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RESEARCH ARTICLE

Resistance–recovery trade-off of soil microbial communities under altered rain regimes: An experimental test across European agroecosystems

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Abstract

1. With the increased occurrence of climate extremes, there is an urgent need to better understand how management strategies affect the capacity of the soil microbial community to maintain its ecosystem functions (e.g. nutrient cycling).
2. To address this issue, intact monoliths were extracted from conventional and ecological managed grasslands in three countries across Europe and exposed under common air condition (temperature and moisture) to one of three altered rain regimes (dry, wet and intermittent wet/dry) as compared to a normal regime. Subsequently, we compared the resistance and recovery of the soil microbial biomass, potential enzyme activities and community composition.
3. The microbial community composition differed with soil management and rain regimes. Soil microbial biomass increased from the wetter to the dryer rain regime, paralleling an increase of available carbon and nutrients, suggesting low sensitivity to soil moisture reduction but nutritional limitations of soil microbes. Conversely, enzyme activities decreased with all altered rain regimes.
4. Resistance and recovery (considering absolute distance between normal and altered rain regime) of the microbial communities depended on soil management. Conventional-intensive management showed higher resistance of two fundamental properties for nutrient cycling (i.e. bacterial biomass and extracellular enzyme activities) yet associated with more important changes in microbial community composition. This suggests an internal community reorganization promoting biomass and activity resistance. Conversely, under ecological management bacterial biomass and enzyme activities showed better recovery capacity, whereas no or very low recovery of these properties was observed under conventional management. These management effects were consistent across the three altered rain

regimes investigated, indicating common factors controlling microbial communities' response to different climate-related stresses.

5. *Synthesis and applications.* Our study provides experimental evidence for an important trade-off for agroecosystem management between (a) stabilizing nutrient cycling potential during an altered rain regime period at the expense of very low recovery capacity and potential long-term effect (conventional sites) and (b) promoting the capacity of the microbial community to recover its functional potential after the end of the stress (ecological sites). Thus, management based on ecologically sound principles may be the best option to sustain long-term soil functioning under climate change.

KEYWORDS

bacteria, copiotrophs, drought, extracellular enzyme, fungi, oligotrophs, PLFA, resilience

1 | INTRODUCTION

With the increased occurrence of extreme climate events (Huntington, 2006; IPCC, 2014), there is an urgent need to better understand how management strategies affect the capacity of natural and agricultural ecosystems to maintain their state and function under altered climate. Following Oliver et al. (2015), this capacity of ecosystems to deal with environmental stress (sometime referred to as overall resilience, see Hodgson et al. (2015) and Mori (2016) for recent discussions on resilience terminologies) can be decomposed in the ecosystem resistance, that is the capacity to maintain its state during stress, and the recovery (also sometimes called 'engineering resilience'), which refers to the capacity to recover after the end of the stress (Hodgson et al., 2015; Ingrisch & Bahn, 2018; Oliver et al., 2015). Although soil microbes underpin carbon and nutrient cycling in ecosystems (Bender et al., 2016; de Vries & Bardgett, 2012; Nannipieri et al., 2003), drivers of the microbial resistance and recovery are still poorly understood (Bardgett & Caruso, 2020; de Vries & Shade, 2013).

Life-strategy (strategy hereafter) concepts in microbial ecology might shed light on the factors that control microbial community resilience (Allison & Martiny, 2008; de Vries & Shade, 2013; Krause et al., 2014; Lavorel & Garnier, 2002; Malik et al., 2019; Piton, Legay, et al., 2020; Wallenstein & Hall, 2012). The copiotrophic-oligotrophic strategy continuum (Fierer et al., 2007), equivalent to *r*-*K* strategy, could help classifying soil microbes according to their traits and resilience under climate change (de Vries & Griffiths, 2018; de Vries & Shade, 2013). Microbes with an oligotrophic strategy are characterized by low growth rate but high resistance to environmental stress, whereas copiotrophic microbes present opposite traits with low stress resistance but high growth rate, favouring recovery after a stress period (de Vries & Griffiths, 2018; de Vries & Shade, 2013). Thus, theory predicts a resistance-recovery trade-off along the copiotrophic-oligotrophic strategy continuum (Pimm, 1984).

Drought effects on soil microbial communities have been extensively studied (see meta-analyses of Canarini et al. (2017) and Ren et al. (2018)), but many alternative patterns of rain regimes are predicted to occur more frequently with climate change and these are still under-investigated (e.g. heavy and intermittent rainfall regimes). This knowledge gap greatly limits our capacity to assess and predict the effects of climate change on microbial communities and ecosystems (de Vries & Griffiths, 2018). Moreover, the extent to which soil microbial communities are impacted by, and can recover from climatic stresses may differ substantially between soils under different management treatments and these interactions are still poorly understood (de Vries et al., 2012, 2018; Fuchslueger et al., 2019; Karlowsky, Augusti, Ingrisch, Hasibeder, et al., 2018; Piton, Legay, et al., 2020). It is known that conventional soil management has a strong impact on microbial community composition and functioning, resulting in a decline in soil biodiversity and biomass (de Vries et al., 2013; Tsiafouli et al., 2015). As an alternative to conventional agriculture, ecological intensification of agriculture has been proposed, on the premise that anthropogenic inputs can be replaced by promoted biodiversity and biological processes, enhancing ecosystem functioning and resilience (Bender et al., 2016; Bommarco et al., 2013). To achieve such ecological intensification of agriculture, there is an urgent need for more studies comparing ecosystem functioning between conventionally and ecologically (i.e. based on ecologically sound principles) managed fields. An ecological system such as an organic agroecosystem can promote soil organic matter content (Garcia-Palacios et al., 2018; Gattinger et al., 2012), microbial abundance and activity (Lori et al., 2017), taxonomic diversity (Mäder et al., 2002) and arbuscular mycorrhizal fungal (AMF) colonization (Mäder et al., 2000). Lower mineral N inputs and higher organic inputs usually used in ecological systems can also modify soil microbial community composition, potentially selecting for higher fungal relative to bacterial abundance and affecting species composition within bacterial and fungal groups (Bossio et al., 1998; de Vries et al., 2006; Hartmann et al., 2015).

Managed grasslands are very common in agricultural landscapes (Lemaire et al., 2005), such as permanent grassland or sown grasslands included in crop rotation, with large variability of management intensity. Few studies have assessed the effect of grassland management on soil microbial community resilience (Cole et al., 2019; de Vries et al., 2012; Jurburg, Natal-da-Luz, et al., 2017; Karlowisky, Augusti, Ingrisch, Hasibeder, et al., 2018), and it is still not clear how conventional and ecological systems might differ in their resilience capacity. Here, we used a cross-country experiment (France, Switzerland and Portugal; Figure S1) with intact monoliths brought to a common environment to test how contrasting management (conventional vs. ecological) affects soil microbial properties and their resistance and recovery to different altered rain regimes (dry, wet and intermittent wet/dry as compared to a control 'normal' level).

Optimization of ecosystem functions (e.g. productivity and nutrient cycling) is usually the first target of agroecosystem management strategies (Oliver et al., 2015). Thus, in this study, we focus on the response of two microbial properties fundamental for nutrient cycling. First, soil microbial biomass was measured to quantify the size of the microbial compartment playing fundamental roles in C, N and P mineralization and stabilization in soil (Kallenbach & Grandy, 2011; Li et al., 2019; Liang et al., 2011; Manzoni & Porporato, 2009). Second, the potential of microbial communities to decompose soil organic matter was also assessed by measuring the potential activities of seven extracellular enzymes degrading C-, N- or P-rich substrates (Nannipieri et al., 2018). In addition, indicators of copiotrophic copiotrophic-oligotrophic oligotrophic strategies (Fungal:Bacterial, Gram-positive:Gram-negative biomass ratio (de Vries & Shade, 2013) and mass-specific enzyme activity (Piton, Legay, et al., 2020) as well as soil microbial community composition (phospholipid fatty acids method) resilience were measured to investigate mechanisms underlying the resilience of the two main properties describe above.

We hypothesized that:

Hypothesis 1 *Ecological and conventional managed soils differ in microbial community composition and traits (mass-specific enzyme activity), with more oligotrophic communities in ecological managed soils.*

Hypothesis 2 *A resistance-recovery trade-off exists, with ecological soil microbial community properties (biomass, activity and composition) having higher resistance but lower recovery compared to conventional microbial communities, for all climate change-induced rain regimes.*

2 | MATERIALS AND METHODS

2.1 | Experimental design and setup

The experiment was setup using terrestrial model ecosystems (TMEs), which are intact soil monoliths defined as controlled, reproducible

systems that attempt to simulate processes and interactions in a portion of the terrestrial ecosystem (Gillett & Witt, 1980; Schäffer et al., 2008). TMEs were extracted at three sites, with for each site eight different plots in different fields, across Europe in October 2015. The three sites were selected across an European Network of ecological intensification sites (Garcia-Palacios et al., 2018). At each site, we selected pairwise comparisons of fields with long-term history (>20 years) under ecological versus conventional management. Ecological management of each pair was selected for their lower N inputs and their lower soil disturbance compared to conventional management at the same site (Table 1). In all selected ecological management regimes, synthetic fertilizers were never used and all meet organic farming requirements. All sites were cultivated for forage at the sampling time: permanent and sown mountain grasslands in France (Vercors), clover-grass in an arable cropping system in Switzerland (Therwil), and permanent and sown grasslands in an agroforestry system in Portugal (Montemor-o-Novo). Detailed information and characterization of the different sites and plots with contrasting management and applied practices are shown in Table 1. In all, 40 TMEs (40 cm depth × 16.5 cm diameter) encased in HDTPE tubes were collected per country (total of 120 TMEs). More precisely, four plots were sampled for each management (ecological and conventional) in each country, totally eight plots per country (Figure S1). Within each of these plots, five TMEs were extracted. Each TME from one plot served as one replicate for each of four different rain regimes and one TME served for collecting T0 data of the soil from that location (see below). The TMEs were collected as described by Knacker et al. (2004), using a retroexcavator and a special stainless-steel extractor.

After sampling, TMEs were transported in a refrigerated truck to the Laboratory of Soil Ecology and Ecotoxicology of Coimbra University (Portugal). Upon arrival, TMEs from the three countries were randomly placed inside special carts creating a temperature gradient between the lower (12–14°C) and the upper (20°C) part as described by Ng et al. (2014). These carts were placed during the entire experiment inside a climate chamber with controlled air humidity (≈60%) and temperature (20°C±), and with a 16 hr:8 hr light:dark photoperiod. Decagon moisture sensors were used to monitor soil moisture in the upper 20 cm layer of each TME three times a week (Mondays, Wednesdays and Fridays) during the entire duration of the experiment (433 days).

Artificial rainwater (Velthorst, 1993) was used to water the TMEs three times a week throughout the experiment. During the first 81 days, the amount of water was adjusted to obtain a soil moisture in the upper 20 cm layer equivalent to 50%–60% of the maximum water holding capacity (WHC_{max}) of the soil from each site where TMEs were collected (Figure 1). These specific values of soil moisture (50%–60% WHC_{max}) are considered as the 'Normal' rain regime for each country. After this acclimation period under 'Normal' rain regime, one TME of each plot origin was sampled to characterize initial soil biotic and abiotic parameters (T0). This first sampling was a destructive sampling, conducted on one TME per plot ($N = 32$, 96 TMEs left). The upper 10 cm of soil was sampled, sieved at 5 mm,

TABLE 1 Characterization of the field sites from which intact soil cores were collected and their contrasting management. MAT, Mean annual precipitation; N, Nitrogen; SOM, Soil Organic Matter; WHC_{max}, maximum Water Holding Capacity. See Lori et al. (2020) for more details

Country (coordinates)	Land use	N fertilizer (average N kg ⁻¹ ha year ⁻¹)	MAT, MAP	Texture	pH	SOM	WHC _{max}
Switzerland 47°30'N 7°33'E	Grassland in rotation	Ecological: Slurry (120) Conventional: Synthetic (140)	9.7°C, 791 mm	Silt/Silt Loam	5.01 (±0.12)	4.15% (±0.67)	58.91% (±1.89)
France 45°07'N 5°31'E	Mountain grassland Ecological: Permanent grassland Conventional: Sown grassland	Ecological: Cow manure (30) Conventional: Cow manure (70)	7.2°C, 1,483 mm	Sandy Loam/Loam	5.71 (±0.86)	9.34% (±2.46)	90.92% (±8.93)
Portugal 38°42'N 8°19'W	Grassland in agroforest	Ecological: None (0) Conventional: Synthetic (56)	16.5°C, 1,093 mm	Sandy Loam	4.62 (±0.35)	3.55% (±0.64)	39.18% (±4.45)

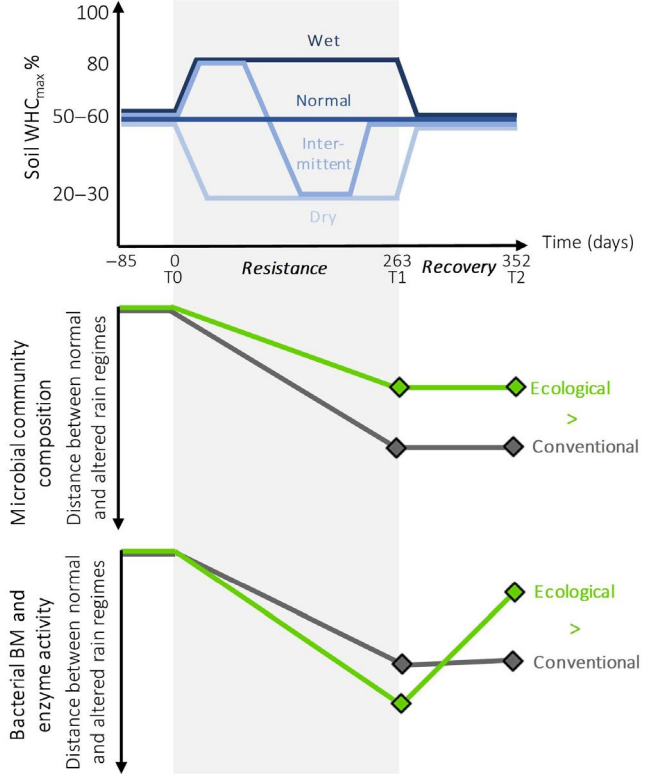


FIGURE 1 Overview of soil moisture dynamics within TMEs since change in rain regimes (at T0), adjusted according to the maximum water holding capacity (WHC_{max}) of each soil (upper panel). Observed (lower panel) resistance and recovery for soil microbial community composition, biomass and enzyme activity in ecological and conventional, described according to the distance to normal (regardless of the direction of the response) during stress period (Resistance) and after the end of stress (Recovery)

plant roots were hand-sorted and samples were stored at 4°C or -20°C for further analyses.

After this acclimation period of 81 days, four rain regimes were simulated during 263 days (Figure 1; Figure S1), with one rain regime simulated on each of the four TMEs from the 32 plots. For the Normal rain regime, soil moisture was maintained at 50%–60% of the WHC_{max}. For the ‘Dry’ rain regime, soil moisture was maintained at 20%–30% of the WHC_{max} simulating a case of severe drought. For the ‘Wet’ rain regime, soil moisture was maintained at 70%–80% of the WHC_{max} simulating a heavy rain regime. Finally, the ‘Intermittent’ rain regime consisted of the simulation of a cycle of wet (74 days), dry (125 days) and normal (64 days) rain regime. The duration of 263 days for all rain regimes was chosen because it was the time needed for this intermittent rain regime treatment to undergo a wet and a dry cycle and back to the normal level.

The exposure to the simulated rain treatments ended after 263 days at which point all TMEs were sampled using non-destructive sampling techniques (T1) so that the TMEs could be subjected to a recovery period. One soil core of 98 cm³ (5 cm diameter and 5 cm height) was collected from each TME. The soil was sieved at 5 mm, plant roots were hand-sorted and samples were stored at 4°C

or -20°C for further analyses. Pure sand encased into a small plastic cylinder was used to fill the holes left after sampling.

All TMEs were then set again to Normal rain regime for 89 days followed by a last destructive sampling (T2) as described for T0 (upper 10 cm).

At the beginning of the experiment, each TME was lined with a 2 cm layer of crop residues from the specific field where TMEs were collected. During the entire experiment, the vegetation of each TME was monitored via cutting the vegetation down to 5 cm (13 harvests in total) for all TMEs at the same time whenever the height in one treatment reached 20 cm. Soil leachates were collected throughout the experiment at the bottom of the TMEs.

2.2 | Soil abiotic properties, microbial community and enzyme activities

The following soil abiotic properties were measured on soil collected at T0, T1 and T2 as explained in more detail in Appendix S1: moisture, pH, organic matter content, total C, dissolved organic C, total N, dissolved mineral and organic N.

Microbial biomass and community composition were characterized by analysis of phospholipid fatty acids (PLFA) according to Frostegård et al. (1993). PLFAs was then associated to different microbial groups (Fungi, Bacteria, Gram-positive and Gram-negative bacteria and Actinobacteria) and converted to microbial biomass C (Appendix S1 for details).

Potential extracellular enzymes activity (EEA) of seven enzymes involved in the degradation of C-rich substrates [α -Glucosidase (AG), β -1,4-Glucosidase (BG), β -D-Cellobiosidase (CB) and β -Xylosidase (XYL)], N-rich substrates (β -1,4-N-acetylglucosaminidase (NAG) and leucine aminopeptidase) and P-rich substrates [phosphomonoesterase (PHOS)] were estimated using standardized fluorimetric techniques (see Appendix S1 for details). Potential enzyme activities were expressed as $\text{nmol g soil}^{-1} \text{ hr}^{-1}$. Then, enzymes activities were summed to represent enzyme activities degrading C-rich ($\text{EEC} = \text{AG} + \text{BG} + \text{CB} + \text{XYL}$), N-rich ($\text{EEN} = \text{LAP} + \text{NAG}$) and P-rich substrates ($\text{EEP} = \text{PHOS}$) and total enzyme activities ($\text{EEA} = \text{EEC} + \text{EEN} + \text{EEP}$; Bell et al., 2013; Piton, Foulquier, Martínez-García, Legay, Hedlund, et al., 2020; Piton, Legay, et al., 2020).

2.3 | Statistical analyses

Redundancy analyses (RDA) were used to assess treatment effects on the microbial community composition (relative abundance of the 27 individuals PLFAs) and the soil bulk abiotic and microbial properties. First, a RDA including the three sampling times was conducted to test management, rain regime, sampling time and their interactions. Second, RDAs were conducted for each sampling time separately if significant interaction between treatments and sampling time were detected. Country was used as condition factor in all RDAs to control for inter-country variations. RDAs were first tested

for overall significance and then for each term using the ANOVA. `cca()` function (Oksanen et al., 2011). Variance partitioning was used to assess the relative proportion of soil microbial community composition explained by each factors using the `varpart()` function (Oksanen et al., 2011).

The effects of management (T0, T1 and T2) and rain regime (T1 and T2) on soil and microbial properties (biomass, activity, F:B, GP:GN and mass-specific EEA) were tested separately for T0, T1 and T2 using linear mixed effect models with rain regime and management as fixed effects, country and plot as random effects. Plot was nested in management nested in country within the random structure to take into account the nested design of the experiment (Crawley, 2005).

To represent microbial community stability (absolute change in response to altered rain regime, whatever the direction, Figure 1), two types of indices were used. For microbial biomass and activities (univariate properties with high and low values), resistance and recovery (i.e. engineering resilience) indices from Orwin and Wardle (2004) were calculated as follows:

$$\text{Resistance}_{ij} = 1 - \frac{2|D_{T1ij}|}{(C_{T1i} + |D_{T1ij}|)},$$

$$\text{Recovery}_{ij} = \frac{2|D_{T1ij}|}{(|D_{T1i}| + |D_{T2ij}|)} - 1,$$

where Resistance_{ij} and Recovery_{ij} are, respectively, the Resistance and Recovery of plot i ($N = 72$) under altered rain regime j (Dry, Wet or Intermittent), with C_{T1i} the value observed in control (normal rain regime) TMEs from the plot i , at the end of the stress period (T1), D_{T1ij} and D_{T2ij} the differences between the value of the TME under altered rain regime j and its associated control (i.e. TME at normal rain regime) from the same plot origin (i) at the end of the stress period (D_{T1ij}), or at the end of the recovery period (D_{T2ij}). These indices are bounded between -1 and $+1$. A value of $+1$ indicates full resistance or recovery (identical value between control and stressed soil). The value 0 for the resistance index indicates either a 100% reduction or increase in the soil under altered rain regime. A value of 0 for the recovery index indicates that the soil previously under altered rain regime is the same distance away from the control as was when the altered rain regime ended. This recovery index from Orwin and Wardle (2004) is impact-normalized and can be seen as the reciprocal of the recovery time (Ingrisch & Bahn, 2018), with time necessary for full recovery decreasing with increasing recovery index value. This 'recovery index' is called 'resilience index' by Orwin and Wardle (2004) because they used a different terminology.

For microbial community composition, different indices to capture resistance and recovery were used. Microbial community composition resistance was measured as Bray–Curtis similarities between microbial community composition (relative abundance of the 27 individual PLFAs) from TMEs under altered rain regime at T1 and their associated control as proposed by de Vries and Shade (2013).

This index is bounded between 0 and 1, with similarity of 1 meaning maximum resistance. To represent recovery of microbial community composition, we used a modified version of the index proposed by de Vries and Shade (2013) by normalizing the community composition recovery by the change initially caused by the stress:

$$\text{Composition - recovery}_{ij} = \frac{(S_{T2i} - S_{T1i})}{(1 - S_{T1i})},$$

where $\text{Composition-recovery}_{ij}$ is the recovery of plot i ($N = 72$) under altered rain regime j (dry, wet or intermittent), with S_{T1ij} and S_{T2ij} the Bray–Curtis similarity between the community composition of the TME under altered rain regime j and its associated control from same plot origin (i) at the end of the stress period (S_{T1ij}), or at the end of the recovery period (S_{T2ij}). This index represents the proportion of the similarity loss during the stress that was recovered between T1 and T2. This way our recovery calculation for community composition was consistent with the impact-normalized recovery index of Orwin and Wardle (2004) used for microbial biomass and activities.

To assess if soil microbial community stability differed between rain regimes and managements, their effects on resistance and recovery indices were tested using mixed effect models with country as random factor. The potential associations between soil microbial community strategy and the resistance and recovery of their biomass, activity and composition were also tested. To do so, mixed effect correlations were conducted between soil microbial community indicators of the copiotrophic–oligotrophic continuum (F:B, GP:GN ratios and mass-specific activities) measured before the stress period (T0) and the resistance and recovery indices of the associated grassland ($N = 24$) to altered rain regimes.

3 | RESULTS

3.1 | Treatments effects

Across all sampling times of the experiment, the microbial community composition (relative abundance of 27 individual PLFAs) was significantly affected by management, rain regime and sampling time but not by their interactions (Table 2). Bulk abiotic and microbial properties were significantly affected by rain regime, sampling time and their interaction (Table 2). The RDA conducted for each sampling time separately to investigate this interaction did not detect any significant effect of treatments at T0 ($RDA_{\text{bulk}}: p = 0.69$) and T2 ($RDA_{\text{bulk}}: p = 0.70$). However, at T1, that is, the end of the stress period, bulk soil properties were affected significantly by rain regime ($RDA_{\text{bulk}}: p < 0.001$). The biplot presenting this treatment effect on bulk soil abiotic and microbial properties separated the rain regimes well along the first axis (Figure 2), with coordinates along this axis also inversely related with the rain gradient: wet, normal and intermittent, and dry. With decreasing soil moisture along this axis, we observed an increase in resources (DOC, DMN, DON, PO_4 , SOM, TC and pH) and microbial biomass (total, fungal, bacterial and

TABLE 2 Effects of management, rain regime, sampling time and country (random factor) on microbial community composition and soil bulk properties. Effects were assessed using RDA and variance partitioning. Variance explained for interaction rows represent the shared explanatory power of the factors included in the interaction

	Community composition		Soil bulk abiotic and microbial properties	
	RDA p value	Variance explained (%)	RDA p value	Variance explained (%)
Management (M)	$p < 0.01$	1	0.253	0
Rain regime (RR)	$p < 0.001$	8	$p < 0.001$	1
Sampling time (ST)	$p < 0.001$	3	$p < 0.001$	10
M \times RR	0.974	0	0.869	0
M \times ST	0.732	0	0.815	0
RR \times ST	0.168	0	$p < 0.01$	3
M \times RR \times ST	0.903	0	1	0
Random factor (Country)		22		36

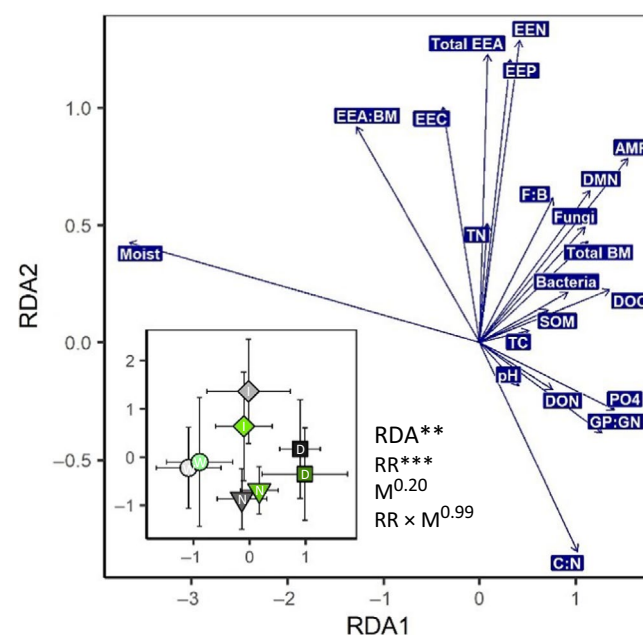


FIGURE 2 Redundancy analysis ordination biplots representing the rain regime and management effects on soil bulk abiotic and microbial properties at the end of the stress period (T1). Ordinations were corrected for variations of soil origin between countries. Points and error bars (small panel) represent means and 95% confidence interval for the treatments coordinates on the first and second axes of the RDA respectively. Point shapes represent the different rain regimes: Circle(W) = Wet, triangle(N) = Normal, diamond(I) = Intermittent, Square(D) = Dry. Grey points = Conventional management, Green points = Ecological management. Significance of the overall RDA and of each term are presented with RDA = overall significance, RR = Rain regime, M = Management, ** = $p < 0.01$, *** = $p < 0.001$. Bacteria = Bacterial biomass-C, Fungi = Fungal biomass-C. See text for other abbreviations

TABLE 3 *p* values associated with the effects of rain regime (RR) and management (M) on soil microbial community resistance and recovery indices. Bold *p* values are significant (<0.05). BM = Biomass-C, AMF = Arbuscular mycorrhizal fungi, EEC, EEN, EEP = Extracellular enzyme activities degrading C-, N- and P-rich substrates, respectively, Total EEA = EEC + EEN + EEP

	Resistance index			Recovery index		
	Rain regime	Management	RR × M	Rain regime	Management	RR × M
Bacterial BM	0.07	0.02	0.73	0.31	0.00	0.48
Fungal BM	0.44	0.51	0.26	0.43	0.46	0.56
AMF BM	0.35	0.51	0.56	0.16	0.81	0.10
Total BM	0.72	0.65	0.55	0.63	0.23	0.34
EEC	0.72	0.05	0.66	0.52	0.05	0.90
EEN	0.81	0.46	0.96	0.73	0.27	0.66
EEP	0.75	0.16	0.51	0.66	0.04	0.40
Total EEA	0.22	0.07	0.88	0.08	0.01	0.11
Community composition	0.61	0.03	0.73	0.34	0.15	0.56

AMF biomass) associated with an increase in F:B and GP:GN ratios. The second axis discriminated the Normal rain regime from the altered ones (wet, dry and intermittent) and was mostly associated with a decrease in enzyme activities (total EEA, EEC, EEN, EEP and EEA:BM) under altered rain regimes. Responses of each bulk soil abiotic and microbial property to the treatments are detailed in the Supporting Information (Tables S1–S2; Figures S3–S5).

3.2 | Resistance and recovery indices response to rain regimes and management

Resistance and recovery indices did not differ between rain regimes (Table 3), indicating similar effects of the three altered rain regimes (dry, wet and intermittent) on the microbial community resilience as compared to the normal rain regime (absolute response regardless of the direction). In contrast, management influenced resistance and recovery of several parameters of the microbial community (Table 3). Resistance of microbial community composition was higher in ecological soil compared to conventional, whereas no difference was found for microbial community composition recovery (Figure 3). A different pattern was observed for bacterial biomass and enzyme activities, since ecological microbial communities showed lower resistance for bacterial biomass and EEC compared to conventional systems (Figure 4). Opposite patterns were observed for recovery with microbial communities of ecological systems showing higher recovery for bacterial biomass, EEC, EEP and total EEA than microbial communities of conventional systems (Figure 4). Soil abiotic properties resistance and recovery indices were not significantly affected by rain regime and management (Table S3).

Resistance and recovery indices were poorly related with the investigated indicators of copiotrophic–oligotrophic continuum (Tables S3–S4) with no consistent correlation observed across rain regimes. Community composition resistance to intermittent rain regime increased with mass-specific activity (EEA:BM) and marginal positive associations were observed for biomass C resistance with GP:GN ($p = 0.07$) and mass-specific activity ($p = 0.10$). For

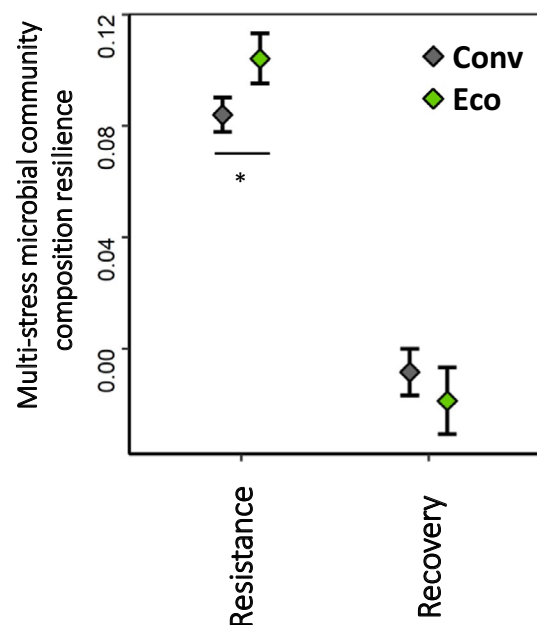


FIGURE 3 Effect of management on microbial community composition resistance and recovery in response to different rain regimes. Resistance was calculated as Bray–Curtis similarity of the microbial community composition between altered rain regime samples and their associated control (Normal rain regime); recovery was calculated as the proportion of the Bray–Curtis similarity loss during the stress and recovery between T1 and T2. All altered rain regimes are plotted together since no interaction between the different rain regimes and management was detected (Table 3). Mean \pm standard error ($n = 36$) from mixed effect model using country as random factor. Black diamonds = Conventional management, Green diamonds = Ecological management. Star indicates significant difference between management according to Tukey's post hoc test ($p < 0.05$)

recovery indices, biomass C recovery to wet rain regime increased with GP:GN, while community composition recovery after the intermittent rain regime was positively associated with GP:GN and F:B ratios (Tables S3–S4).

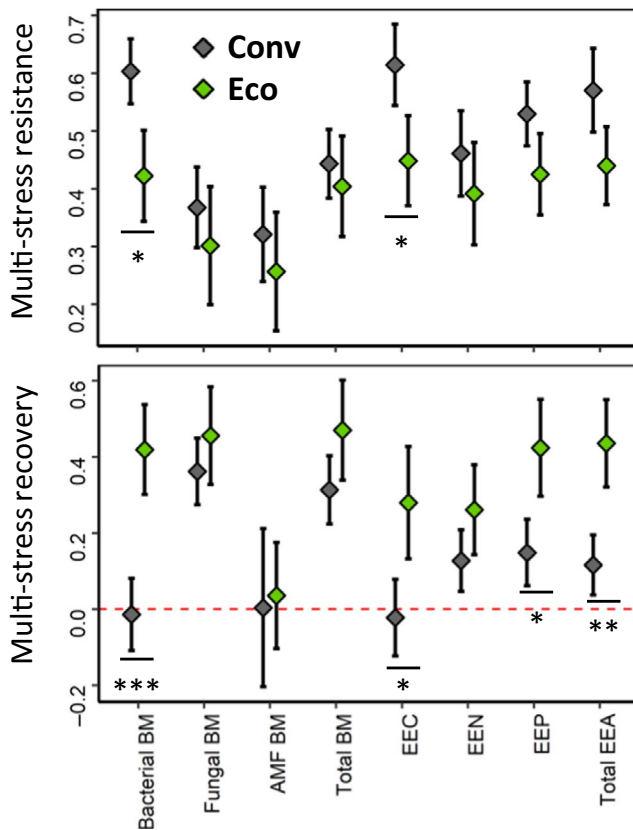


FIGURE 4 Effect of management on multi-stress resistance and recovery of soil microbial communities, calculated following Orwin and Wardle (2004). All altered rain regimes are plotted together since no interaction between rain regime and management was detected (Table 3). Mean \pm SE ($n = 36$) from mixed effect model using country ($n = 3$) as random factor. Grey diamonds = Conventional management, Green diamonds = Ecological management. Stars indicate significant difference between management treatments according to Tukey's post hoc test (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$). Horizontal red dashed line on recovery plot emphasizes the value of zero of the Orwin and Wardle (2004) index, with values under this threshold indicating no evidence for a recovery, that is, difference between disturbed and controlled community still as important after recovery period as it was at the end of the simulated stresses). BM = Biomass-C, AMF = Arbuscular mycorrhizal fungi, EEC, EEN, EEP = Extracellular enzyme activities degrading C-, N- and P-rich substrates, respectively, Total EEA = sum of EEC, EEN and EEP

4 | DISCUSSION

4.1 | Limitations of the approach

We hypothesized more oligotrophic communities in ecological managed soils, based on the rationale of lower N input compared to conventional management (Table 1). While we observed distinct microbial community compositions between management treatments (see Section 4.3), this was not associated with a modification of the indicators of copiotrophic–oligotrophic strategy assessed in this study (F:B, GP:GN biomass ratio and mass-specific enzymatic activity). Moreover,

we did not find a general association between our indicators of copiotrophic–oligotrophic strategy and our microbial resistance and recovery indices. This suggests that such indicators of microbial strategy might only be relevant to explain difference of ecosystem functioning, resistance and recovery from soils that are more contrasting in their characteristics than our soils, for example, with larger differences in nutrient inputs (Bardgett et al., 1996; Cole et al., 2019; de Vries & Bardgett, 2012; de Vries et al., 2006, 2012; Piton, Legay, et al., 2020). Thus, a deeper investigation of microbial community composition and traits will be necessary to compare less contrasting systems such as the conventional and ecological systems of our study.

Our experimental conditions were designed to isolate the rain regime effects from other environmental changes. Thus, it is important to note that other factors acting under field conditions were controlled. First, the continuation of the field fertilization and plant harvesting practices from the original plots where the TMEs were extracted were not mimicked during our experiment. This may have contributed to the absence of a management effect on soil nutrients and copiotrophic–oligotrophic indicators, although one would expect to see this distinction still at T0 unless effects are transient and quickly fade after nutrient applications. Second, temperature was kept constant in our experiment, whereas rain and temperature regimes often covary in the field and can have combined effect on the soil microbial community (Bérard et al., 2015).

4.2 | Effect of rain regimes on soil microbial community composition, biomass and related enzyme activities

Within TMEs from each country, microbial community composition and biomass mostly followed the gradient of rain intensity and moisture imposed during our experiment (Figure 2). Interestingly, microbial biomass of all microbial groups was inversely related with the moisture gradient, with higher biomass under dryer conditions which was also associated with higher nutrient and C availability. In the same experiment, Lori et al. (2020) showed the inverse response for plant growth and N uptake, increasing along the rain intensity gradient. These findings indicate a higher sensitivity of plants to water limitation compared to the microbes that seemed more limited by the availability of C and nutrients in the soil. Thus, dryer conditions might have reduced plant nutrient uptake capacity and promoted rhizodeposition, increasing nutrient and C availability, thus inducing a bottom-up stimulation of microbial biomass build-up (Preece & Peñuelas, 2016; Williams & Vries, 2020). Moreover, higher sensitivity of soil fauna to dry condition compared to microbes might have released top-down control of microbial biomass (Crowther & Grossart, 2015; Crowther et al., 2015; Vestergård et al., 2015), contributing to the observed pattern.

Potential enzyme activities did not follow the same response and decreased under all altered rain regimes. In a recent metanalysis, Xiao et al. (2018) reported a very large variability in soil enzyme activities in response to water manipulation, suggesting complex controlling

mechanisms and likely context dependency. In our experiment, the response of total enzyme activity was mostly associated with variation of the activity per unit of microbial biomass (biomass-specific enzyme activity), which has been shown to be controlled by changes in microbial community composition, functional acclimation and/or evolutionary adaptation (Piton, Foulquier, Martínez-García, Legay, Hedlund, et al., 2020).

4.3 | Effect of management on soil microbial community composition

Our results show distinct microbial community compositions between soils under conventional and ecological management types (Hypothesis 1, Table 2), although this variation of community composition (detected using relative abundance of PLFAs) was small compared to the difference between countries or rain regimes. This result is consistent with previous studies from the same experiment or from the same study sites, also reporting management effect on microbial community composition using different methods (amplicon sequencing), with plant community composition, litter-P traits and fertilization types as important drivers of differences in soil microbial properties between the two management types (Hartmann et al., 2015; Lori et al., 2018, 2020). These findings add to the growing body of evidence that distinct soil microbial community compositions might play a fundamental role in the functional differences between different agroecosystems (Bender et al., 2016).

4.4 | Effect of management on soil microbial community resistance and recovery

To assess microbial community stability (absolute change in response to altered rain regime as compared to the control, whatever the direction), we calculated resistance and recovery indices (with such recovery also called resilience or engineering resilience in the literature Hodgson et al., 2015; Mori, 2016)). We compared these indices between rain regimes and management types. Our results showed that management affects the capacity of the soil microbial community to resist and recover from altered rain regimes (Hypothesis 2, Figures 1, 3 and 4).

Our results showed that microbial community composition is more resistant in ecological managed soils as hypothesized (Figure 3). Conversely, the resistance of bacterial biomass and enzymatic activity was lower for these soils (Figure 4). Thus, our results showed an inverse relationship between microbial community internal stability (PLFA relative abundances resistance) and the resistance of the biomass and activity of the whole community (two ecosystem properties). This suggests that microbial community reorganization (species turnover) might have underpinned ecosystem stability through functional compensation among species responding inversely to an environmental change (Allison & Martiny, 2008; Jurburg, Nunes, et al., 2017; Tilman, 1996). However, it is important

to note that alteration of microbial membrane composition associated with microbial physiological state changes may also have influenced PLFA relative abundances independent of community composition (Frostegård et al., 2011).

Recovery of bacterial biomass and enzymatic activity showed the opposite pattern compared to resistance, with higher recovery capacity (shorter estimated recovery time) for ecological soil compared to conventional (Figures 1 and 4). However, in contrast to enzyme activities and microbial biomass, the recovery of the soil microbial community composition was similarly low among management types (Figure 3). These findings suggest that there is not a fundamental role of community reorganization in the recovery of bacterial biomass and enzyme activity, as for resistance. It is noteworthy that recovery indices of bacterial biomass and enzyme activities under conventional management were very low with values close to zero (Figure 4). A value of zero for the recovery index indicates that difference between disturbed and controlled communities was still as important after the period for recovery as at the end of the simulated stresses (Orwin & Wardle, 2004). While we acknowledge that more than one sampling time after the end of the stress period would have been necessary to fully conclude on the recovery dynamics, these very low values of recovery indices suggest no, or very low recovery potential under conventional management.

All the management effects observed for resistance and recovery were consistent across the three applied rain regimes (Table 3). Simulated dry, wet and intermittent rain regimes were symmetric around the normal regime in our experiment (Figure 1). This symmetry might explain the similarity in the magnitude of microbial responses across rain regimes. Nevertheless, this suggests that the responses of the soil microbial communities to different environmental variations (albeit all water related) might be similarly controlled, consistent with theoretical model predictions that organisms can either promote general high stress tolerance or rapid growth under low stress, whatever the stress (de Vries & Griffiths, 2018; de Vries & Shade, 2013; Malik et al., 2019; Pimm, 1984). Thus, long-term management effects (decades) on this trade-off seem able to overrule potential difference in the resistance and recovery capacity in response to short-term (months) altered rain regimes. While we acknowledge that our data volume is limited, these results bring some first empirical evidence that management that affects microbial community resistance and recovery for one stress (e.g. drought) can have a similar effect on its resistance and recovery capacity to other climate change-induced stress (e.g. heavy rain). As both wet and dry extreme events are predicted to increase in future (Huntington, 2006), such consistency would have very important implications. Thus, we highly encourage studies investigating simultaneously the capacity of microbial communities to respond to several climatic stresses (in terms of type and/or temporal dynamics), across ecosystems and climates, to further assess if some general drivers of microbial community and ecosystem responses to climate change exist.

To conclude, our results support a general resistance–recovery trade-off (de Vries et al., 2012; Karlowsky, Augusti, Ingris, Hasibeder, et al., 2018; Pimm, 1984; Piton, Legay, et al., 2020) for

bacterial biomass and enzyme activity. This trade-off seems associated with distinct capacity of communities to reorganize their species and/or membrane compositions. We hypothesized that the main driver of this trade-off was the difference in microbial community composition we observed, associated with functional differences which we could not detect with our approach. Isotopic approaches (e.g. Canarini et al., 2020; Karlowsky, Augusti, Ingrisch, Hasibeder, et al., 2018) will be necessary to fully test such potential link between distinct responses of overall communities and functional differences among their constituents. Meta-omics approaches (Malik et al., 2019, 2020) will further help to elucidate the taxa and traits driving these differences. We acknowledge that other properties not measured in our study might have also contributed to this management effect. Our ecological systems (excepted the Swiss site) had higher abundance of forbs (Lori et al., 2020) which may have had reduced resistance but increase recovery of C transfer to soil microbes in response to the different rain regimes, compared to our conventional systems which were more grass dominated (Karlowsky, Augusti, Ingrisch, Akanda, et al., 2018; Karlowsky, Augusti, Ingrisch, Hasibeder, et al., 2018), and this may have triggered the differential responses of bacterial biomass and enzyme activity we observed. Soil structure (not assessed in this study) can also influence microbial community resistance and recovery, independently of community composition differences (Griffiths et al., 2008). For instance, distinct crop residues between ecological and conventional management (Garcia-Palacios et al., 2018) may have affected soil aggregation structure, influencing microbial community response to rain variability (Sun et al., 2017). Nevertheless, the combined management practices of ecological management appear to limit long-term effect on microbial community biomass and functioning in response to both dry, wet and intermittent altered rain regimes, by increasing recovery capacity of these fundamental properties for soil fertility. Such functional attributes of microbial communities under ecological management can have positive cascading effect on forage growth and nutrients uptakes under altered rain regimes as demonstrated in previous studies (Lori et al., 2018, 2020; Piton, Legay, et al., 2020). To sum up, management based on ecologically sound principles, typically comprising lower fertilization load, the use of organic fertilizer and more diversified plant communities from the local species pool (Bender et al., 2016; Bommarco et al., 2013; Lori et al., 2020) should be encouraged to maintain long-term soil fertility. More specific management recommendations to promote soil functioning under climate changes will require factorial experiments where specific individual treatments are being tested and to verify if and how beneficial attributes of different management systems can be combined.

5 | CONCLUSIONS

Using terrestrial model ecosystems extracted from grassland under different pedoclimatic and management conditions (Table 1), our experiment demonstrated that long-term management can have important consequences for the resistance and recovery of the

microbial community biomass, activity and composition to different short-term alterations of the rain regime. More precisely, our results suggest that compared to ecological management, conventional management can increase climate stress resistance of soil microbial properties fundamental for nutrient cycling (bacterial biomass and extracellular enzyme activities), but that this goes at the expense of a very low capacity of its microbial communities to recover these properties after the stress. Distinct microbial community compositions and community reorganization capacities seem to underpin these resistance and recovery patterns while the relative importance of these drivers needs further investigation. Future experiments would benefit of including the influence of mowing and fertilization as treatments during the incubation (controlled in this experiment), while the relative importance of the mechanisms demonstrated here will need to be also assessed in the field. Nevertheless, this study presents a potential crucial trade-off for managers between stabilizing nutrient cycling potential during an altered rain regime period or promoting a recovery of this nutrient cycling potential. Agroecosystem management strategies may need to account for such trade-offs when seeking to rely on long-term soil biological functioning to provide ecosystem services. Under unpredictable precipitation regimes, promoting soil microbial communities with recovery capacities may be the best option to sustain long-term soil functioning along with maintenance of plant productivity, and our results indicate that management based on ecologically sound principles (e.g. organic agriculture) can contribute to achieving this.

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AUTHORS' CONTRIBUTIONS

A.F., L.B., K.H., P.M.d.S., J.C.C. and G.B.D.D. designed the experiment together with other partners of the ECO-SERVE project; P.M.d.S., E.N., F.R. and P.M.d.S. carried out the experiment in the Laboratory of Soil Ecology and Ecotoxicology of the University of Coimbra; All authors participated in sampling; G.P., N.L., J.C.C., A.F. conducted the enzymatic assays; K.H. measured the PLFA. L.B.M.-G. conducted the soil chemical analyses; G.P. ran all the statistical analyses, wrote the first draft of this paper and edited it based on significant comments from A.F., L.B.M.-G., N.L., L.B., K.H., J.C.C. and G.B.D.D. All authors gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.hmgqnk9f6> (Piton, Foulquier, Martinez-Garcia, Legay, Brussard, et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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