformatics/btr087>.
- Wang, G., Or, D., 2013. Hydration dynamics promote bacterial coexistence on rough surfaces. *ISME J* 7, 395–404. <https://doi.org/10.1038/ismej.2012.115>.
- Wang, J.-T., Zheng, Y.-M., Hu, H.-W., Li, J., Zhang, L.-M., Chen, B.-D., Chen, W.-P., He, J.-Z., 2016. Coupling of soil prokaryotic diversity and plant diversity across latitudinal forest ecosystems. *Sci. Rep.* 6, 19561. <https://doi.org/10.1038/srep19561>.
- Wang, Q., Garrity, G.M., Tiedje, J.M., Cole, J.R., 2007. Naive Bayesian classifier for rapid assignment of rRNA sequences into the new bacterial taxonomy. *Appl. Environ. Microbiol.* 73, 5261–5267. <https://doi.org/10.1128/AEM.00062-07>.
- Weiss, S., Xu, Z.Z., Peddada, S., Amir, A., Bittinger, K., Gonzalez, A., Lozupone, C., Zaneveld, J.R., Vázquez-Baeza, Y., Birmingham, A., Hyde, E.R., Knight, R., 2017. Normalization and microbial differential abundance strategies depend upon data characteristics. *Microbiome* 5, 27. <https://doi.org/10.1186/s40168-017-0237-y>.
- Wickham, H., 2009. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag, New York.
- Zavala, L.M., García-moreno, J., Gordillo-rivero, Á.J., Jordán, A., Mataix-solera, J., 2014. Natural soil water repellency in different types of Mediterranean woodlands. *Geoderma* 226–227, 170–178. <https://doi.org/10.1016/j.geoderma.2014.02.009>.
- Zeppenfeld, T., Balkenhol, N., Kovacs, K., Carminati, A., Bennett, M., Green, S., 2017. Rhizosphere hydrophobicity: a positive trait in the competition for water. *PLoS One* 12, e0182188. <https://doi.org/10.1371/journal.pone.0182188>.