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Highlights

- Flood and drought events had negative impact on indicators of ecosystem function
- This grassland was more resistant and resilient to drought than flood
- Flooding led to pronounced and persistent shift in plant and microbial communities
- The combination of flood and drought stress increased the resilience of the system

Resilience of ecosystem service delivery in grasslands in response to single and compound extreme weather events

Rosalind J. Dodd[a,b], David R. Chadwick[b], Paul W. Hill[b], Felicity Hayes[c], Antonio R. Sánchez-Rodríguez[b,d], Dylan Gwynn-Jones[e], Simon M. Smart[f], Davey L. Jones[b,g]

[a]*UK Centre for Ecology and Hydrology, Lancaster Environment Centre, Library Ave, Bailrigg, LA1 4AP, UK*

[b]*Environment Centre Wales, School of Natural Sciences, Bangor University, Bangor, Gwynedd, LL57 2UW, UK*

[c]*UK Centre for Ecology and Hydrology, Environment Centre Wales, Bangor, Gwynedd, LL57 2UW, UK*

[d]*Departamento de Agronomía, Universidad de Córdoba, Córdoba, 14071, Spain*

[e]*Department of Life Sciences, Aberystwyth University, Aberystwyth, Ceredigion, SY23 3DA, UK*

[f]*UK Centre for Ecology & Hydrology, Lancaster Environment Centre, Lancaster, LA1 4AP, UK*

[g]*SoilsWest, Centre for Sustainable Farming Systems, Food Futures Institute, Murdoch University, Murdoch WA 6105, Australia*

*Correspondence: rosdod@ceh.ac.uk

Abstract

Extreme weather events are increasing in frequency and magnitude with profound effects on ecosystem functioning. Further, there is now a greater likelihood that multiple extreme events are occurring within a single year. Here we investigated the effect of a single drought, flood or compound (flood+drought) extreme event on temperate grassland ecosystem processes in a field experiment. To assess system resistance and resilience, we studied changes in a wide range of above- and below-ground indicators (plant diversity and productivity, greenhouse gas emissions, soil chemical, physical and biological metrics) during the 8 week stress events and then for 2 years post-stress. We hypothesized that agricultural grasslands would have different degrees of resistance and resilience to flood and drought stress. We also investigated two alternative hypotheses that the combined flood+drought treatment would either, (A) promote ecosystem resilience through more rapid recovery of soil moisture conditions or (B) exacerbate the impact of the single flood or drought event. Our results showed that flooding had a much greater effect than drought on ecosystem processes and that the grassland was more resistant and resilient to drought than to flood. The immediate impact of flooding on all indicators was negative, especially for those related to production, and climate and water regulation. Flooding stress caused pronounced and persistent shifts in soil microbial and plant communities with large implications for nutrient cycling and long-term ecosystem function. The compound flood+drought treatment failed to show a more severe impact than the single extreme events. Rather, there was an indication of quicker recovery of soil and microbial parameters suggesting greater resilience in line with hypothesis (A). This study clearly reveals that contrasting extreme weather events differentially affect grassland ecosystem function but that concurrent events of a contrasting nature may promote ecosystem resilience to future stress.

Keywords: Climate change, soil quality, drought, flooding, greenhouse gas emissions, microbial community

1. Introduction

Grasslands represent an important global agroecosystem covering an area of ca. 11 million km^2 and 7 % of the earth's terrestrial area (O'Mara, 2012). In addition to food production, grasslands provide a wide range of ecosystem services (ES), such as biodiversity provision, climate regulation and natural hazard protection (MEA, 2005; O'Mara, 2012) which rely on effective belowground soil functioning (Adhikari and Hartemink, 2016; Brussaard, 1997; Wagg et al., 2014). The effects of climate change are already being felt, with the frequency and severity of extreme weather events increasing in every region of the globe (IPCC, 2021). Such extreme events have been shown to negatively affect grassland yields and biomass production (Environment Agency, 2006; Niu et al., 2014). Recent spatial analysis of long-term temperature and precipitation records, in combination with land use data, highlighted an increasing risk of flooding and drought (single and in combination/succession) in many UK pastoral landscapes (Dodd et al., 2021). To safeguard the vital ES provided by agricultural grasslands, we need to fully understand the impact of such events on the whole ecosystem.

Precipitation regimes regulate grassland ecosystem structure and function due to the influence on soil moisture, a major driver of plant growth and microbial activity (Bloor and Bardgett, 2012). While there is some uncertainty in the response pattern (Evans et al., 2022), plants and microbes are considered to exhibit a hump-shaped response to moisture with substrate diffusivity and oxygen limitation constraining growth at the low and high extremes respectively. Consequently, extreme events which rapidly and dramatically change the moisture conditions (such as flood and drought) have the potential to cause a large-scale change in above and below ground ecosystem processes. A wealth of research on drought has demonstrated large scale changes in ecosystem properties including reductions in primary production (Ciais et al., 2005; Hoover et al., 2014), changes in above and below ground community structure (de Vries et al., 2018; Knapp et al., 2020; Ochoa-Hueso et al., 2020; Ochoa-Hueso et al., 2018) and altered C and nutrient cycling (Bloor and Bardgett, 2012; Deng et al., 2021; Dijkstra et al., 2015). However, research into ecosystem responses to prolonged flooding at the field scale have been largely neglected, and while some experiments include increased precipitation regimes, these rarely examine prolonged flooding (Abbasi et al., 2020), despite evidence of widespread impacts on vegetation across the globe (Famiglietti et al., 2021). Flooding disruption of nutrient cycles (Sánchez-Rodríguez et al., 2019a,b) and increased N_2O emissions (Oram et al., 2021; Sánchez-Rodríguez et al., 2019a; Sánchez-Rodríguez et al., 2019b) along with changes in microbial communities (Sánchez-Rodríguez et al., 2019a,b; Unger et al., 2009) have been observed in mesocosm studies under controlled conditions. However, such studies may exhibit differing responses to the field scale (Unger et al., 2009). Alternatively, flood impacts have been assessed following natural flood events on existing field trials (González Macé et al., 2016; Harvey et al., 2019; Wagner et al., 2015). Nevertheless, these opportunistic trials often have limited ability to regulate the experimental conditions and are often poorly instrumented and lack appropriate controls and plot scale flood experiments remain a key gap in the literature.

In addition to single extreme events, there is growing recognition that many ecosystems can experience a combination of multiple climatic drivers or hazards often termed compound extremes (Zscheischler et al., 2018). Such compound events are likely to have a larger effect on ecosystem function, through a reduction in the systems resilience, amplifying the impact and potentially leading to bi-modal response-recovery patterns indicative of a regime shift (Rillig et al., 2019). While research into the impact of compound events on ecosystems is growing, these have been mainly focused on combinations of drivers with additive properties, for example heatwaves and droughts (Arain et al., 2022) or storm surge and flooding (Wahl et al., 2015). However, recent research suggests that the occurrence of multiple extreme events, with contrasting drivers, within the same year is also increasing; for example a swift transition from flood to drought events or *vice versa* (Dodd et al., 2021).

As ecosystem function is highly dependent on soil moisture, contrasting events of extreme precipitation amount, occurring in quick succession, are likely to have a different impact to each event alone. A deluge event during summer drought was seen to alleviate reductions in plant production and soil respiration in a natural semi-arid grassland (Post and Knapp, 2020) and numerous studies have examined the effect of rewetting of dry soils on many aspects of ecosystem function (Birch, 1958; Borken and Matzner, 2009; Fierer and Schimel, 2002; Gordon et al., 2008). However, there has been little investigation of the reverse, where rapid drying of wet soils may occur due to reduced rainfall. The frequency of winter and spring flooding and that of summer droughts is predicted to increase (Fowler and Kilsby, 2003; Thompson et al., 2017). Furthermore, as extreme events are becoming more frequent and intense (Li et al., 2019; Trenberth, 2011), the likelihood of a second extreme occurring before the system has fully recovered also increases, potentially magnifying the impact (Schwalm et al., 2017) and tipping the system to a new functional state. We propose two alternative hypotheses of ecosystem response to this scenario: (A) the drawdown of soil moisture may be slower in previously flooded soils promoting resilience to subsequent drought and a reduction in observed ecosystem impact (Post and Knapp, 2020), or (B) if the drought event occurs prior to ecosystem recovery, a second stress event may lead to adverse impacts on biotic communities and potential community collapse, with multi-year impacts on ecosystem function.

Our study directly addresses gaps in knowledge surrounding the short and medium-term impact of simulated severe drought and flood events on the resilience of grassland ecosystems at the field plot scale. Further, we assess the impact of compound weather events characterised by a spring flood followed by a summer drought. Here, we use a set of above and below ground biotic and abiotic indicators to quantify the effect of these extreme events on ecosystem process of six essential grassland ES: forage production, nutrient cycling, organic matter decomposition, climate regulation, pollution regulation and biodiversity provision. Changes in these indicators were used to assess the impact of each event type immediately post stress (reflecting system resistance) and the legacy implications for longer-term ecosystem function through monitoring indicator recovery (reflecting system resilience). We hypothesised that (1) extreme weather events will negatively impact on ecosystem processes; (2) grassland ecosystems will have different degrees of resistance and resilience to flood or drought stress. Additionally, we investigated the two alternative hypotheses presented above (A and B) for the combined flood and drought event.

2. Materials and methods

2.1. Treatments and plot establishment

The study site was located at the Henfaes Agricultural Research Station, Abergwyngregyn, Gwynedd, North Wales, UK (53º14′21”N, 4º00′57”W) on sheep-grazed, *Lolium perenne* L. dominated, low intensity grassland. The soil at the site is a sandy loam textured Eutric Cambisol (Typic Hapludalf) overlying a mixed glacial till parent material. The site has a temperate-oceanic climate with a mean annual rainfall of 1060 mm and temperature of 10 °C.

Sixteen 3 m × 3 m plots were established in winter 2015. The experiment consisted of four treatments and was conducted in three phases. The treatments consisted of (1) spring flood (flood), (2) summer drought (drought), (3) spring flood followed by summer drought (flood+drought), and (4) ambient conditions (control). Each treatment had four replicates (*n* =

4) arranged in a randomised plot design. The three data collection phases were (1) flood period, (2) drought period and (3) recovery.

Although the site was previously grazed with sheep (*Ovis aries* L.), livestock were excluded from the plots during the construction phase. Two weeks prior to the start of the trial (April 2016), sheep were briefly reintroduced (0.22 sheep m^{-2}; 2 d) to mimic mob grazing and trampling in this sheep-based pasture system.

To prevent lateral water escape, the eight flood plots were hydrologically isolated. This was achieved by vertically inserting 80 cm deep PVC plastic boards (5 cm thick; Tatra-Rotalac Ltd., Manchester, UK) lined with an impermeable butyl rubber membrane (Pondkeepers Pond Liners Ltd., Billingham, UK; Fig. S1) around the plot boundary. The boards were buried to a depth of 30 cm in the soil, leaving 50 cm aboveground to hold the flood water. A physical barrier was also inserted to a similar depth to isolate the eight non-flood plots to ensure a similar level of physical disturbance.

To mimic on-farm management practices, lime (3 t ha^{-1}) and NPK compound fertiliser (25:5:5; 50 kg N ha^{-1}) were applied to all plots in April 2016 (14 d prior to flooding), in line with past fertiliser application rates in this field. The same rate of NPK fertiliser was applied again in August 2016 during the drought period.

2.2. Experimental details

The flooding treatments were designed to simulate a fluvial flood event, reflecting the scale and duration of similar events which have occurred within the local and wider region in the last decade (Defra, 2014; Harvey et al., 2019; Huntingford et al., 2014; Slingo et al., 2014). However, it should be noted that the site had no previous history of flooding. Figure S1 shows the layout of the field trial.

Flood phase: In spring 2016, eight flood plots were submerged with water from the adjacent river to a depth of 20 cm, which was sufficient to fully submerge all vegetation (Fig. S1.c). Sediment was added to each of the plots following the initial flooding to a depth of 2-3 mm to simulate the deposition of eroded soil and sediment typically associated with river flooding and observed in recent extreme flood events (ADAS, 2014). This was achieved by suspending 13.5 kg of surface soil in the floodwater. The soil was taken adjacent to the plots (0-7 cm depth) under the same management regime.

The plots were maintained at a constant flood level of 20 cm for eight weeks during April to June, by topping up the flood water, via a ball float valve connected to a reservoir of river water, reflecting the unprecedented flooding events observed across UK agroecosystems in the winter of 2013 - 2014 (Defra, 2014; Slingo et al., 2014). At the end of the flood period the floodwater was removed using a pump over a 4 h period.

Recovery phase 1: All plots were left under ambient conditions for four weeks following the end of the flood phase and before the initiation of the drought phase.

Drought phase: At the end of recovery phase 1, rain-out shelters (4 m × 4 m area) were erected over eight plots, four of which were previously subjected to the spring flood. The rain-out shelters were constructed with PalSun® polycarbonate sheets (2 mm thick; Plastock Ltd, High Wycombe, UK), mounted on wooden frames, angled towards the direction of the prevailing wind (Fig. S1d) with a maximum height of 1.8 m. The slight reduction (10 ± 1%) in light transmission under the rain-out shelters (measured using a PAR sensor; 400 to 750 nm; PP Systems International Inc., Amesbury, MA) was deemed unlikely to impact significantly on grass growth, during the drought treatment. Rain was excluded from the four drought and four flood+drought plots for 8 weeks during July to September 2016.

Recovery phase 2: All plots were monitored for two years following the end of the drought period to determine the impact on ecosystem recovery in the absence of management intervention. During this time, all plots were subjected to ambient conditions and livestock and rabbits were excluded.

2.3. Plot measurement frequency and ecosystem service assessment

To determine the impact on ES, a range of above and below ground indicators were identified which are directly linked to the provision of the six identified ecosystem services, forage production, nutrient cycling, organic matter decomposition, climate regulation, pollution regulation and biodiversity provision (Table 1; Adhikari and Hartemink, 2016; Dominati et al., 2010; Rutgers et al., 2012; van Eekeren et al., 2010). Additionally, soil biota play a key role regulating the ecosystem processes underpinning these ES (Creamer et al., 2022). The importance of soil biodiversity in ecosystem multifunctionality is becoming increasingly apparent (Creamer et al., 2022; Delgado-Baquerizo et al., 2020) along with the role of plant-soil interactions (Forero et al.; Valencia et al., 2018). As such, the following above and below ground biotic indicators supporting ecosystem processes were also included: pasture community composition, microbial community characteristics (biomass and PLFA), and earthworm abundance and biomass. Each plot was divided into dedicated areas for monitoring (Fig. S1). During the flood, drought and recovery phases regular measurements were taken from all plots (see Table S1).

2.4. Above ground measurements

Biomass was harvested from 40 × 40 cm quadrats within each plot on 5 occasions (1 month post flood, 1 week post drought, and at 6-, 12- and 24-months recovery). Plant material was oven dried (80 °C, 24 h), weighed, ground (< 2 mm) and analysed for forage quality including crude protein, metabolizable energy and digestibility (Sciantec Analytical Laboratories, York, UK). Annual biomass yield was calculated as tonnes per hectare for the four treatments as the sum of the first 4 cuts for year 1 and as the 5th cut for year 2.

Plant surveys were undertaken over each entire plot by the same expert botanist in the growing seasons throughout the duration of the experiment at the same time as the biomass harvest. Presence and percentage cover (rounded to the nearest 1%) of all vascular plants and bryophytes were recorded in each experimental plot. Cover of bare ground plus litter and total bryophyte were also recorded and the species richness and Shannon-Wiener Diversity were calculated (Magurran, 2013).

The percentage cover of each species was converted to a fraction. The proportion of forage grasses which directly support livestock grazing and hence food production and injurious weeds which detract from this provision (Maskell et al. 2020) were calculated along with indicators of important species supporting biodiversity, namely; butterfly larval food plants; supporting invertebrate populations (Lepidoptera) (Smart et al., 2000; Smart et al., 2017); crop wild relatives as genetic insurance for food production (Jarvis et al., 2015) and nectar-providing plants supporting pollinator biodiversity (Baude et al., 2016).

2.5. Below ground measurements

The plots were instrumented with SDI-12 soil moisture sensors (Acclima Inc., Meridian, ID) inserted horizontally at a depth of 5 cm, a static greenhouse gas chamber and three MacroRhizon soil solution samplers (0.15 μm pore size; Rhizosphere Research Products, Wageningen, The Netherlands) inserted at a 45° angle to a depth of 5 cm for collection of soil pore water with two inserted within the main plot and one within the greenhouse gas chamber. Soil sampling was undertaken immediately following the removal of the flood or drought stress and at 6-, 12- and 24-month post drought recovery stages.

During each soil sampling event multiple soil cores (n = 6, ϕ = 1 cm, depth = 0-10 cm) were randomly taken from the indicated plot area (Fig. S1), homogenised and sieved (< 2 mm) for analysis.

Soil physical indicators: An intact core (100 cm^3, 0-10 cm depth) was taken from each plot and weighed, dried (105 °C, 16 h), reweighed and dry bulk density and water filled pore space determined.

Soil (and floodwater) chemical indicators: Soil moisture content was determined gravimetrically (105 °C, 24 h). Soil pH and electrical conductivity (EC) were measured in 1:5 (w/v) soil to distilled water suspension using standard electrodes. Within 24 h of collection, soils were extracted with 1:5 (w/v) soil-to-AcOH (0.5 M) and 1:5 (w/v) soil-to-K_2SO_4 (0.5 M). Macronutrient and trace element (P, K, Ca, Na, Al, Fe, Mg, Mn, Al) concentrations were determined in the AcOH extracts via ICP analysis (Varian 720 ICP-OES). NO_3^- and NH_4^+ in the K_2SO_4 extracts were measured colorimetrically according to Miranda et al. (2001) and Mulvaney (1996), respectively.

Total soil C and N were determined on oven-dried, ground soil using a TruSpec CN Analyser (Leco Corp. St. Joseph, MI, USA). The tea-bag index (TBI) was used as a standardised method to estimate both C decomposition (k) and C stabilisation (S) rate in soil (Keuskamp et al., 2013). The difference between the two rates provides an indication of C storage. Tea-bags were buried at 5 cm depth within each plot immediately prior to stress initiation (Keuskamp et al., 2013) and recovered at the end of each stress period.

Soil redox measurements were taken on a weekly basis during the experiment with a handheld SenTix® redox probe (n = 3 $plot^{-1}$; Wissenschaftlich-Technische Werkstätten GmbH, Weilheim, Germany) inserted into the top 2 cm of soil. During the flood phase, soil solution and the overlying floodwater was sampled weekly from the flood plots. Where possible, the soil solution was sampled from the control treatment, however, there was only sufficient soil moisture to extract a sample on limited sampling dates. These samples were analysed for pH, EC, NH_4^+ and NO_3^- as described above and dissolved organic C (DOC) using a Multi N/C 2100-S Analyser. Dissolved reactive P (DRP) and total dissolved P (TDP), after acid persulfate digestion (Rowland and Haygarth, 1997) were determined using the molybdate blue method of Watanabe and Olsen (1965). Dissolved organic P (DOP) was calculated as the difference between TDP and DRP (AnalytikJena, Jena, Germany).

Soil biological indicators: Following collection, soil samples were immediately frozen (-80 °C), freeze-dried and phospholipid fatty acid (PLFA) analysis undertaken according to Bartelt-Ryser et al. (2005) to determine the soil microbial community profile. Taxonomic groups were ascribed to individual PLFAs using the Sherlock® PLFA Method and Tools Package (PLFAD1: Microbial ID Inc., Newark, DE) as outlined in Sánchez-Rodríguez et al. (2019b).

Earthworm surveys were undertaken at the same timepoints as for soil sampling, by excavating a soil pit (20 cm × 20 cm × 20 cm) and recovering live earthworms by hand. Following soil excavation, 1 L of allyl isothiocyanate (1.3% v/v) in deionised water was poured into the pit and left for 30 min to expel any deeper dwelling earthworms (Pelosi et al., 2009). Collected earthworms were transported live to the laboratory in moist soil where numbers of juvenile and mature earthworms were recorded and weighed.

Greenhouse gas emissions: A closed static chamber (40 cm × 40 cm × 25 cm) was fitted to an aluminium frame installed in each plot at the beginning of the field experiment. Immediately after closing each static chamber, a 20 ml gas sample was taken from the headspace through a septum inserted in the lid using a needle attached to a 25 ml syringe at time T0 and T60 mins. The gas samples were transferred to pre-evacuated glass vials (20 ml) and analysed for CH_4, CO_2 and N_2O using a Clarus 500 gas chromatograph equipped with a HS-40 Turbomatrix autoanalyzer (PerkinElmer Inc., Waltham, MA).

Gas sampling was repeated 40 times between the start of the flood phase to day 235, for each plot when no differences in gas flux had been observed between the treatment and control plots for 90 days The frequency of gas sampling was higher during the flood phase, recovery phase 1 and the drought phase, and lower in recovery phase 2. At each gas sampling time, soil temperature was recorded (0-2 cm depth) (T0 and T60 min) and the temperature was used to correct the GHG fluxes. GHG fluxes were calculated using the difference in each gas concentration between T0 and T60, the ratio between chamber volume and soil surface area (Chadwick et al., 2014), and based on tests showing linearity (MacKenzie et al., 1998). During the flood phase, an extension (25 cm height) was used to extend the static chamber in the flood plots. Total cumulative fluxes were estimated using the trapezoidal rule (Rahman and Forrestal, 2021) for the different phases of the experiment; the flood phase (0 to 58 d), the flood and recovery phase 1 (0 to 85 d), the drought phase (93 to 142 d), the drought and recovery phase 2 (93 to 142 d), and the whole period of gas sampling (0 to 235 d). The total GHG flux in CO_2 equivalents (kg C_{eq} ha^{-1}) was calculated by multiplying the total cumulative fluxes of CH_4 by 28, CO_2 by 1, and N_2O by 265 (IPCC, 2013) and summing them.

2.6. Data processing and statistical analyses

Soil moisture data from the Acclima moisture probes was converted to water filled pore space (WFPS) as follows:

$$WFPS\ (\%) = \frac{SWC}{\left(1-\frac{BD}{PD}\right)}\ x\ 100 \qquad \text{(Eqn. 1)}$$

where *SWC* = volumetric soil water content (vol. %), *BD* = soil bulk density (g cm^{-3}) and *PD* = particle density (2.65 g cm^{-3}).

To examine the response of the above- and below-ground metrics to the treatments, natural log response ratios (*lnRR*) were calculated as follows (Hedges et al., 1999):

$$lnRR = \ln\left(\frac{X_{treatment}}{X_{control}}\right) \quad \text{(Eqn. 2)}$$

where $X_{treatment}$ and $X_{control}$ are the mean values of each indicator under the treatment (flood, drought and flood + drought) and the ambient control plots. In accordance with (Hedges et al., 1999), we calculated the variance as follows:

$$Variance = (SD^2_{treatment}/(nX_{treatment}) + (SD^2_{control}/(nX_{control}) \quad \text{(Eqn. 3)}$$

Subsequently the variance was converted to a 95 % confidence as shown below:

$$Confidence\ interval = 1.96\ x\ \sqrt{Variance} \quad \text{(Eqn. 4)}$$

Finally, the response ratio and the corresponding confidence intervals were transformed to a percentage change of the indicator from the control as follows:

$$(e^{lnRR\ or\ Variance} - 1)\ \times 100 \quad \text{(Eqn. 5)}$$

The percent change and associated confidence interval was calculated for each above- and below-ground indicator and the result plotted for three time periods: (1) immediately post stress treatment; (2) after 1 year recovery; and (3) after 2 years recovery. If the 95 % confidence interval did not overlap with zero, this indicated a significant change in the indicator metric.

Changes in soil microbial communities were assessed by principal component analysis (PCA) of PLFA taxonomic groups based on a data correlation matrix with principal components (PCs). Analysis of variance (ANOVA) with Tukey's HSD post-hoc testing was used to assess differences in the four treatments (for plant food production and biodiversity provision plant indicators and greenhouse gas fluxes for each of the identified time periods). The statistical cut-off for significance was $p < 0.05$. ANOVA and PCA were performed in the statistical package SPSS software v22.0 (IBM Inc., Armonk, NY).

3. Results

3.1. Assessment of treatment impacts

Measurements of WFPS were used to validate the success of the treatments imposed on the plots. At the initiation of flooding, WFPS increased from 34 % to a maximum of 85 %, and remained at 79 ± 1 % for the duration of the flood period. The control plots fluctuated between 20 and 45 % WFPS during the same period (Fig. S2). The drought treatments resulted in a 71 % reduction in WFPS from 32 %, reaching 9 % by the end of the drought period which was 63 % lower than the control. While the % reduction in WFPS over the drought period was similar in the previously flooded plots, exhibiting a 70 % reduction from 54 % to 16 %, due to a higher initial value, this was only 47 % below the control. Both flooding and drought exhibited a legacy effect from the stress, slowly converging toward the control. The WFPS remained elevated in the flood plots and reduced in the drought plots, compared to the control for the 6 months post drought when the sensors were removed. In contrast, the flood+drought treatments showed a quicker recovery in WFPS following drought treatment and WFPS was comparable to the control plots within 2 months (Fig. S2).

Flooding reduced the redox potential (Eh) from +297 mV (aerobic) to -92 mV (anaerobic) after 50 d of flooding (Fig. S3), while in the control and drought plots Eh values remained between +200 and +300 mV, throughout the trial. On removal of the flood water, Eh rapidly increased to a maximum of 348 mV in the first 14 days and remained higher than the control for 28 days before returning to the control range (+200 to +300 mV). While no clear trends emerged during the drought phase all treatments plots showed a general trend of higher Eh compared to the control during recovery 2 in the order of flood > flood+drought > drought > control.

Neither flooding nor drought led to a change in soil temperature. In addition, no unexpected periods of flooding or drought occurred during the experiment which might have compromised the control treatments.

3.2. Above-ground indicator metrics

The response of each above-ground indicator immediately following the stress period and following the three recovery periods are summarised in Figure 1. The annual above-ground plant biomass for the flood plots was reduced by 30 % (CI: 24 %) compared to the control, while the drought treatment did not significantly impact annual biomass production (Fig. 1b). The reduction in annual biomass in flood+drought plots was greater than for flood-only (54 % decrease, CI: 30 %). However, these changes in biomass were not carried over to the following year (Fig. 1c). The change in pasture community which established post flood (Table S2a) was accompanied by a change in the plant species supporting food provision and biodiversity ES. The first month's pasture regrowth following flood stress showed a reduced abundance of forage grasses, crop wild relatives (CWR) and plant species known to provide food for butterfly lava (Fig. 2). There was also a slight increase in the number of tree and shrub species seedlings (comprised of *Fraxinus excelsior*) and an increase in the number of nectar-producing species. The reduction in forage grasses, CWR and butterfly lava food remained for the first-year post flood, and the abundance of CWR and butterfly lava food species remained reduced in the second year of recovery. Immediately following the drought, the previously flooded plots continued to show a reduction in forage grasses, CWR and butterfly lava food species. Additionally, these plots showed a small reduction in legumes. The reduction in CWR and butterfly lava food species was still evident in the first year along with an increase in the nectar species, but these changes were not present in the second year of recovery. In contrast, post drought there was no change in these indicator species in drought-only plots across the whole trial (Fig. 2, Table S2b).

3.3. Below-ground indicator metrics

The response of below-ground soil quality indicators to flooding and drought are summarised in Figure 1. Overall, significant changes in a range of soil quality indicators were apparent immediately post-stress removal, however, these changes progressively lessened over the 2-year recovery period. In addition, the response of the combinatorial flood+drought treatment was similar to the flood treatment.

3.3.1. Soil chemical indicators

Flooding reduced soil EC, soil available P (P_{acOH}), and C storage compared to the control (Fig. 1a), and increased extractable NH_4^+, Mn (Mn_{acOH}), and Fe (Fe_{acOH}). Drought also reduced C storage and increased extractable NH_4^+, NO_3^-, and Fe_{acOH} along with the soil EC. The flood+drought reduced available P (P_{acOH}) and increased soil EC, Mn_{acOH}, Fe_{acOH}, NH_4^+ and NO_3^-.

During the first year of recovery P_{acOH} was reduced in all stress combinations (Fig. 1b) but was increased compared to the control in the second-year post stress in the flood and flood+drought plots (Fig. 1c). Extractable Fe_{acOH} and Mn_{acOH} concentrations were increased in the flood plots and Mn_{acOH} increased in the flood+drought plots during the first year. Two years post stress Fe_{acOH} concentrations were reduced in both treatments. Flooding increased soil NH_4^+, and drought increased both soil NH_4^+ and NO_3^- but this did not persist through the recovery phase. However, at the two-year recovery point NO_3^- concentrations were increased in the flood plots.

Due to low moisture conditions in some treatments, soil solution samples were only consistently collectable from the flood plots, and only during the flood phase and recovery phase 1. There was a general trend of increasing DOC and decreasing DRP and NO_3^- as the flood period progressed (Fig. 3). On removal of the flood water there was a spike in DOC concentrations accompanied by a spike in DOP followed by a sharp decline. Additionally, there was a large spike in the NH_4^+ concentrations 13 d following removal of the flood water to a maximum of 131 mg N L^{-1} which quickly declined to background levels (0.04 mg N L^{-1}) by day 21. A sharp spike in NO_3^- concentrations to a maximum concentration of 34.9 mg N L^{-1} was observed 7 days after flood removal followed by a more gradual decline to background levels (0.83 mg N L^{-1}) by day 27.

3.3.2. Soil biological indicators

Distinct changes in microbial community structure were observed with respect to both sampling time and treatment. Seasonality played a key role in controlling the distribution of PLFA markers with marked separation between the stress and recovery periods and a clear shift towards more Gram-positive dominated communities as time progressed. However, treatment effects on community structure were also observed (Fig. 4). Flood stress increased the dominance of Gram-negative bacteria while drought led to a shift towards actinomycete markers. The flood and flood+drought plots also had a reduction in the fungi-to-bacteria ratio and amount of arbuscular mycorrhizal fungi (AMF) in the first- and second-year post stress (Fig 1.b.c). The PLFA markers within the flood plots showed a larger separation from the control treatments compared to the drought and flood+drought plots after the first and second year of recovery. After 1-year of recovery there were three distinct groups of PLFA distributions, (1) control, (2) drought and flood+drought, and (3) flood. At the 2-year recovery point the control group remained separated from the three stress treatments (Fig. 4). The size of the microbial biomass was also slightly increased in the flood and drought plots during the first year and in the flood-only and flood+drought plots in the second year relative to the control. Earthworm abundance increased following removal of flooding, however, it decreased following the removal of drought (Fig. 1).

3.3.3. Greenhouse gas emissions

During the flood phase, CO_2 emissions were higher in the control plots in comparison with the flood plots (up to 300 mg C m^{-2} h^{-1} vs. <1 mg C m^{-2} h^{-1}, respectively; Fig. 5b). During the drought CO_2 emissions were similar for the control and flood plots and reduced in the drought and flood+drought plots (between 80–320 mg C m^{-2} h^{-1} vs. 30–190 mg C m^{-2} h^{-1}, respectively; Fig. 5b). During recovery phase 1 and 2, the CO_2 emissions were similar between all treatments. Overall, flood or drought caused a large decrease in cumulative CO_2 emissions while their combination (flood+drought) resulted in the lowest cumulative emissions (Table 2).

No N_2O emissions were observed during the flood phase for the control or flood plots. During the drought phase, application of N fertiliser resulted in a peak in N_2O emissions in the control and flood plots (up to 0.43 and 0.82 mg N m^{-2} h^{-1}, respectively) while no emissions were observed in the drought or flood+drought plots (<0.07 mg N m^{-2} h^{-1}). The spring flood caused N_2O peaks of 0.2–1.2 mg N m^{-2} h^{-1} (60-85 d after flooding) that were more frequent and higher than the fluxes observed following N fertilization in the control (Fig. 5c). No N_2O emissions were observed in any of the plots in the second recovery phase (Fig. 5c). The highest total cumulative N_2O emissions were calculated for the flood+drought plots (4.16 kg N ha^{-1}), followed by flood plots (3.35 kg N ha^{-1}), control plots (1.01 kg N ha^{-1}) and drought plots (0.41 kg N ha^{-1}); the differences were significant between the flood+drought and the drought plots (Table 2). These emissions occurred mainly during recovery phase 1 (Table S3). The expected increase in N_2O emissions due to N fertilisation (during the drought phase) was influenced by the treatment where total cumulative N_2O emissions followed the order flood ≥ control = flood+drought ≥ drought (Table S3).

CH_4 emissions remained close to zero except immediately after flood water removal (58 d after flooding) when they peaked (1-2 mg C m^{-2} h^{-1}) in the flooded plots (Fig. 5a).

Mean cumulative CH_4 fluxes were small and not significant between treatments over the 2-year experiment (Table 2). Overall, the control and drought treatments acted as a sink for CH_4 (−0.38 and −0.20 kg C ha^{-1}, respectively) while the flood and flood+drought were a minor source of CH_4 (0.98 and 1.49 kg C ha^{-1}, respectively). Table S3 shows that (i) the control plots were a sink during most of the experiment (except in the second recovery phase), (ii) flood induced CH_4 emissions (mainly immediately following flood water removal), and (iii) drought reduced CH_4 emissions (only during the drought phase).

When considering the combined emissions of GHGs in terms of total CO_2-equivalents, significant differences were apparent and followed the series control ≥ flood ≥ drought = flood+drought (Table 2). If direct CO_2 emissions are excluded, the pattern was similar to total cumulative N_2O emissions (i.e. flood+drought ≥ flood ≥ control ≥ drought) over the 2-year period.

4. Discussion

This study utilised a suite of above and below ground properties of an improved sheep grazed pasture to determine the impact of both single extreme events characterised by contrasting rainfall patters (flood or drought), and the combined impact of a swift transition from flood to drought conditions on ecosystem functioning. Our results clearly show three key findings: (1) this grassland system was more resistant and resilient to drought conditions than flooding, (2) the combination of flood and drought did not magnify the impact of the single stressors with some indication of faster recovery times and (3) persistent changes in plant and microbial communities post flood likely have implications for future ecosystem service provision.

4.1. Impact of contrasting single extreme events (i.e. flood vs. drought).

Both flooding and drought were found to have a large impact on the above and below ground indicators of ecosystem function in improved grasslands supporting out hypothesis that extreme weather events will negatively impact ecosystem processes. However, flooding was more detrimental with 17 indicators being different to the control immediately post stress compared to 8 indicators for drought (Fig. 1). Flood plots also showed a difference in 7 indicators two years after the stress compared to just 1 indicator two years post drought. Together these results show lower resistance and resilience to flooding than drought. Further evidence of this was found in the shifts in microbial community, as indicated by PLFA markers. Larger shifts occurred for the flood plots and remained more distinct for longer compared to drought. This prolonged shift in microbial communities agrees with previous mesocosm studies, where a shift in PLFA markers occurred following extreme flooding (80 days) and persisted for the length of the monitored recovery period of 60 days (Sánchez-Rodríguez et al., 2018). In contrast, microbial communities in grasslands have been shown to be largely resistant to drought (Birkhofer et al., 2021; Blankinship et al., 2011) and unlike for flooding there was no change in microbial biomass during the drought period Drought did induce a larger shift towards actinomycete taxa which have been shown to be more resistant to dry and wetting cycles (Acosta-Martínez et al., 2014; Ochoa-Hueso et al., 2020; Ochoa-Hueso et al., 2018). However, seasonality had a large control on PLFA marker distribution likely due to changing environmental conditions. Interestingly, the shift towards actinomycetes compared to the control also occurred in the flood plots post drought, despite no drought treatment being imposed. This indicates that immediately following environmental stress, microbial communities are more responsive to changes in environmental conditions compared to unstressed communities demonstrating lower resilience.

Environmental stressors can have detrimental impacts on earthworm communities (Singh et al., 2020). Earthworms are considered keystone species within soil environments due to their influence on soil chemical, physical and biological processes (Blouin et al., 2013; Jones et al., 1994). Generally, prolonged flooding has been shown to reduce earthworm abundance across different ecosystems (Singh et al., 2020). However, our study showed a 76 % increase in earthworm numbers (predominantly juveniles) immediately following removal of the overlying floodwater. Visual observation suggested this was the result of recent hatching, with some earthworms still attached to cocoons. This finding has only been reported for one study in annually flooded Alder forests (Emets, 2018). We hypothesise that a sudden change in osmotic potential ruptured the cocoons outer shell leading to premature emergence. In contrast drought did not impact on earthworm biomass or abundance, likely due to their ability to enter estivation in response to low moisture conditions, indication of which was observed in the post drought sampling with many individuals exhibiting characteristic knot configurations (McDaniel et al., 2013). The trend post flood did not persist into the recovery phase once cocoons within the control soils hatched, and under the single flood stress condition this short-lived increase in earthworm numbers is unlikely to influence overall ecosystem function.

Above and below-ground biodiversity has been shown to be positively related to ecosystem multifunctionality (Delgado-Baquerizo et al., 2020) and even small changes in microbial structure (such as community composition shifts) can have a large impact on function due to altered metabolic capability of the ecosystem (Crowther et al., 2019). The pronounced and persistent change microbial communities induced by flooding were also accompanied by increased plant diversity and richness which will influence soil function with knock-on effects on the provision of ecosystem services while the impact of drought appears to be minimal and immediate with limited longer-term impacts. Where significant indicator responses to treatments were found, their impact on the 6 highlighted ES will be discussed in section 4.3.

4.2. Impact of consecutive contrasting extreme event types (i.e. flood vs. drought).

The combination of flood and drought stress did not increase the number of indicators affected compared to flood alone either immediately post stress (15 for flood+drought cf. 17 for flood) or at the 2-year recovery (5 flood+drought cf. 6 for flood). In fact, there was some indication within the microbial community of faster recovery in community composition evidenced by reduced separation of PLFA markers from the control plots 1 year post stress compared to flood alone. We suggest that the more rapid reduction in soil moisture post flood in the flood+drought plots may have increased the resilience of microbial population in line with the first of the two alternative hypotheses that subsequent events of contrasting typology will promote ecosystem recovery (hypothesis A).

However, while hypothesis A may fit the microbial community response the impact on earthworm populations showed contrasting results. The large increase in juvenile earthworm numbers post flood was followed by a dramatic decrease of 85 % in abundance compared to the control post drought despite no significant change in the drought plots. We suggest that the premature emergence of juveniles during flooding may have implications for the resilience of the community if a second extreme event occurs prior to this community reaching maturity, in line with the second alternative hypothesis B. Larger soil invertebrates including earthworms are especially important for maintaining optimal ecosystem functions (Delgado-Baquerizo et al., 2020) and loss of earthworm populations could have large-scale consequences for ecosystem service provision.

4.3 Implications for ecosystem service provision

Flood, drought and the combined flood+drought had an impact on both the indicators directly related to the 6 specific ecosystem services considered.

Forage production: The reduction in annual biomass and the slow recovery of forage grass species following flooding will likely decrease production at least during the event year. Additionally, flooding resulted in large periods of increased bare ground while the plant community re-established itself. The extremes of wet and dry conditions will limit the pool of successful colonists. A likely scenario in the longer term is larger areas of bare ground with varying cover of transient and persistent weed species. Recolonisation of bare ground with invasive weed species is a concern to farmers (ADAS, 2014). However, in our study neither flooding nor drought or the combination led to a change in the % cover of injurious weeds compared to ambient conditions.

These results indicate that flooding will lead to a reduction in forage provision and subsequent production metrics at least during the stress year while drought may have limited impact in this grassland. Farmers may need accept reductions in profit margins to bring in additional forage to meet feed demands, increasing production costs or reduce stocking rates.

Nutrient cycling: The impact of extreme weather events on soil fertility was evidenced through immediate and prolonged changes in extractable soil nutrients. While soil P concentrations were largely unaffected by drought stress, flooding altered soil P in different directions at the various timescales. The reduction in plant-available P post flood is consistent with the reductive dissolution of P bound to iron or manganese oxides within the clay fraction of the soil under the observed negative redox potentials (Sánchez-Rodríguez et al., 2019a; Sánchez-Rodríguez et al., 2019b). The P released from the clay surfaces is prone to leaching while the iron and manganese oxides are quickly precipitated within aerobic micro-sites leading to the accumulation of Fe_{acOH} and Mn_{acOH}. A general downward trend in soil solution DRP as the flood period progressed supports this theory. This reduction in P_{acOH} persisted for the first year of recovery potentially impacting sward recovery. Hence, farmers should be encouraged to test for soil P status following prolonged flooding, as this may have changed.

N dynamics in soils are tightly coupled to soil moisture (Bowles et al., 2018). Consequently, in contrast to P, soil mineral N concentrations were influenced by both drought and flood stress. Suppression of plant growth combined with low soil moisture and limited leaching potential during drought led to the accumulation of NH_4^+ and NO_3^- in the soil. While the accumulation of NH_4^+ during flood stress was accompanied by no change in NO_3^- concentration despite reduced plant N requirements. We ascribe the greater accumulation of NH_4^+ during the flood phase compared to the drought to a combination of (1) supressed microbial nitrification at low Eh potentials during flooding, and (2) increased mineralisation of organic matter introduced as dead plant material. Waterlogged conditions increase the leaching potential of NO_3^-, and the rate of denitrification (Rohe et al., 2021) explaining the lack of soil NO_3^- response. The accumulation of mineral N immediately post drought or flood stress provides essential nutrients for plant growth following removal of the stress and is essential to the resilience of pasture systems (Oram et al., 2020). This likely contributed to the lack of annual yield loss seen post drought but was not sufficient to mitigate the within-event year impact of flooding on annual biomass.

Drought did not influence soil fertility metrics in the longer term. However, differing P_{acOH} and NO_3^- responses post flood and during the recovery periods suggest a longer-term impact on N and P dynamics in the flood plots. During recovery phase 2, no fertiliser was applied, and livestock were excluded, therefore the increase in P_{acOH} and NO_3^- concentrations in the flood plots suggests increased biogeochemical cycling of nutrients to replace those lost from the system. This recovery of soil fertility in the flooded plots was further evidenced by a recovery of annual biomass to that of the control plots in year 2.

The exact mechanisms for these patterns of soil fertility are unclear but may be due to a change in soil-plant-microbe interactions. In the absence of fertiliser inputs, soil fertility is largely driven by microbial processing of organic matter (Risch et al., 2019). Manipulation of rainfall has been shown to alter soil microbial community structure (Ochoa-Hueso et al., 2020) and microbial activity via increased extracellular enzyme expression (Ochoa-Hueso et al., 2018). The higher microbial biomass in flooded soils 1 and 2 years post stress can be attributed to increased inputs of dead organic matter and an associated resource pulse post flooding (Wright et al., 2015). Furthermore, plant-soil feedback mechanisms are key drivers of ecosystem processes and plant associated microbiomes are profoundly influenced by abiotic factors and changing environmental conditions (Pugnaire et al., 2019; Saijo and Loo, 2020). The shift in plant and microbial community composition observed during pasture regrowth may have influenced the soil chemistry and the root associated microbiome, as evidenced by the shift in PLFA markers, including markers for AMF, with implications for nutrient acquisition strategies (Lozano et al., 2021). Further work, on the detailed changes in microbial communities, especially gene expression of N and P cycling and investigation of the changes in extracellular enzyme expression may further elucidate the mechanisms involved.

Organic matter decomposition: Results from the tea-bag index found reduction in the C stabilisation rate during both the flood and drought phase, and a reduction in C decomposition rate during the flood with impacts on below ground C storage.

Anoxic conditions are generally considered to decrease C decomposition and favour C accumulation (Greenwood, 1961; Reichstein et al., 2013). However, while the decomposition rate decreased during flooding, C storage also decreased during both the flood and the drought phases. The reduction in C storage was driven by a reduction in C stabilisation rates, likely due to reduced rhizodeposition. Drought has been shown to alter allocation of C within plants (Bahn et al., 2013) and affect exudate quantity and quality (Williams and de Vries, 2020) but the impact of flooding on these dynamics remains a significant gap in the literature. Additionally, iron redox cycles during flooding can release mineral protected C with leaching of DOC via the soil solution. Measurable changes in soil C stores take time to develop. However, the persistent shift in microbial composition post flood, could impact on C turnover especially if more resource-conservative stress tolerant traits are favoured over enzyme expression (Wang and Allison, 2021).

Climate regulation: Soil plays an important role in regulating the climate and can act both as a sink for C and a source of GHGs (Lal et al., 2021). Flood and drought decreased CO_2 emissions and cumulative CO_2 fluxes during the stress period due to a reduction in soil microbial and root respiration with the largest effect on total flux seen for the combined events. However, the lower cumulative CO_2 emissions during drought in the previously flooded plots indicates that the negative impact of the combination of stresses on soil was not additive.

Flooding has a significant impact on the production of CH_4 due to the generation of negative redox potentials (Zhang and Furman, 2021). Supressed gas exchange under waterlogged conditions delayed the pulse of CH_4 release until the removal of the flood water. In the flooded soils, the drought period produced a switch from a CH_4 source to a CH_4 sink. The sustained release of CH_4 from the flooded soils is likely due to the lag in WFPS recovery, but changes in the microbial community structure may also play a role.

Nitrous oxide makes an important contribution to GHG emissions from grazed pasture systems with soil moisture, N fertiliser application (Cardenas et al., 2019) and excreta deposition (Chadwick et al., 2018) being the main drivers of N dynamics. Flood stress had the largest impact on N_2O emissions with a large pulse emitted once the floodwater was removed and a second pulse associated with fertiliser application. During the flood and the first days of recovery, NH_4^+ is the predominant inorganic N form within the soil mineral and solution phases as anaerobic conditions supress nitrification. Subsequent mineralization of dead vegetation, mesofauna and soil microorganisms resulted in a pulse of C and N release facilitated by favourable summer temperatures (Kirwan and Blum, 2011; Sánchez-Rodríguez et al., 2019b). This resulted in a peak in NH_4^+ during soil recovery. Concurrent nitrification and denitrification occurring at microsites within the soil led to the observed N_2O emissions in the soil recovery phase after flooding (Miniotti et al., 2016; Zhu et al., 2013) and contributed to the observed decrease in NH_4^+ and NO_3^-, in the soil solution. Additionally, NH_3 volatilization (when the soil was flooded and saturated) would have reduced the NH_4^+ concentration in the soil solution (Verhoeven et al., 2018). During longer-term recovery, increased N demand due to a resumption of the growth of plants (seed bank) and soil microorganisms under non-anoxic conditions led to a gradual decline in NO_3^- in the soil solution, in line with N_2O peaks. However, this reduction was slower than for NH_4^+, which indicates that the gradual recovery of plants and microorganisms which was insufficient to fully utilise the available N resource. Current understanding of N dynamics in agricultural systems identifies N fertilisation as the main driver of spikes in N_2O emissions. However, the N_2O pulse following floodwater recession was greater than that produce by N fertilisation. Consequently, flooding caused the highest GWP (excluding CO_2) in line with Hou et al. (2000), especially in combination with drought. These data can help to fill knowledge gaps related to GHG emissions from agricultural soils (Bianchi et al., 2021). Furthermore, alteration of the soil microbial communities is likely to play a large role through the alteration of N dynamics and the long-term effect of flood induced shifts in microbial structure on GHG emissions requires further investigation.

Pollution regulation: The risk of erosion and runoff generation immediately post flood is increased due to the severe reduction in plant cover and the high WFPS, reducing infiltration capacity of the soil, and remains a threat for the first year of recovery along with an increased risk of nutrient and sediment transport. Conversely, 8 weeks of drought did not increase the proportion of bare ground present retaining soil protection to future heavy rain events, minimising the erosion risk and impact on water quality.

Flood events have been shown to export significant amounts of P to receiving waterbodies (Ockenden et al., 2017). Traditionally, P leaching has not been considered to be a major transport pathway in clay-rich soils. However, evidence of P leaching to groundwater in certain soil, hydrologic and management conditions is growing (McDowell et al., 2019; Stuart and Lapworth, 2016) and in flooded soils this may be enhanced by reductive dissolution cycles of Fe/Mn oxides. The general downward trend in DRP over the flood period indicates loss of P to leaching while the spikes in concentration are likely due to localised release of P from iron oxides in response to anoxic conditions developing. Further evidence of loss of P from the soil is seen through the reduction in P_{acOH} post flood. Unlike P, NO_3^- is prone to leaching and the general downward trend in soil solution NO_3^-, coupled with low N_2O emissions during the flood phase suggest possible loss to groundwater. During this period, the concentrations detected were low (< 0.25 mg NO_3^- L^{-1}) and unlikely to pose a significant water quality risk. However, immediately post flood there is an increased risk of N and P leaching due resumption of microbial activity leading to mineralisation of dead plant material and nitrification processes converting accumulated NH_4^+ to NO_3^-, evidenced by a large, and environmentally significant, spike in DOC, DOP and NO_3^-concentrations within the soil solution followed by a sharp decline.

Biodiversity provision: Grasslands provide important floral resources for pollinating species. However, the low biodiversity within many agricultural pastures supporting livestock production is contributing to global declines in species (Sánchez-Bayo and Wyckhuys, 2019). While drought had no impact on plant community composition, the increase in diversity and richness recolonising the flood plots post stress may promote greater insect populations including pollinating species evidenced by a persistent increase in nectar-containing species in the flood plus drought treatment. However, in contrast grassland crop wild relatives are largely composed of flooding-intolerant grass species (Jarvis et al., 2015) and flooding reduced their abundance for 1 year post-flood. Crop wild relatives contribute towards an ecosystem's genetic resource provision (Jarvis et al., 2015) and often exhibit useful traits related to stress tolerance (Castañeda-Álvarez et al., 2016). However, if flooding becomes more widespread, reduction of this valuable resource could have negative impacts for biodiversity provision and future agricultural plant breeding programs aimed at producing plant varieties more resilient to climate change.

5. Conclusions

Extreme weather events are increasing in frequency and magnitude. Here we show that flooding and drought have a significant impact on a range of above and below ground indicators of ecosystem function and that this pasture system is more resistant and resilient to drought than to flood. Contrary to our prediction, the compound flood+drought treatment did not further exacerbate the flood impact. In fact, there was some indication of more resilience in soil and microbial parameters suggesting contrasting event types may promote recovery through a more rapid return to ambient soil moisture conditions. The immediate impact of flooding on all ecosystem services was negative, especially for production and climate and water regulation. Flooding stress caused pronounced and persistent shifts in soil microbial and plant communities with large implications for nutrient cycling and long-term ES provision. However, determination of the mechanisms behind these changes and the impact of these shifts along with the complex plant-soil-microbe interactions, on whole ecosystem function remains a key research priority. The observed increase in soil nutrient concentrations immediately post flood and drought stress has the potential to provide a resource pulse for pasture growth and recolonization. Soil testing is essential when determining fertiliser rates to minimise nutrient loss and minimise impacts on water quality and GHG emissions. Furthermore, the large pulse of N_2O emissions is striking and with the projected increase in the frequency, severity and spatial extent of flood events further research is required to factor flood-induced N_2O pulses into GHG emission projections.

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Author contribution

Davey L. Jones, David R. Chadwick, Dylan Gwynn-Jones, Rosalind J. Dodd and Paul. W. Hill conceived the study and set up the experiment. Rosalind J. Dodd, Antonio R. Sánchez-Rodríguez and Simon M. Smart undertook the main fieldwork, laboratory studies and data analysis. Rosalind J. Dodd wrote the first draft of the manuscript and all authors contributed substantially to revisions and have given final approval of the submitted manuscript.

Conflict of interest

The authors declare no competing interests.

References

Abbasi, A.O., Salazar, A., Oh, Y., Reinsch, S., del Rosario Uribe, M., Li, J., Rashid, I., Dukes, J.S. (2020) Reviews and syntheses: Soil responses to manipulated precipitation changes – an assessment of meta-analyses. Biogeosciences 17, 3859-3873.

Acosta-Martínez, V., Cotton, J., Gardner, T., Moore-Kucera, J., Zak, J., Wester, D., Cox, S. (2014) Predominant bacterial and fungal assemblages in agricultural soils during a record drought/heat wave and linkages to enzyme activities of biogeochemical cycling. Applied Soil Ecology 84, 69-82.

ADAS, (2014) The Economic Impact of 2014 Winter Floods on Agriculture in England. ADAS, Wolverhamption, UK, p. 46pp.

Adhikari, K., Hartemink, A.E. (2016) Linking soils to ecosystem services — A global review. Geoderma 262, 101-111.

Arain, M.A., Xu, B., Brodeur, J.J., Khomik, M., Peichl, M., Beamesderfer, E., Restrepo-Couple, N., Thorne, R. (2022) Heat and drought impact on carbon exchange in an age-sequence of temperate pine forests. Ecological Processes 11, 7.

Bahn, M., Lattanzi, F.A., Hasibeder, R., Wild, B., Koranda, M., Danese, V., Brüggemann, N., Schmitt, M., Siegwolf, R., Richter, A. (2013) Responses of belowground carbon allocation dynamics to extended shading in mountain grassland. New Phytologist 198, 116-126.

Bartelt-Ryser, J., Joshi, J., Schmid, B., Brandl, H., Balser, T. (2005) Soil feedbacks of plant diversity on soil microbial communities and subsequent plant growth. Perspectives in Plant Ecology, Evolution and Systematics 7, 27-49.

Baude, M., Kunin, W.E., Boatman, N.D., Conyers, S., Davies, N., Gillespie, M.A.K., Morton, R.D., Smart, S.M., Memmott, J. (2016) Historical nectar assessment reveals the fall and rise of floral resources in Britain. Nature 530, 85-88.

Bianchi, A., Larmola, T., Kekkonen, H., Saarnio, S., Lång, K. (2021) Review of Greenhouse Gas Emissions from Rewetted Agricultural Soils. Wetlands 41, 108.

Birch, H.F. (1958) The effect of soil drying on humus decomposition and nitrogen availability. Plant and Soil 10, 9-31.

Birkhofer, K., Fliessbach, A., Gavín-Centol, M.P., Hedlund, K., Ingimarsdóttir, M., Jørgensen, H.B., Kozjek, K., Meyer, S., Montserrat, M., Moreno, S.S., Laraño, J.M., Scheu, S., Serrano-Carnero, D., Truu, J., Kundel, D. (2021) Conventional agriculture and not drought alters relationships between soil biota and functions. Scientific Reports 11, 23975.

Blankinship, J.C., Niklaus, P.A., Hungate, B.A. (2011) A meta-analysis of responses of soil biota to global change. Oecologia 165, 553-565.

Bloor, J.M.G., Bardgett, R.D. (2012) Stability of above-ground and below-ground processes to extreme drought in model grassland ecosystems: Interactions with plant species diversity and soil nitrogen availability. Perspectives in Plant Ecology, Evolution and Systematics 14, 193-204.

Blouin, M., Hodson, M.E., Delgado, E.A., Baker, G., Brussaard, L., Butt, K.R., Dai, J., Dendooven, L., Peres, G., Tondoh, J.E., Cluzeau, D., Brun, J.-J. (2013) A review of earthworm impact on soil function and ecosystem services. European Journal of Soil Science 64, 161-182.

Borken, W., Matzner, E. (2009) Reappraisal of drying and wetting effects on C and N mineralization and fluxes in soils. Global Change Biology 15, 808-824.

Bowles, T.M., Atallah, S.S., Campbell, E.E., Gaudin, A.C.M., Wieder, W.R., Grandy, A.S. (2018) Addressing agricultural nitrogen losses in a changing climate. Nature Sustainability 1, 399-408.

Brussaard, L. (1997) Biodiversity and Ecosystem Functioning in Soil. Ambio 26, 563-570.

Cardenas, L.M., Bhogal, A., Chadwick, D.R., McGeough, K., Misselbrook, T., Rees, R.M., Thorman, R.E., Watson, C.J., Williams, J.R., Smith, K.A., Calvet, S. (2019) Nitrogen use efficiency and nitrous oxide emissions from five UK fertilised grasslands. Science of The Total Environment 661, 696-710.

Castañeda-Álvarez, N.P., Khoury, C.K., Achicanoy, H.A., Bernau, V., Dempewolf, H., Eastwood, R.J., Guarino, L., Harker, R.H., Jarvis, A., Maxted, N., Müller, J.V., Ramirez-Villegas, J., Sosa, C.C., Struik, P.C., Vincent, H., Toll, J. (2016) Global conservation priorities for crop wild relatives. Nature Plants 2, 16022.

Chadwick, D.R., Cardenas, L., Misselbrook, T.H., Smith, K.A., Rees, R.M., Watson, C.J., McGeough, K.L., Williams, J.R., Cloy, J.M., Thorman, R.E., Dhanoa, M.S. (2014) Optimizing chamber methods for measuring nitrous oxide emissions from plot-based agricultural experiments. European Journal of Soil Science 65, 295-307.

Chadwick, D.R., Cardenas, L.M., Dhanoa, M.S., Donovan, N., Misselbrook, T., Williams, J.R., Thorman, R.E., McGeough, K.L., Watson, C.J., Bell, M., Anthony, S.G., Rees, R.M. (2018) The contribution of cattle urine and dung to nitrous oxide emissions: Quantification of country specific emission factors and implications for national inventories. Science of The Total Environment 635, 607-617.

Ciais, P., Reichstein, M., Viovy, N., Granier, A., Ogée, J., Allard, V., Aubinet, M., Buchmann, N., Bernhofer, C., Carrara, A., Chevallier, F., De Noblet, N., Friend, A.D., Friedlingstein, P., Grünwald, T., Heinesch, B., Keronen, P., Knohl, A., Krinner, G., Loustau, D., Manca, G., Matteucci, G., Miglietta, F., Ourcival, J.M., Papale, D., Pilegaard, K., Rambal, S., Seufert, G., Soussana, J.F., Sanz, M.J., Schulze, E.D., Vesala, T., Valentini, R. (2005) Europe-wide reduction in primary productivity caused by the heat and drought in 2003. Nature 437, 529-533.

Creamer, R.E., Barel, J.M., Bongiorno, G., Zwetsloot, M.J. (2022) The life of soils: Integrating the who and how of multifunctionality. Soil Biology and Biochemistry 166, 108561.

Crowther, T.W., van den Hoogen, J., Wan, J., Mayes, M.A., Keiser, A.D., Mo, L., Averill, C., Maynard, D.S. (2019) The global soil community and its influence on biogeochemistry. Science 365, eaav0550.

de Vries, F.T., Griffiths, R.I., Bailey, M., Craig, H., Girlanda, M., Gweon, H.S., Hallin, S., Kaisermann, A., Keith, A.M., Kretzschmar, M., Lemanceau, P., Lumini, E., Mason, K.E., Oliver, A., Ostle, N., Prosser, J.I., Thion, C., Thomson, B., Bardgett, R.D. (2018) Soil bacterial networks are less stable under drought than fungal networks. Nature Communications 9, 3033.

Defra, (2014) Legacy effects of extreme flood events on soil quality and ecosystem functioning: Project LM0316 Final Report. Department for the Environment, Fodd & Rural Affairs, London, UK.

Delgado-Baquerizo, M., Reich, P.B., Trivedi, C., Eldridge, D.J., Abades, S., Alfaro, F.D., Bastida, F., Berhe, A.A., Cutler, N.A., Gallardo, A., García-Velázquez, L., Hart, S.C., Hayes, P.E., He, J.-Z., Hseu, Z.-Y., Hu, H.-W., Kirchmair, M., Neuhauser, S., Pérez, C.A., Reed, S.C., Santos, F., Sullivan, B.W., Trivedi, P., Wang, J.-T., Weber-Grullon, L., Williams, M.A., Singh, B.K. (2020) Multiple elements of soil biodiversity drive ecosystem functions across biomes. Nature Ecology & Evolution 4, 210-220.

Deng, L., Peng, C., Kim, D.-G., Li, J., Liu, Y., Hai, X., Liu, Q., Huang, C., Shangguan, Z., Kuzyakov, Y. (2021) Drought effects on soil carbon and nitrogen dynamics in global natural ecosystems. Earth-Science Reviews 214, 103501.

Dijkstra, F.A., He, M., Johansen, M.P., Harrison, J.J., Keitel, C. (2015) Plant and microbial uptake of nitrogen and phosphorus affected by drought using 15N and 32P tracers. Soil Biology and Biochemistry 82, 135-142.

Dodd, R.J., Chadwick, D.R., Harris, I.M., Hines, A., Hollis, D., Economou, T., Gwynn-Jones, D., Scullion, J., Robinson, D.A., Jones, D.L. (2021) Spatial co-localisation of extreme weather events: a clear and present danger. Ecology Letters 24, 60-72.

Dominati, E., Patterson, M., Mackay, A. (2010) A framework for classifying and quantifying the natural capital and ecosystem services of soils. Ecological Economics 69, 1858-1868.

Emets, V.M. (2018) Long-term Dynamics of Population Parameters of the Aporrectodea caliginosa Earthworm in an Annually Flooded Alder Forests in the Voronezh Nature Reserve. Russian Journal of Ecology 49, 349-355.

Environment Agency, (2006) The impact of climate change on severe droughts in England and Wales from1800 and evidence of impact Bristol, U.K., p. 54.

Evans, S.E., Allison, S.D., Hawkes, C. (2022) Microbes, memory and moisture: Predicting microbial moisture responses and their impact on carbon cycling. Functional Ecology 36, 1430-1441.

Famiglietti, C.A., Michalak, A.M., Konings, A.G. (2021) Extreme wet events as important as extreme dry events in controlling spatial patterns of vegetation greenness anomalies. Environmental Research Letters 16, 074014.

Fierer, N., Bradford, M.A., Jackson, R.B. (2007) Toward an ecological classification of soil bacteria. Ecology 88, 1354-1364.

Fierer, N., Schimel, J.P. (2002) Effects of drying–rewetting frequency on soil carbon and nitrogen transformations. Soil Biology and Biochemistry 34, 777-787.

Forero, L.E., Kulmatiski, A., Grenzer, J., Norton, J. Plant–soil feedbacks help explain plant community productivity. Ecology n/a, e3736.

Fowler, H.J., Kilsby, C.G. (2003) A regional frequency analysis of United Kingdom extreme rainfall from 1961 to 2000. International Journal of Climatology 23, 1313-1334.

González Macé, O., Steinauer, K., Jousset, A., Eisenhauer, N., Scheu, S. (2016) Flood-Induced Changes in Soil Microbial Functions as Modified by Plant Diversity. PLOS ONE 11, e0166349-e0166349.

Gordon, H., Haygarth, P.M., Bardgett, R.D. (2008) Drying and rewetting effects on soil microbial community composition and nutrient leaching. Soil Biology and Biochemistry 40, 302-311.

Greenwood, D.J. (1961) The effect of oxygen concentration on the decomposition of organic materials in soil. Plant and Soil 14, 360-376.

Harvey, R.J., Chadwick, D.R., Sánchez-Rodríguez, A.R., Jones, D.L. (2019) Agroecosystem resilience in response to extreme winter flooding. Agriculture, Ecosystems & Environment 279, 1-13.

Hedges, L.V., Gurevitch, J., Curtis, P.S. (1999) The meta-analysis of response ratios in experimental ecology. Ecology 80, 1150-1156.

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

Hou, A.X., Chen, G.X., Wang, Z.P., Van Cleemput, O., Patrick Jr., W.H. (2000) Methane and Nitrous Oxide Emissions from a Rice Field in Relation to Soil Redox and Microbiological Processes. Soil Science Society of America Journal 64, 2180-2186.

Huntingford, C., Marsh, T., Scaife, A.A., Kendon, E.J., Hannaford, J., Kay, A.L., Lockwood, M., Prudhomme, C., Reynard, N.S., Parry, S., Lowe, J.A., Screen, J.A., Ward, H.C., Roberts, M., Stott, P.A., Bell, V.A., Bailey, M., Jenkins, A., Legg, T., Otto, F.E.L., Massey, N., Schaller, N., Slingo, J., Allen, M.R. (2014) Potential influences on the United Kingdom's floods of winter 2013/14. Nature Climate Change 4, 769-777.

IPCC, (2021) Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change., in: Masson-Delmotte, V., Zhai, P, Pirani, A., Connors, S.L., Pean, C., Berger, S., Caud, N., Chen, Y., Goldfarb, L., Gomis, M.I., Huang, M., Leitzell, K., Lonnoy, E., Matthews, J.B.R., Maycock, T.K., Waterfield, T., Yelekci, O., Yu, R., and Zhou, B. (Ed.).

Jarvis, S., Fielder, H., Hopkins, J., Maxted, N., Smart, S. (2015) Distribution of crop wild relatives of conservation priority in the UK landscape. Biological Conservation 191, 444-451.

Jones, C.G., Lawton, J.H., Shachak, M. (1994) Organisms as Ecosystem Engineers. Oikos 69, 373-386.

Keuskamp, J.A., Dingemans, B.J.J., Lehtinen, T., Sarneel, J.M., Hefting, M.M. (2013) Tea Bag Index: a novel approach to collect uniform decomposition data across ecosystems. Methods in Ecology and Evolution 4, 1070-1075.

Kirwan, M.L., Blum, L.K. (2011) Enhanced decomposition offsets enhanced productivity and soil carbon accumulation in coastal wetlands responding to climate change. Biogeosciences 8, 987-993.

Knapp, A.K., Chen, A., Griffin-Nolan, R.J., Baur, L.E., Carroll, C.J.W., Gray, J.E., Hoffman, A.M., Li, X., Post, A.K., Slette, I.J., Collins, S.L., Luo, Y., Smith, M.D. (2020)

Resolving the Dust Bowl paradox of grassland responses to extreme drought. Proceedings of the National Academy of Sciences 117, 22249-22255.

Lal, R., Monger, C., Nave, L., Smith, P. (2021) The role of soil in regulation of climate. Philosophical Transactions of the Royal Society B: Biological Sciences 376, 20210084.

Li, C., Zwiers, F., Zhang, X., Chen, G., Lu, J., Li, G., Norris, J., Tan, Y., Sun, Y., Liu, M. (2019) Larger Increases in More Extreme Local Precipitation Events as Climate Warms. Geophysical Research Letters 46, 6885-6891.

Lozano, Y.M., Aguilar-Trigueros, C.A., Roy, J., Rillig, M.C. (2021) Drought induces shifts in soil fungal communities that can be linked to root traits across 24 plant species. New Phytologist 232, 1917-1929.

MacKenzie, A.F., Fan, M.X., Cadrin, F. (1998) Nitrous Oxide Emission in Three Years as Affected by Tillage, Corn-Soybean-Alfalfa Rotations, and Nitrogen Fertilization. Journal of Environmental Quality 27, 698-703.

Magurran, A.E. (2013) Measuring Biological Diversity, 1 ed. Wiley-Blackwell, Oxford.

McDaniel, J.P., Barbarick, K.A., Stromberger, M.E., Cranshaw, W. (2013) Survivability of Aporrectodea caliginosa in Response to Drought Stress in a Colorado Soil. Soil Science Society of America Journal 77, 1667-1672.

McDowell, R.W., Gray, C.W., Cameron, K.C., Di, H.J., Pellow, R. (2019) The efficacy of good practice to prevent long-term leaching losses of phosphorus from an irrigated dairy farm. Agriculture, Ecosystems & Environment 273, 86-94.

MEA, (2005) Millennium Ecosystem Assessment: Ecosystems and human wellbeing, Washington D.C.

Miniotti, E.F., Romani, M., Said-Pullicino, D., Facchi, A., Bertora, C., Peyron, M., Sacco, D., Bischetti, G.B., Lerda, C., Tenni, D., Gandolfi, C., Celi, L. (2016) Agro-environmental sustainability of different water management practices in temperate rice agro-ecosystems. Agriculture, Ecosystems & Environment 222, 235-248.

Miranda, K.M., Espey, M.G., Wink, D.A. (2001) A rapid, simple spectrophotometric method for simultaneous detection of nitrate and nitrite. Nitric Oxide 5, 62-71.

Mulvaney, R.L., (1996) Nitrogen—Inorganic Forms, Methods of Soil Analysis, pp. 1123-1184.

Niu, S., Luo, Y., Li, D., Cao, S., Xia, J., Li, J., Smith, M.D. (2014) Plant growth and mortality under climatic extremes: An overview. Environmental and Experimental Botany 98, 13-19.

O'Mara, F.P. (2012) The role of grasslands in food security and climate change. Annals of Botany 110, 1263-1270.

Ochoa-Hueso, R., Arca, V., Delgado-Baquerizo, M., Hamonts, K., Piñeiro, J., Serrano-Grijalva, L., Shawyer, J., Power, S.A. (2020) Links between soil microbial communities, functioning, and plant nutrition under altered rainfall in Australian grassland. Ecological Monographs 90, e01424.

Ochoa-Hueso, R., Collins, S.L., Delgado-Baquerizo, M., Hamonts, K., Pockman, W.T., Sinsabaugh, R.L., Smith, M.D., Knapp, A.K., Power, S.A. (2018) Drought consistently alters the composition of soil fungal and bacterial communities in grasslands from two continents. Global Change Biology 24, 2818-2827.

Ockenden, M.C., Hollaway, M.J., Beven, K.J., Collins, A.L., Evans, R., Falloon, P.D., Forber, K.J., Hiscock, K.M., Kahana, R., Macleod, C.J.A., Tych, W., Villamizar, M.L., Wearing, C., Withers, P.J.A., Zhou, J.G., Barker, P.A., Burke, S., Freer, J.E., Johnes, P.J., Snell, M.A., Surridge, B.W.J., Haygarth, P.M. (2017) Major agricultural changes required to mitigate phosphorus losses under climate change. Nature Communications 8, 161-161.

Oram, N.J., De Deyn, G.B., Bodelier, P.L., Cornelissen, J.H., van Groenigen, J.W., Abalos, D. (2020) Plant community flood resilience in intensively managed grasslands and the role of the plant economic spectrum. Journal of Applied Ecology 57, 1524-1534.

Oram, N.J., Sun, Y., Abalos, D., van Groenigen, J.W., Hartley, S., De Deyn, G.B. (2021) Plant traits of grass and legume species for flood resilience and N2O mitigation. Functional Ecology 35, 2205-2218.

Pelosi, C., Bertrand, M., Capowiez, Y., Boizard, H., Roger-Estrade, J. (2009) Earthworm collection from agricultural fields: Comparisons of selected expellants in presence/absence of hand-sorting. European Journal of Soil Biology 45, 176-183.

Post, A.K., Knapp, A.K. (2020) The importance of extreme rainfall events and their timing in a semi-arid grassland. Journal of Ecology 108, 2431-2443.

Pugnaire, F.I., Morillo, J.A., Peñuelas, J., Reich, P.B., Bardgett, R.D., Gaxiola, A., Wardle, D.A., van der Putten, W.H. (2019) Climate change effects on plant-soil feedbacks and consequences for biodiversity and functioning of terrestrial ecosystems. Science Advances 5, eaaz1834.

Rahman, N., Forrestal, P.J. (2021) Ammonium Fertilizer Reduces Nitrous Oxide Emission Compared to Nitrate Fertilizer While Yielding Equally in a Temperate Grassland. Agriculture 11, 1141.

Reichstein, M., Bahn, M., Ciais, P., Frank, D., Mahecha, M.D., Seneviratne, S.I., Zscheischler, J., Beer, C., Buchmann, N., Frank, D.C., Papale, D., Rammig, A., Smith, P., Thonicke, K., van der Velde, M., Vicca, S., Walz, A., Wattenbach, M. (2013) Climate extremes and the carbon cycle. Nature 500, 287.

Rillig, M.C., Ryo, M., Lehmann, A., Aguilar-Trigueros, C.A., Buchert, S., Wulf, A., Iwasaki, A., Roy, J., Yang, G. (2019) The role of multiple global change factors in driving soil functions and microbial biodiversity. Science 366, 886-890.

Risch, A.C., Zimmermann, S., Ochoa-Hueso, R., Schütz, M., Frey, B., Firn, J.L., Fay, P.A., Hagedorn, F., Borer, E.T., Seabloom, E.W., Harpole, W.S., Knops, J.M.H., McCulley, R.L., Broadbent, A.A.D., Stevens, C.J., Silveira, M.L., Adler, P.B., Báez, S., Biederman, L.A., Blair, J.M., Brown, C.S., Caldeira, M.C., Collins, S.L., Daleo, P., di Virgilio, A., Ebeling, A., Eisenhauer, N., Esch, E., Eskelinen, A., Hagenah, N., Hautier, Y., Kirkman, K.P., MacDougall, A.S., Moore, J.L., Power, S.A., Prober, S.M., Roscher, C., Sankaran, M., Siebert, J., Speziale, K.L., Tognetti, P.M., Virtanen, R., Yahdjian, L., Moser, B. (2019) Soil net nitrogen mineralisation across global grasslands. Nature Communications 10, 4981.

Rohe, L., Apelt, B., Vogel, H.J., Well, R., Wu, G.M., Schlüter, S. (2021) Denitrification in soil as a function of oxygen availability at the microscale. Biogeosciences 18, 1185-1201.

Rowland, A.P., Haygarth, P.M. (1997) Determination of Total Dissolved Phosphorus in Soil Solutions. Journal of Environmental Quality 26, 410-415.

Rutgers, M., van Wijnen, H.J., Schouten, A.J., Mulder, C., Kuiten, A.M.P., Brussaard, L., Breure, A.M. (2012) A method to assess ecosystem services developed from soil attributes with stakeholders and data of four arable farms. Science of The Total Environment 415, 39-48.

Saijo, Y., Loo, E.P.-i. (2020) Plant immunity in signal integration between biotic and abiotic stress responses. New Phytologist 225, 87-104.

Sánchez-Bayo, F., Wyckhuys, K.A.G. (2019) Worldwide decline of the entomofauna: A review of its drivers. Biological Conservation 232, 8-27.

Sánchez-Rodríguez, A.R., Chadwick, D.R., Tatton, G.S., Hill, P.W., Jones, D.L. (2018) Comparative effects of prolonged freshwater and saline flooding on nitrogen cycling in an agricultural soil. Applied Soil Ecology 125, 56-70.

Sánchez-Rodríguez, A.R., Hill, P.W., Chadwick, D.R., Jones, D.L. (2019a) Typology of extreme flood event leads to differential impacts on soil functioning. Soil Biology and Biochemistry 129, 153-168.

Sánchez-Rodríguez, A.R., Nie, C., Hill, P.W., Chadwick, D.R., Jones, D.L. (2019b) Extreme flood events at higher temperatures exacerbate the loss of soil functionality and trace gas emissions in grassland. Soil Biology and Biochemistry 130, 227-236.

Schwalm, C.R., Anderegg, W.R.L., Michalak, A.M., Fisher, J.B., Biondi, F., Koch, G., Litvak, M., Ogle, K., Shaw, J.D., Wolf, A., Huntzinger, D.N., Schaefer, K., Cook, R., Wei, Y., Fang, Y., Hayes, D., Huang, M., Jain, A., Tian, H. (2017) Global patterns of drought recovery. Nature 548, 202-205.

Singh, J., Schädler, M., Demetrio, W., Brown, G.G., Eisenhauer, N. (2020) Climate change effects on earthworms - a review. SOIL ORGANISMS 91, 113–137.

Slingo, J.M., Belcher, S.E., Scaife, A.A., McCarthy, M., Saulter, A., McBeath, K., Jenkins, A., Huntingford, C., Marsh, T., Hannaford, J., Parry, S., (2014) The recent storms and floods in the UK. NERC, Exeter.

Smart, S.M., Firbank, L.G., Bunce, R.G.H., Watkins, J.W. (2000) Quantifying Changes in Abundance of Food Plants for Butterfly Larvae and Farmland Birds. Journal of Applied Ecology 37, 398-414.

Smart, S.M., Henrys, P.A., Norton, L.R., Wallace, H., Wood, C.M., Williams, B., Bunce, R.G.H. (2017) Changes in the frequency of common plant species across linear features in Wales from 1990 to 2016: implications for potential delivery of ecosystem services. New Journal of Botany 7, 112-124.

Stuart, M.E., Lapworth, D.J. (2016) Macronutrient status of UK groundwater: Nitrogen, phosphorus and organic carbon. Science of The Total Environment 572, 1543-1560.

Thompson, V., Dunstone, N.J., Scaife, A.A., Smith, D.M., Slingo, J.M., Brown, S., Belcher, S.E. (2017) High risk of unprecedented UK rainfall in the current climate. Nature Communications 8.

Trenberth, K.E. (2011) Changes in precipitation with climate change. Climate Research 47, 123-138.

Unger, I.M., Motavalli, P.P., Muzika, R.-M. (2009) Changes in soil chemical properties with flooding: A field laboratory approach. Agriculture, Ecosystems & Environment 131, 105-110.

Valencia, E., Gross, N., Quero, J.L., Carmona, C.P., Ochoa, V., Gozalo, B., Delgado-Baquerizo, M., Dumack, K., Hamonts, K., Singh, B.K., Bonkowski, M., Maestre, F.T. (2018) Cascading effects from plants to soil microorganisms explain how plant species richness and simulated climate change affect soil multifunctionality. Global Change Biology 24, 5642-5654.

van Eekeren, N., de Boer, H., Hanegraaf, M., Bokhorst, J., Nierop, D., Bloem, J., Schouten, T., de Goede, R., Brussaard, L. (2010) Ecosystem services in grassland associated with biotic and abiotic soil parameters. Soil Biology and Biochemistry 42, 1491-1504.

Verhoeven, E., Decock, C., Barthel, M., Bertora, C., Sacco, D., Romani, M., Sleutel, S., Six, J. (2018) Nitrification and coupled nitrification-denitrification at shallow depths are responsible for early season N2O emissions under alternate wetting and drying management in an Italian rice paddy system. Soil Biology and Biochemistry 120, 58-69.

Wagg, C., Bender, S.F., Widmer, F., van der Heijden, M.G.A. (2014) Soil biodiversity and soil community composition determine ecosystem multifunctionality. Proceedings of the National Academy of Sciences 111, 5266-5270.

Wagner, D., Eisenhauer, N., Cesarz, S. (2015) Plant species richness does not attenuate responses of soil microbial and nematode communities to a flood event. Soil Biology and Biochemistry 89, 135-149.

Wahl, T., Jain, S., Bender, J., Meyers, S.D., Luther, M.E. (2015) Increasing risk of compound flooding from storm surge and rainfall for major US cities. Nature Climate Change 5, 1093-1097.

Wang, B., Allison, S.D. (2021) Drought legacies mediated by trait trade-offs in soil microbiomes. Ecosphere 12, e03562.

Watanabe, F.S., Olsen, S.R. (1965) Test of an Ascorbic Acid Method for Determining Phosphorus in Water and NaHCO3 Extracts from Soil. Soil Science Society of America Journal 29, 677-678.

Williams, A., de Vries, F.T. (2020) Plant root exudation under drought: implications for ecosystem functioning. New Phytologist 225, 1899-1905.

Wright, A.J., Ebeling, A., de Kroon, H., Roscher, C., Weigelt, A., Buchmann, N., Buchmann, T., Fischer, C., Hacker, N., Hildebrandt, A., Leimer, S., Mommer, L., Oelmann, Y., Scheu, S., Steinauer, K., Strecker, T., Weisser, W., Wilcke, W., Eisenhauer, N. (2015) Flooding disturbances increase resource availability and productivity but reduce stability in diverse plant communities. Nature Communications 6, 6092.

Zhang, Z., Furman, A. (2021) Soil redox dynamics under dynamic hydrologic regimes - A review. Science of The Total Environment 763, 143026.

Zhu, X., Burger, M., Doane, T.A., Horwath, W.R. (2013) Ammonia oxidation pathways and nitrifier denitrification are significant sources of N2O and NO under low oxygen availability. Proc Natl Acad Sci U S A 110, 6328-6333.

Zscheischler, J., Westra, S., van den Hurk, B.J.J.M., Seneviratne, S.I., Ward, P.J., Pitman, A., AghaKouchak, A., Bresch, D.N., Leonard, M., Wahl, T., Zhang, X. (2018) Future climate risk from compound events. Nature Climate Change 8, 469-477.

Figure legends

Fig. 1. Response of above- and below-ground indicators (a) immediately post flood or drought stress, (b) 1 year and (c) 2 years following the stress event. Effect sizes represent variation from the control calculated from the LnR/R response ratio as outlined in the methods. Error bars represent the 95 % confidence interval. Open symbols represent significant effects (95 % CI not overlapping Zero). The number of indicators significantly different to the control at the three time-points for the three treatments are shown in (d). In all panels AMF denotes arbuscular mycorrhizal fungi.

Fig. 2. Ecosystem service indicator scores provided by the pasture community (a) at the 1-month pasture regrowth stage post flood, (b) immediately post drought, (c) 6-months post drought, (d) 1-year post drought and (e) 2-years post drought. The letters denote significant differences between treatments at the $p < 0.05$ as determined by the Tukey HSD test of multiple comparisons and *n.s.* denotes no significant difference.

Fig. 3. Mean temporal dynamics of soil solution (a) dissolved organic carbon (DOC), (b) dissolved reactive phosphorus (DRP), (c) dissolved organic phosphorus (DOP), (d) ammonium (NH_4^+) and (e) nitrate (NO_3^-) within the flood plots during the flood phase and recovery phase 1. Error bars show the standard error of the mean.

Fig. 4. Principle component analysis for PLFA (a) in the four treatments across the five sampling dates, immediately post flood, immediately post drought and 6, 12 and 24 months post drought and (b) vectors indicate the direction of shift towards specific taxonomic groups 85 % of the variance in PLFA markers was explained by PC1 (x-axis) and a further 10 % was

explained by PC2 (y-axis). Ellipses group the responses to the specific time period and errors bars show the standard error of the mean for the four treatments.

Fig. 5. Greenhouse gas emissions for each treatment showing hourly CH_4 (a-d), CO_2 (d-h) and N_2O (i-l) fluxes (mean ± standard error, n = 4) in each period of the experiment (flood phase, recovery phase 1, drought phase and recovery phase 2) for the different treatments assessed in this study (control, flood, drought and flood + drought). The arrow and F indicate a fertilization event.

Table 1. Indicator metrics associated with the 6 selected provisioning, supporting and regulating services provided by agricultural grasslands.

Environment Service category	**Service**	**Indicators**	**Measurement**
Provisioning	Food provisioning	Biomass, forage grass cover, weed species cover	Pasture cut, plant surveys
	Biodiversity provision	Plant species richness + diversity, nectar producing species, butterfly larvae food species, crop wild relatives	Plant surveys
Regulating	Climate regulation	CO_2, CH_4, N_2O emissions	Static chamber greenhouse gas emission measurements
	Pollution regulation	% ground cover, soil solution chemistry (DOC, NO_3^-, NH_4^+, DRP, DOP)[1]	Plant surveys, rhizon sampling of soil solution (during flood phase only)
Supporting	Nutrient cycling	Soil extractable NO_3^-, NH_4^+, P	Soil samples
	Organic matter decomposition	C stabilisation rate (*S*), C decomposition rate (*k*)	Tea-bag index

[1] DRP = dissolved reactive phosphorus, DOC = dissolved organic phosphorus, DOC = dissolved organic carbon.

Table 2. Mean cumulative GHG fluxes and total CO_2 equivalents with and without CO_2 emissions along with the standard error. The letters denote significant differences between treatments according to the Tukey's HSD test at the $p < 0.05$ level of significance.

Treatment	CH_4 (kg C ha^{-1})	CO_2 (kg C ha^{-1})	N_2O (kg N ha^{-1})	GWP (exc. CO_2) (kg $CO_{2\ eq}$ ha^{-1})	GWP (inc. CO_2) (kg $CO_{2\ eq}$ ha^{-1})
Control	-0.38 ± 0.18 a	8111 ± 192 a	1.01 ± 0.14 ab	273 ± 40 ab	7915 ± 274 a
Flood	0.98 ± 0.72 a	4651 ± 1213 ab	3.35 ± 1.03 ab	874 ± 264 ab	5238 ± 1347 a
Drought	-0.20 ± 0.03 a	4726 ± 1059 ab	0.41 ± 0.06 b	108 ± 15 b	4602 ± 1062 a
Flood & drought	1.49 ± 1.16 a	2942 ± 617 b	4.16 ± 1.43 a	1060 ± 343 a	3813 ± 925 a
p value	0.215	**0.009**	**0.031**	**0.025**	0.059

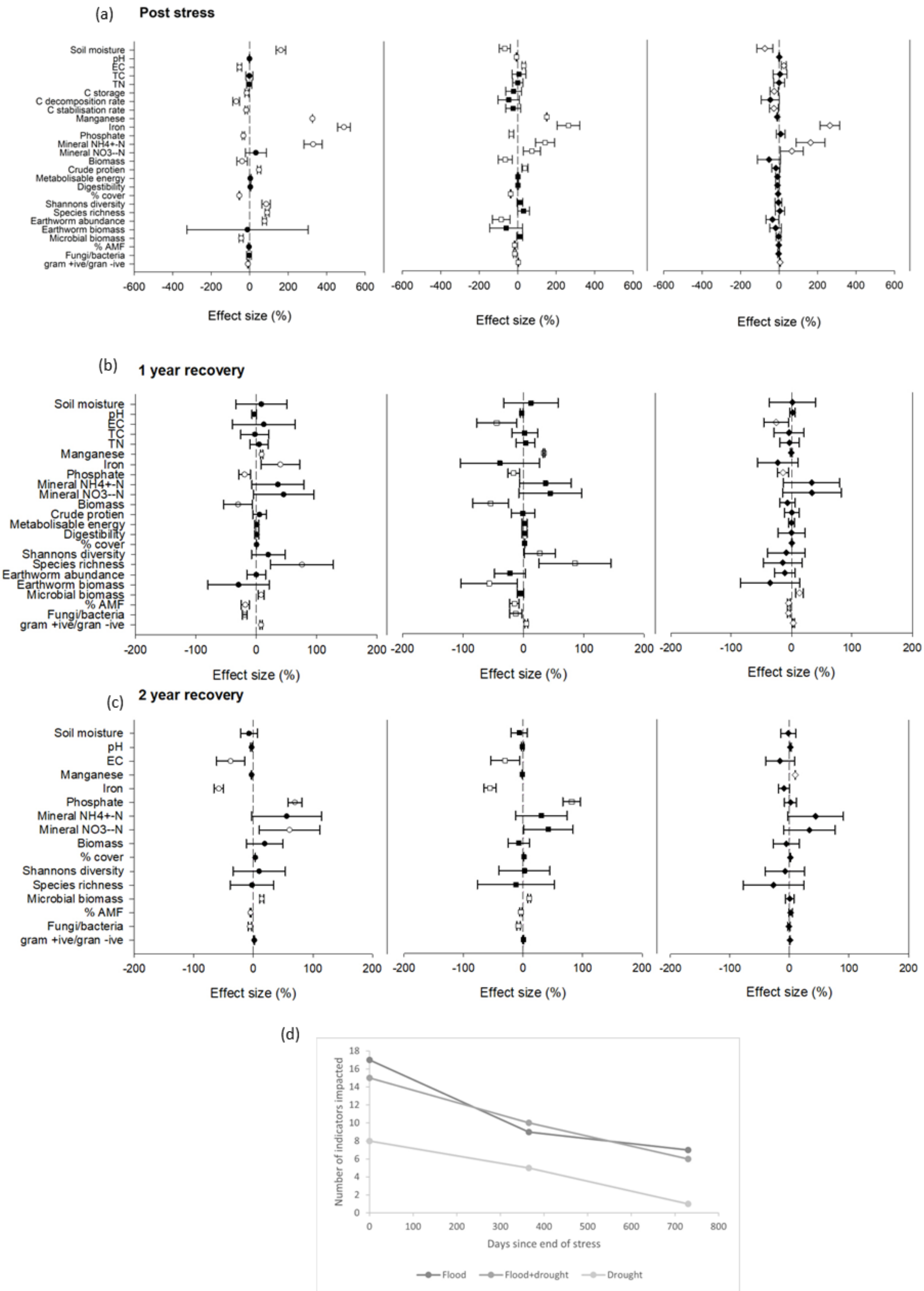

(a) Post stress
Soil moisture
pH
EC
TC
TN
C storage
C decomposition rate
C stabilisation rate
Manganese
Iron
Phosphate
Mineral NH4+-N
Mineral NO3--N
Biomass
Crude protien
Metabolisable energy
Digestibility
% cover
Shannons diversity
Species richness
Earthworm abundance
Earthworm biomass
Microbial biomass
% AMF
Fungi/bacteria
gram +ive/gran -ive
-600 -400 -200 0 200 400 600
Effect size (%)
(b) 1 year recovery
-200 -100 0 100 200
Effect size (%)
(c) 2 year recovery
Effect size (%)
(d)
Number of indicators impacted
Days since end of stress
Flood
Flood+drought
Drought

Figure 1

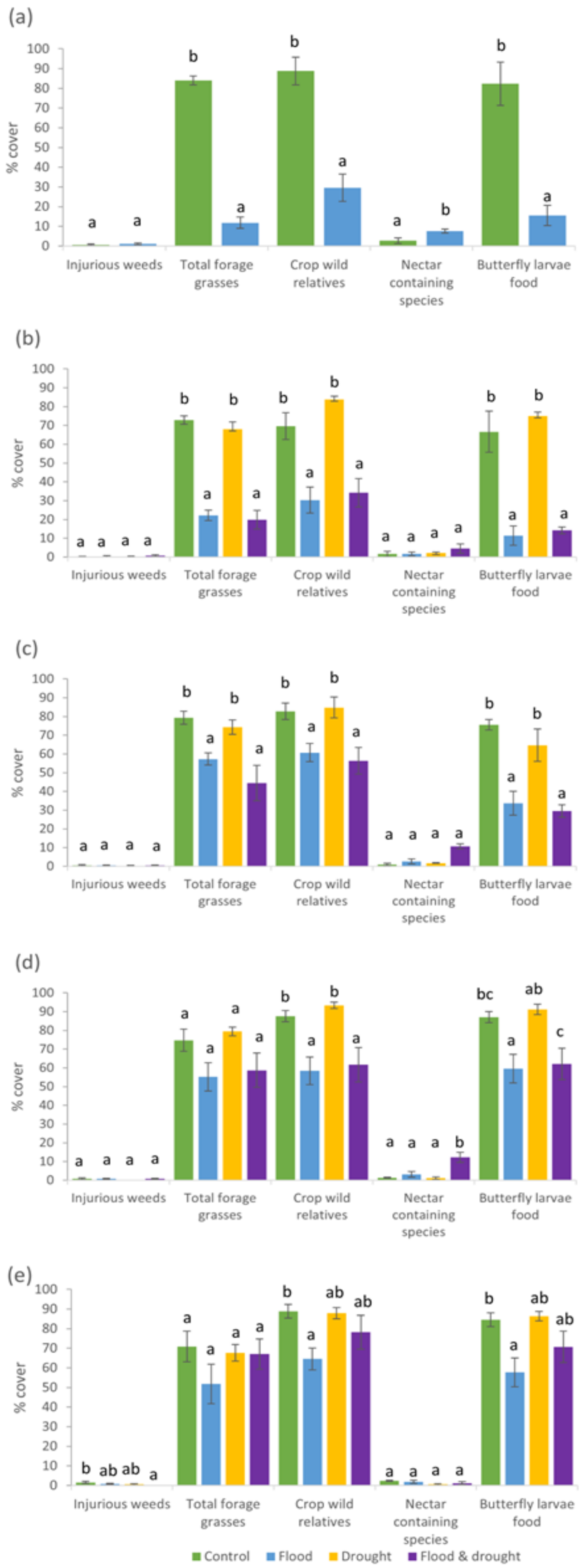

(a)
(b)
(c)
(d)
(e)
% cover
Injurious weeds
Total forage grasses
Crop wild relatives
Nectar containing species
Butterfly larvae food
Control
Flood
Drought
Flood & drought

Figure 2

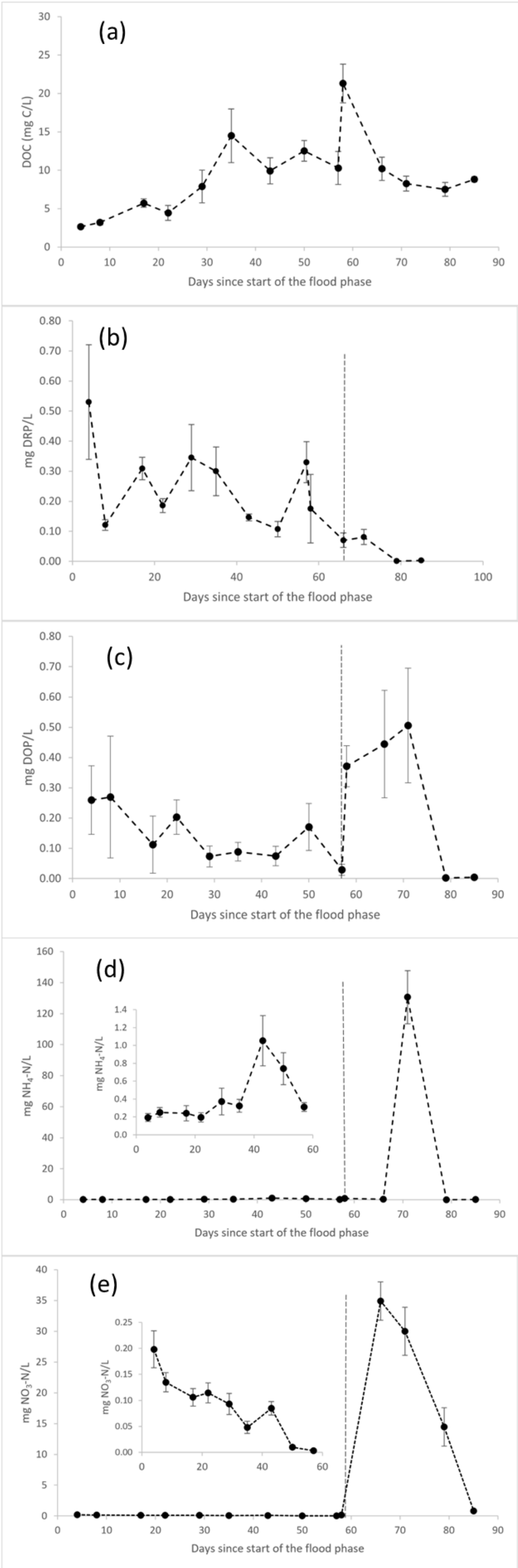

(a)
DOC (mg C/L)
Days since start of the flood phase
(b)
mg DRP/L
Days since start of the flood phase
(c)
mg DOP/L
Days since start of the flood phase
(d)
mg NH_4-N/L
mg NH_4-N/L
Days since start of the flood phase
(e)
mg NO_3-N/L
mg NO_3-N/L
Days since start of the flood phase

Figure 3

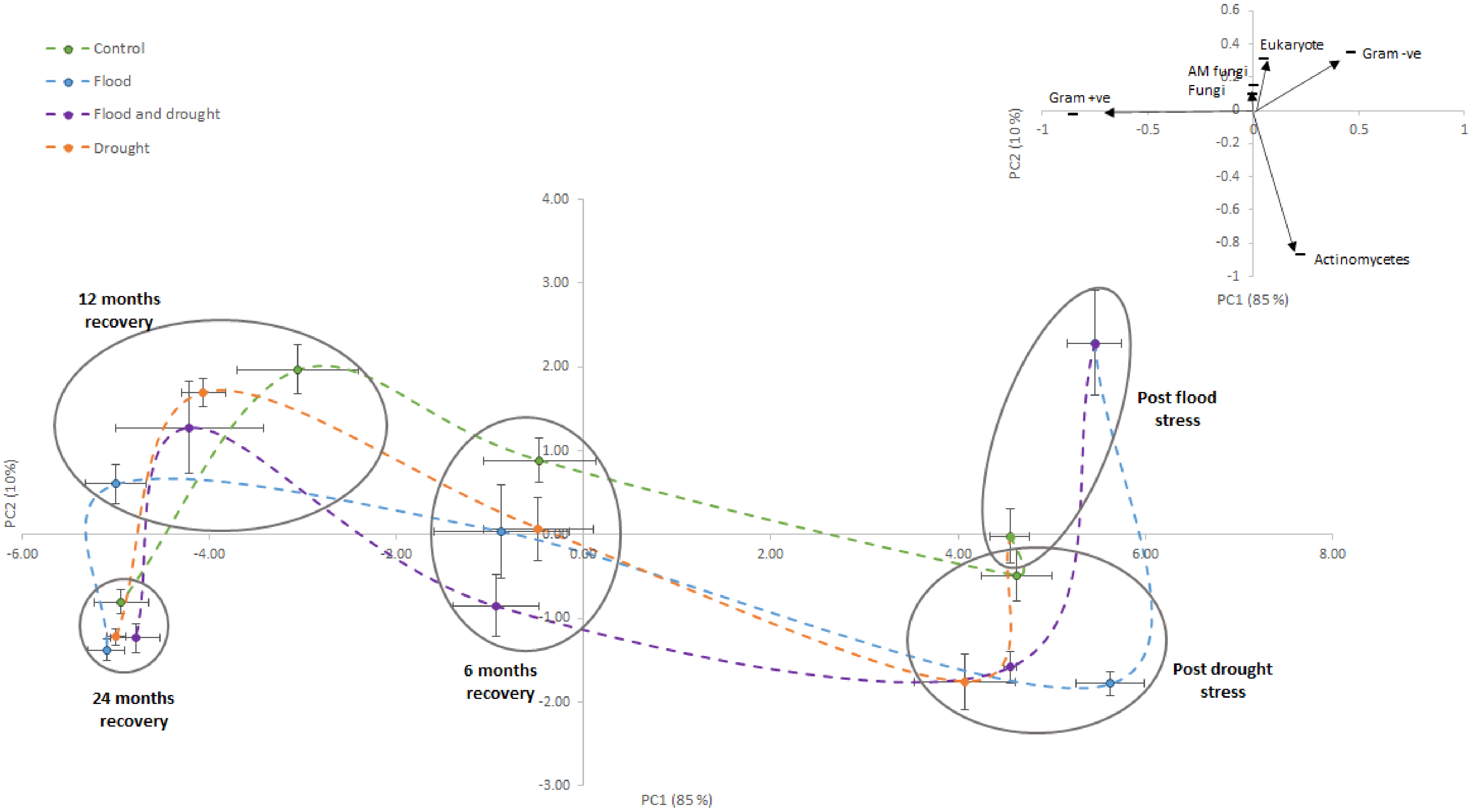
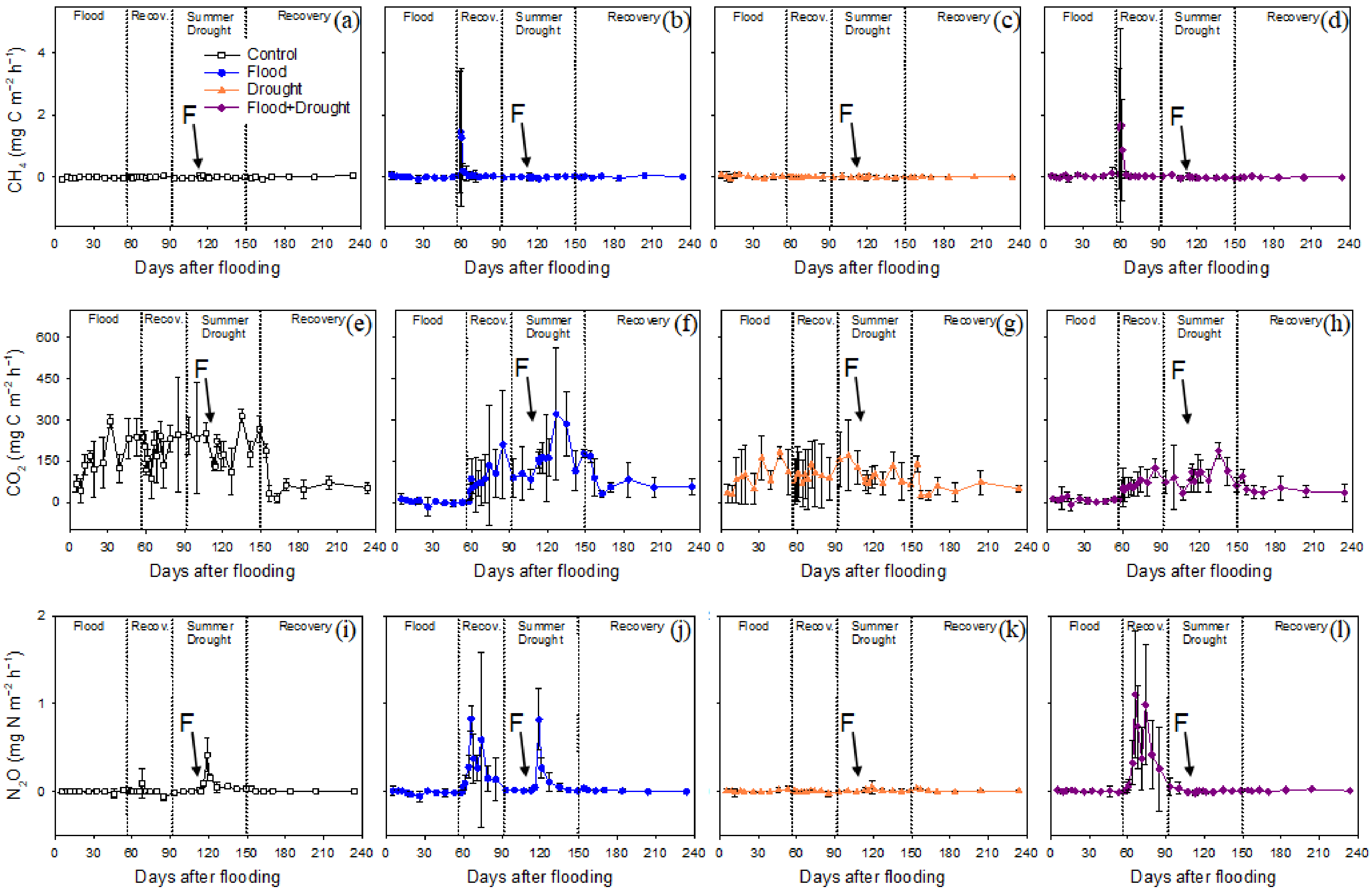

Control
Flood
Flood and drought
Drought
12 months recovery
6 months recovery
24 months recovery
Post flood stress
Post drought stress
PC1 (85 %)
PC2 (10%)
Eukaryote
Gram -ve
AM fungi
Fungi
Gram +ve
Actinomycetes
PC2 (10 %)
PC1 (85 %)

Figure 4

1176



Flood
Recov.
Summer Drought
Recovery
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
(j)
(k)
(l)
Control
Flood
Drought
Flood+Drought
F
CH4 (mg C m-2 h-1)
CO2 (mg C m-2 h-1)
N2O (mg N m-2 h-1)
Days after flooding
0
30
60
90
120
150
180
210
240

Figure 5