ECOLOGY LETTERS

Ecology Letters, (2015) **18**: 612–625 doi: 10.1111/ele.12451

IDEAS AND PERSPECTIVE

Resilience vs. historical contingency in microbial responses to environmental change

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Abstract

How soil processes such as carbon cycling will respond to future climate change depends on the responses of complex microbial communities, but most ecosystem models assume that microbial functional responses are resilient and can be predicted from simple parameters such as biomass and temperature. Here, we consider how historical contingencies might alter those responses because function depends on prior conditions or biota. Functional resilience can be driven by physiological, community or adaptive shifts; historical contingencies can result from the influence of historical environments or a combination of priority effects and biotic resistance. By modelling microbial population responses to environmental change, we demonstrate that historical environments can constrain soil function with the degree of constraint depending on the magnitude of change in the context of the prior environment. For example microbial assemblages from more constant environments were more sensitive to change leading to poorer functional acclimatisation compared to microbial assemblages from more fluctuating environments. Such historical contingencies can lead to deviations from expected functional responses to climate change as well as local variability in those responses. Our results form a set of interrelated hypotheses regarding soil microbial responses to climate change that warrant future empirical attention.

Keywords

Acclimation, acclimatisation, adaptation, climate change, competition, dormancy, ecosystem function, legacy, microbial community, plasticity.

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CONSIDERING MICROBIAL DRIVERS OF SOIL PROCESSES

Broad interest in microbial responses to environmental change is largely based on the uncertainty surrounding belowground responses to global climate change. Some of that uncertainty reflects our lack of a basic mechanistic understanding for how soil microbes respond to environmental change and how those responses scale to the ecosystem level. Perhaps the largest challenge we face in developing such a framework is that the majority of available information on microbial responses to climate change is at the whole-soil or community level, reflecting the aggregate functioning of many taxa responding simultaneously to the environment. We have a limited understanding of species-level responses (e.g. Lennon *et al*. 2012) and how those scale up to function. Aggregate, community-level soil function might be sufficient for models at the ecosystem scale; alternatively, models that only consider aggregate functioning may miss dynamics related to variation among individuals or functional groups, or to diversity *per se*, that could create variability within and across sites. The scale and degree of mechanism in models required to optimise model function remains unknown (e.g. Lawrence *et al*. 2009).

Historically, ecosystem models have largely ignored explicit microbial controls, with process rates often directly proportional to pool sizes (e.g. Parton *et al*. 1988; Li *et al*. 1997). Such first-order models have nevertheless successfully simulated ecosystem processes such as soil carbon cycling at large spatial and long temporal scales (e.g. Melillo *et al*. 1995). Ecosystem process models are becoming more mechanistically sophisticated, simulating process rates as a function of both substrate and microbial biomass or enzyme pools (e.g. Sinsabaugh & Moorhead 1994; Schimel & Weintraub 2003; Wang *et al*. 2013). For example the recently developed 'CLM microbial model' explains 50% of the variation in soil carbon by explicitly simulating microbial biomass pools and decomposition via enzyme-driven, temperature-dependent Michaelis–Menten kinetics (Wieder *et al*. 2013).

A common assumption in many models is that all microbial taxa are functionally equivalent (Lawrence *et al*. 2009); this assumption arises from the idea that high microbial diversity and apparently broad distributions equate to ecological redundancy (Allison & Martiny 2008). There is also mounting evidence, however, for high beta-diversity in both bacteria (Fierer *et al*. 2009) and fungi (Öpik *et al*. 2009). Furthermore, microbial communities that differ in composition typically also realise differential function under controlled conditions, consistent with the idea of local specialisation (Strickland *et al*. 2009). Hence, improved prediction may be achieved by incorporating microbial diversity into process models. To date, this has been done via functional groups, either within or across trophic levels, and by varying traits among taxa (e.g. Allison 2012). The simplest approaches to functional groups include separate fungal and bacterial pools (Waring

et al. 2013), active and dormant states in the microbial biomass (Wang *et al*. 2014b) or generalists and specialists (Moorhead & Sinsabaugh 2006). However, because community-level function is an accumulation of individual life-history events that determine population sizes and individual activity rates, it makes sense to consider microbial community function from the standpoint of population growth and regulation.

A multitude of factors regulate populations, but resource depletion and associated competition are factors common to nearly all populations (Tilman 1986). Given that microbial soil decomposers, at least to first approximation, compete for carbon as a single limiting resource, we are confronted with Hutchinson's 'paradox of the plankton,' in which there are far more coexisting entities than limiting resources (Hutchinson 1961). What then allows for coexistence in microbial decomposer communities? An obvious hypothesis is the storage effect, where temporal variation in the environment combined with dormancy allows different players to flourish at different times (Chesson & Huntly 1997). While it is known that a storage effect can facilitate coexistence, less is known about how temporal environmental variation affects the resilience of communities to systematic environmental change and how that affects soil function.

Here, we address two aggregate, community-level functional responses that represent a range of possible responses to environmental change: resilience, in which function is maintained as expected purely based on abiotic conditions in the face of environmental change, or historical contingency, in which function depends on prior conditions or biota (Fig. 1, Box 1). We consider microbial physiological, community and evolutionary mechanisms that can impact aggregate function in biogeochemical processes, how historical contingencies can constrain those mechanisms, and how the interactions of mechanisms and constraints scale up to community-level functional responses using a simulation model.

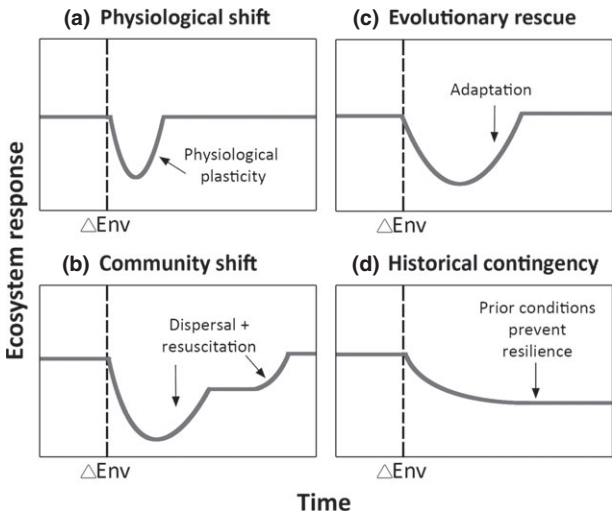

Figure 1 Microbial community-level functional responses to environmental change (ΔEnv) can show resilience (a–c) or legacies (d). Functional resilience results from acclimatisation via (a) individual-level physiological plasticity, (b) community shifts from either internal turnover or immigration, or (c) evolutionary rescue in the form of rapid adaptation to the new conditions. Legacy effects (d) occur when function deviates from expectations based on abiotic conditions. Such legacies can result from historical contingencies caused by effects of the previous environment on either microbial genetic and functional capacity, or by priority effects and biotic resistance, which can also positively feedback to each other. Here, historical contingencies are shown as a reduction in ecosystem resilience, but legacies could also result in elevated responses.

Box 1 Glossary of responses, mechanisms and constraints

Term	Definition
Acclimation	Adjustment of individual organisms to a controlled or induced change in the environment, such as in laboratory or field experiments
Acclimatisation	Adjustment of individual organisms to a natural change in the environment
Adaptation	Evolutionary process by which organisms become better suited to the environment via population genetic change resulting from natural selection
Aggregate function	Soil function resulting from sum of all activities in the soil microbial community
Historical contingency	Constraints on microbial responses created by prior conditions that result in aggregate functional responses to environmental change dependent on either previous biota or environments
Legacy	Biotic and abiotic conditions created by prior environments that persist when the environment changes
Plasticity	Degree to which an organism can change phenotype in response to a change in the environment
Priority effects	Species present before or arriving first after a change in the environment can affect the community successional trajectory or reassembly process
Recovery	Time required for an ecosystem to recover to a pre-disturbance state
Resilience	Capacity of an ecosystem to tolerate disturbance without switching to a qualitatively different state controlled by a different set of processes; here we consider resilience to translate into aggregate functional responses to environmental change that reflect purely abiotic conditions
Resistance	Degree of change in an ecosystem variable following disturbance

In the model, we link individual microbial response mechanisms to the broader question of how historical patterns of environmental variation influence the resiliency of competitively structured communities to a change in the environment. This takes the form of a simple population-based model of a microbial community vying for a single resource pool. Each of the populations is given an environmental optimum analogous to a preferred soil moisture or temperature, and the environmental value is varied through time according to a stochastic process. Using this model, we ask to what extent does historical variation in the environment influence the outcome of a systematic environmental change: is the community

resilient or is its performance highly contingent on the past environmental regime? Our intention in introducing a community model is not to present an alternative to, or improve upon, existing microbial models. Rather, we isolate a very specific mechanism related to resource competition influenced by a fluctuating environment.

ECOLOGICAL AND EVOLUTIONARY RESPONSE MECHANISMS IN MICROBIAL COMMUNITIES

Soil function can exhibit resilience to a change in the environment via acclimatisation. In plants, acclimatisation occurs largely through shifts in individual plant physiology (Atkin *et al.* 2000). In soils, however, there are several potential underlying mechanisms, as a consequence of aggregate function being driven by a diverse microbial community (Fig. 1, Box 1, Table 1). Community-level functional acclimatisation can occur in response to environmental change if functionally dominant microbial populations are generalists with broad physiological capabilities that can adjust to new conditions (Fig. 1a), if more specialised taxa with distinct functional capabilities become active from dormant pools or via the arrival of immigrants (Fig. 1b), or if the environmental perturbation leads to rapid microbial adaptation of functionally dominant microbial populations (Fig. 1c). Alternatively, legacy effects may be present whereby historical contingencies prevent functional acclimatisation, resulting in potential deviations from responses expected based purely on abiotic conditions when the environment changes (Fig. 1d). For example evolutionary specialisation to the previous environment via local adaptation could determine the degree of functional resilience to a change in the environment (Fig. 1d). Each of these mechanisms is discussed in more detail below; understanding their relative importance will allow us to be more broadly predictive about belowground responses to environmental change across the landscape.

Physiological responses

Community-level functional plasticity and acclimatisation through individual physiological changes appears to be common (Fig. 1a, Table 1) (Malcolm *et al.* 2009). At the individual level, physiological response curves to soil moisture can be taxon-specific, and both generalist and specialist strategies are found (Lennon *et al.* 2012). Yet functional plasticity does not always occur, nor is it necessarily adaptive. For example among 12 ectomycorrhizal fungi, there was a wide range of variability in respiratory acclimation across a range of temperatures, with only three isolates acclimating to higher temperature (Malcolm *et al.* 2008).

Physiological plasticity in microbial taxa may reflect a generalist strategy with regard to a given set of environmental conditions. We incorporate this concept into our modelling by assigning each population a one-dimensional environmental niche function, which determines resource assimilation rate and ultimately competitive ability. This niche function integrates to a constant value so that it either possesses a high peak and narrow tails, corresponding to a specialist, or gentle peak and broad tails, corresponding to a generalist. Taxa with broader fundamental climatic niches may have a higher probability of avoiding extinction and maintaining continuous activity as the environment changes compared to taxa with narrower environmental tolerances. However, plasticity can also be costly to maintain and can reduce fitness if environmental predictability is poor or if novel environmental conditions generate low-fitness phenotypes (Chevin *et al.* 2013). Furthermore, generalists are expected to have lower overall function compared to specialists, given observed trade-offs between, for example stress tolerance and growth rate (Lennon *et al.* 2012), optimal growth and metabolic switching (Schuetz *et al.* 2012), and growth rate and growth yield (Lipson *et al.* 2009). Based on such trade-offs, the proportion of generalists vs. specialists in the microbial community will directly affect the rate and extent of community-level functional change in response to a large change in the environment.

Shifts in community composition

Microbial community composition can play a role in both plastic and constrained soil functional responses to altered environments based on the influence of composition on ecosystem process rates (e.g. Gulledge *et al.* 1997; Strickland *et al.* 2009; Hawkes *et al.* 2011). As the environment fluctuates, rapid changes in microbial community composition can be caused by shifts in the relative abundance of taxa already present (Table 1) (DeAngelis *et al.* 2010; Cregger *et al.* 2012) via classic resource-based competitive dynamics (Tilman 1986). Alternatively, community composition can be altered by local dormancy and resuscitation or by immigration from the regional species pool (Lennon & Jones 2011; Wang *et al.* 2014b). For example in soils that experience periods of drying and rewetting, microbial communities can cycle through repeated and predictable states based on distinct resuscitation strategies of different taxa that reflect physiological traits (Fig. 1b) (Placella *et al.* 2012). Dispersal from the regional species pool may rescue local function if species sorting results in the presence of taxa best suited to the changed environment (Fig. 1b) (Van der Gucht *et al.* 2007; Lindström & Langenheder 2012). Species sorting may occur more often for environmental specialists, whereas generalists should be more likely to assemble stochastically (Langenheder & Szekely 2011).

Evolutionary processes

Microbial evolution plays a role in determining whether aggregate functional responses to environmental change are plastic or locally specialised. Adaptation to the new environment can allow populations to recover, a process termed 'evolutionary rescue' (Gonzalez & Bell 2013) (Fig. 1c, Table 1). For example evolutionary rescue was observed in yeast populations subjected to salt stress and was more likely in larger populations with prior stress exposure (Gonzalez & Bell 2013). Conversely, microbial evolutionary responses to a change in the environment may be restricted by existing local adaptation, which can inhibit selective sweeps (Dykhuizen & Dean 2004) and hinder the potential for evolutionary rescue

Table 1 Examples of reported microbial responses to a change in rainfall, moisture or osmotic stress

Climate/habitat	Treatment	Duration	Community or population response	Functional response	HC	References
Field experiments						
Atlantic heathland, continental forest-steppe, Mediterranean shrubland	Summer rain exclusion	10–13 years	Growth rates of fungi and bacteria and microbial community composition differed among sites, but not treatments	Soil respiration differed among sites, but not treatments	N	Rousk *et al.* (2013)
Chihuahuan desert grassland	Supplemental precipitation (+25% in summer, winter or both)	7 years	Resistance for 2 years, then increased microbial biomass and shift in microbial community structure	Elevated enzyme activities after initial 2 years	Y	Bell *et al.* (2014)
Temperate old-field	Field rain 50% or 150% of ambient	1.1–2.6 years		Enzyme activity more sensitive to moisture in drought plots	N	Steinweg *et al.* (2012)
Mediterranean grassland	Summer drought & rewetting	5 months	Bacteria community composition shifted, but fungi were resistant		Y	Barnard *et al.* (2013)
Humid tropical forest	Summer rain exclusion with and without prior summer exclusion	2 summers	Shifts in microbial community composition, but resistance with repeat exposure		Y	Bouskill *et al.* (2013)
Semiarid piñon-juniper woodland	Increased (+18%) or decreased (−50%) precipitation	1 summer	Soil microbial community composition and abundance varied more with seasonal monsoons than treatments		N	Cregger *et al.* (2012)
Temperate grassland, wheat field	Field rainfall exclusion, laboratory drought (40%) and rewetting	4 months field, 2 weeks laboratory	Field drought legacies, with microbial community composition and abundance affected more in soils with prior drought		Y	de Vries *et al.* (2012)
Combined field and laboratory experiments						
Semiarid shortgrass steppe	Field rainfall at 25, 50, or 100% of ambient; laboratory incubations at five soil water potentials	11 years field, 36 h and 6 months laboratory	All drought treatments caused a change in bacteria community composition relative to ambient; active bacteria depended more on current than historical moisture in laboratory	Prior field treatment contributed to respiration in short-term laboratory incubations, but in the longer-term only current moisture mattered	N	Evans *et al.* (2013)
Continental tallgrass priarie	Increased summer field rain (160%), constant or wet-dry cycles in laboratory	10–12 years field, 6 h laboratory	Microbial community composition reflected both field and laboratory moisture conditions		Y	Williams (2007)
Temperate tallgrass prairie	Field drought 50% longer than ambient; four 20-day dry-rewet periods in laboratory	10 years field, 80 days laboratory	Shift to more stress-tolerant life history strategies with more frequent dry-wet cycles	Lower initial respiration in delayed compared to ambient	Y	Evans & Wallenstein (2012, 2014)
Mediterranean meadow	Increased rainfall (120%) in winter or spring; constant moisture in laboratory	4–7 years field; 4 weeks laboratory incubation	Community composition of fungi and bacteria shifted seasonally more than with rain addition; treatments affected fungi at some dates	Decomposition rates higher in spring rain plots during time period when fungal communities shifted	N	Cruz-Martinez *et al.* (2009), Hawkes *et al.* (2011)
Temperate managed grassland	Soils dried and rewet to 50% moisture	4 days or 1 year drying, 150 h incubation	Growth rates of bacteria and fungi depended on duration of prior drying	Respiration response to rewetting depended on duration of prior drying	Y	Meisner *et al.* (2013)
Continental tall- and mixed-grass prairies	Field rain gradient, laboratory short or long wet-dry cycles	12 weeks laboratory (six, 2-week cycles)		Respiration and enzyme activities responded similar to laboratory treatments regardless of site origin	N	Tiemann & Billings (2011)

(continued)

Table 1. (continued)

Climate/habitat	Treatment	Duration	Community or population response	Functional response	HC	References
Maritime forest	Field growing season rain reduction (70%), laboratory dry-rewet	2 years field, 1 week laboratory	Bacterial growth curves shift based on field history, but cumulative growth indistinguishable	Respiration response to rewetting slower and reduced in field drought soils	Y	Göransson *et al.* (2013)
Laboratory experiments						
Yeast strains grown in 96-well plates in laboratory	Initial osmotic stress across initial range of 0 to 150 g/L NaCl, then all in final 150 g/L	Transfer every 72 h, 8 initial and 4 final transfers	Adaptation to high salt stress in initial conditions; evolutionary rescue events in final concentration depended on initial conditions		Y	Gonzalez & Bell (2013)

Field and laboratory experiments are included; the combination of field and laboratory allows for a more robust assessment of potential historical contingency effects.
HC, historical contingencies; observations indicated by Y (yes) or N (no).

(Schiffers *et al.* 2013). Local adaptation to the previous climate can constrain responses to a novel climate (Fig. 1d); for example the magnitude of soil responses to rewetting can be limited by prior drought events (Göransson *et al.* 2013), which may act as selective sweeps. Similarly, taxa that are locally adapted to non-climatic conditions, such as soil properties (Belotte *et al.* 2003), can create biotic resistance in the community if this prevents establishment of taxa better suited to the new climate (Fig. 1d).

HISTORICAL CONTINGENCIES IN SOIL FUNCTIONAL RESPONSES TO ENVIRONMENTAL CHANGE

Historical contingencies can occur in aggregate soil function when the environment changes, but unexpected or novel responses occur because the previous microbial community continues to dominate or other aspects of the environment that drive microbial function endure (Fig. 1d). In some cases, prior conditions can lead to an increase in anticipated functional responses, such as when earlier genetic change in the community positions microbial taxa for unique evolutionary responses to environmental change (Blount *et al.* 2008). In other cases, reduced or sub-optimal function occurs (Table 1, Fig. 1d). Analogous processes may occur in our modelling, where a diverse range of niche optima can be maintained in a fluctuating environment. Under a rapid environmental shift, rare types able to persist in the historical community may emerge as dominants in the changed environment. Any lag in community-level functional acclimatisation created by historical contingencies is directly pertinent to how we model ecosystem responses to climate change, as it determines the time frame and magnitude of response, as well as whether or not predictions can be made based on a straightforward relationship of microbial activity to environmental conditions. If legacies occur, the underlying mechanisms and temporal scale of persistence will be key to understanding their relevance for predicting future ecosystem function in a changing climate.

Soil legacies related to climate change are a current topic of debate (Table 1). For example legacy effects have been observed in soil microbial responses to altered precipitation in both temperate grasslands and wet tropical forests (Evans & Wallenstein 2012; Bouskill *et al.* 2013), but not in five European shrublands subjected to long-term growing season warming and drought treatments (Rousk *et al.* 2013). The disparity in results may reflect different experimental treatments, initial conditions such as microbial functional diversity and redundancy, or prior environmental conditions, but the small number of studies precludes simplification. More broadly, we might expect historical contingencies to be more common when the new environment falls outside the range of conditions experienced previously (Waldrop & Firestone 2006).

The characteristics of previous environmental conditions also affect how soil microbes will respond to a novel climate. Fluctuations can create community-level functional resilience to future climate change either through greater physiological breadth of individual taxa (generalists) or the presence of a range of taxa with specific physiologies (specialists). Fluctuating environments can lead to coexistence via temporal or spatial niche differentiation (Chesson & Huntly 1997), which could generate broader specialist diversity and buffer community-level aggregate function in the system. This effect is enhanced when greater differentiation among species in their environmental responses leads to asynchrony among taxa (Loreau & de Mazancourt 2008). Conversely, a lack of fluctuations may reduce the ability of local microbial communities to respond to change, resulting in a dependency on immigration to drive acclimatisation.

Beyond the absolute magnitude of historical environmental variation, we may also consider the pattern of fluctuations. Environmental fluctuations are typically autocorrelated, either tending to move in the same direction as recent changes (positive autocorrelation) or tending to switch directions in an oscillatory fashion (negative autocorrelation). Greater autocorrelation (either positive or negative) leads to a larger long-term deviation from the mean. These patterns could influence community composition directly by increasing the overall magnitude of fluctuation, or indirectly by possibly altering, for example the balance of specialists versus generalists. Temporal autocorrelation of environmental drivers varies across landscapes (Jones & Briffa 1992), possibly generating commu-

nities with different degrees of sensitivity to future climate shifts. Thus, we expect the degree of functional resilience to depend not only on the magnitude of the environmental shift relative to historical conditions, but also on the pattern of historical environmental fluctuation.

MODELLING COMMUNITY RESPONSES TO ENVIRONMENTAL CHANGE

The factors outlined here that influence microbial community responses to climate change suggest complex outcomes that may defy simple extrapolation. Under these circumstances modelling can be used to explore potentially non-intuitive behaviour owing to the simultaneous effects of multiple governing factors. We constructed a simplified model to examine how individual-level microbial responses scale up to ecosystem responses in a changing environment (Fig. 2, Table 2, Supporting Information). While not a microbial model *per se*, we extract a number of essential features of microbial community responses to a change in the environment. We explicitly modelled the following response mechanisms: (1) Physiological plasticity via specialist-generalist trade-off in physiological breadth, and (2) community composition shifts via competitive dynamics and dormancy. We explored these response mechanisms in the context of environmental change, given different historical patterns of environmental variation that could constrain responses. See Supporting Information for the full model code.

Other factors not explicitly included in the current version of the model have some implicit parallels. For example the ability to adapt to new conditions and create evolutionary rescue is not included, but local adaptation is partly reflected in the idea of specialists. Similarly, immigration is not modelled, but effects may be similar to those generated by the introduction of microbial strategies from dormant pools. In contrast, there is no parallel for abiotic legacies such as soil properties; on their own, these might constrain responses in a manner similar to that of environmental history modelled here, but undoubtedly their explicit consideration would interact with the environmental fitness function to create greater complexity. Incorporation of these other factors is the logical next step in this modelling effort.

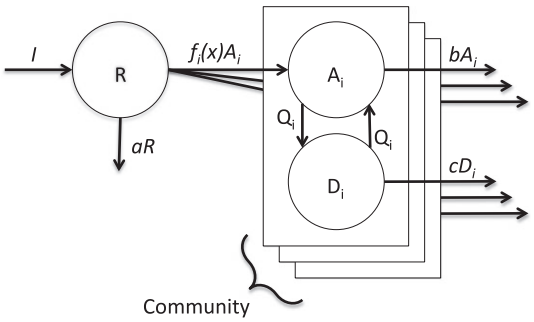

Figure 2 Model diagram showing state variables (circles) and material 'carbon' fluxes (arrows). The expressions give the flux rates for the resource and *i*th species. For symbol definitions, see text and Table 1.

Physiological responses: specialist-generalist trade-off

Our starting point for understanding microbial responses and resilience in a variable environment is the assumption of a specialist-generalist trade-off, which affects the potential to acclimatise to new environments. Although we do not explicitly model physiological acclimatisation within species, community-level selection for generalist species has much the same effect, albeit without the ability of individuals to dynamically adjust allocations influencing specialisation.

We focus on the concept of a trade-off in environmental tolerance. This species-specific environmental tolerance influences both the rate of resource consumption, and hence competitive dynamics, and the rate of transition between dormant and active states. We begin with a univariate descriptor of the environment $X = X(t)$ (for more details on $X(t)$ see section on environmental conditions below). We then model the fitness of species i according to the Gaussian density function $g_i(X) = \mathcal{N}(X; \mu_i, \sigma_i)$. The species-specific parameters μ_i and σ_i determine the niche optimum and niche breadth respectively. This formulation introduces an explicit trade-off in the maximum fitness: $g_i(\mu_i) \propto 1/\sigma_i$. Hence, species can be more tolerant of a wide-range of environmental conditions, but at the cost of reduced competitive ability relative to specialists. Generalists also exhibit a more gradual switch to dormancy as the environment departs from μ_i, the niche optimum (see section on dormancy below).

Changes in community composition: competitive dynamics

We focus here on competition for a single resource pool. This formulation isolates the role of environmental variation in maintaining diversity from other potential niche mechanisms such as resource specialisation. In addition, this allows us to

Table 2 Model parameters, dimensions and default values, as well as relative sensitivities of resource, active biomass and dormant biomass to the parameters

Symbol	Description	Dimensions	Default value	Resource	Active biomass	Dormant biomass
I	Resource input rate	Mass/time	0.01	74 ± 0.2	5.1 ± 0.58	4 ± 1.2
a	Per-unit resource loss rate constant	1/time	0.0025	−3.4 ± 0.19	−0.61 ± 0.57	0.47 ± 1.2
s	Uptake half-saturation	Mass	0.2	6.1 ± 0.2	−8.7 ± 0.58	−5.8 ± 1.2
r	Maximum resource uptake rate constant	1/time	0.095	−14 ± 0.19	20 ± 0.56	16 ± 1.2
b	Active biomass loss rate constant	1/time	0.019	2.1 ± 0.19	−26 ± 0.55	−22 ± 1.2
u,v	Dormancy function shape parameters	None	8.0	2.5 ± 0.18	−19 ± 0.53	55 ± 1.1
ϕ	Dormancy flux rate constant	1/time	0.48	−2.9 ± 0.21	21 ± 0.63	−61 ± 1.3
c	Dormant biomass loss rate constant	1/time	0.0038	−0.39 ± 0.19	−0.094 ± 0.57	−0.67 ± 1.2

understand impacts on resource pools, analogous to soil carbon or nutrients. Resource dynamics are given by

$$\frac{dR}{dt} = I - aR - \sum_{i=1}^{N} f_i(X)A_i$$

where R is resource quantity, I is resource supply rate, a is resource loss rate, and A_i is the active biomass of species i. Here, upper-case symbols denote dynamic quantities (time indices are omitted) and lower-case symbols denote constants. Species-specific resource uptake is given by

$$f_i(X) = g_i(X)\frac{rR}{s+R}$$

where r is the maximum growth rate and s is the half-saturation coefficient. Fluxes of the active microbial biomasses are given by

$$\frac{dA_i}{dt} = (f_i(X) - b)A_i - Q_i$$

where b accounts for respiration and mortality and Q_i is the flux of biomass into the dormant state (see next section on dormancy). Because the biomass loss rate b is the same across species, in a constant environment we expect that the species with the greatest fitness $f_i(X)$, that is the species closest to its optimal niche for whom $|\mu_i - X|$ takes the smallest value, will deterministically exclude all other species. Hence, the only mechanism maintaining diversity in our model is temporal variation in fitness rank owing to a fluctuating environment.

Changes in community composition: dormancy

Particularly for environmental specialists, dormancy can be a key mechanism allowing for survival in a changing environment. We modelled the flux between dormant and active pools as a function of a species' perceived environmental stress. We define stress as fitness relative to its maximum, $\hat{g}_i(X) = g_i(X)/g_i(\mu_i)$, and furthermore assume that the transition to dormancy is a nonlinear switch-like function. We chose the cumulative density of the Beta distribution, which we denote by $\beta(z; u, v)$, where u and v are shape parameters that influence how sharply function switches as z approaches unity. This formulation captures the essential features of stress-induced transition to dormancy. A more detailed consideration of microbial dormancy mechanisms can be found in Wang *et al.* (2014a).

With the definition $\psi_i = \beta[\hat{g}_i(X); u, v]$, the dormancy flux is given by

$$Q_i = \phi[(1 - \psi_i)A_i - \psi_i D_i]$$

where ϕ is the maximum rate and D_i is the dormant biomass. This function has two extremes: ϕA_i when fitness is zero and $-\phi D_i$ when environmental conditions lead to maximal fitness. Our parameterisation of the Beta function ($u = v = 8$) results in a roughly linear increase in ϕ_i over relative fitness $0.25 < \hat{g}_i(X) < 0.75$ and approximately constant (either near 0 or near 1) outside this range. Note that relative fitness in this context is relative to a species' own maximum, not relative to the community-wide average fitness.

With these assumptions, change in the dormant biomass of the ith species is simply

$$\frac{dD_i}{dt} = Q_i - cD_i$$

where c sets the mortality rate of dormant biomass. Species transition to dormancy when their fitness is low and become active when the environmental conditions are more favourable.

Environmental conditions

We modelled environmental variation using a first-order autoregressive time series model. Because the community model is continuous in time, we simulated time series according to a two-scale process. Below a threshold time scale, $d\tau$, we generated a locally smooth deterministic function $X(t) = j(x_{\tau_0+d\tau}, x_{\tau_0+2d\tau}, x_{\tau_0+3d\tau}, \ldots, x_{\tau_0+nd\tau})$ where $j(\cdot)$ is a linear interpolating function and x_τ are samples from a coarse-scale stochastic model. For the coarse-scale component, we used a first-order autoregressive model

$$x_{\tau+d\tau} - \bar{x} = \rho(x_\tau - \bar{x}) + \varepsilon_\tau$$

where $\bar{x}$ is the mean environmental value. Environmental noise ε_τ was sampled from the normal distribution $\mathcal{N}(0, \sigma_E)$ where σ_E sets the magnitude of environmental variation (the label 'sd' is used in the tables and figures to designate σ_E). The autoregressive parameter ρ determines the autocorrelation pattern of environmental fluctuations (the label 'ac' is used in the tables and figures to designate ρ). For $\rho < 0$, the environment rapidly oscillates between high and low values. This leads to 'blue noise' with a spectrum biased towards high-frequency variance. When $\rho < 0$, the environmental values take long excursions above and below the mean. This produces a 'red noise' spectrum dominated by low-frequency variation. The time series mean $\bar{x}$ is bounded and stationary for $-1 < \rho < 1$. We used a threshold time scale $d\tau = 1$ day.

Parameterisation and parameter sensitivities

As the model was as a theoretical exercise, we did not base parameters on measured data. Modelled turnover times of carbon and microbial pools vary widely in the literature, in part because different models partition these pools in different ways and in part because empirical estimates vary among studies. We chose our default parameters (Table 2) such that the turnover times of the resource and active and dormant biomass pools were reasonably consistent with those of Wang *et al.* (2013), a particularly well-documented and calibrated study, whose representation of dissolved carbon and microbial pools is analogous to our resource and active biomass pools. For a single species with $\mu_i = 0.0$ and $\sigma_i = 1.0$ simulated in a constant optimal environment ($\bar{x} = 0.0$, $\sigma_E = 0.0$), the turnover of the resource pool was 20 days, consistent with the 20 day turnover of dissolved organic carbon in the model of Wang *et al.* (2013). Active biomass under these conditions turned over every 53 days compared to 132 days in Wang *et al.* (2013). Turnover time of dormant biomass was set at five times that of active biomass, or 265 days. Order of

magnitude variation in these turnover rates will have little impact on our basic conclusions.

We also conducted a sensitivity analysis of our model. We varied all parameters simultaneously over 1000 replicate runs. Parameters were perturbed in each replicate by multiplying each by a log-normal deviate with log-mean = 0.0 and log-standard-deviation = 0.25. We equated sensitivity to the regression coefficients of a model with the steady-state output as the dependent variables and parameter values as the independent variables.

Simulations with environmental history and environmental change

We examined the influence of two historical environmental factors, environmental variation (sd = σ_E) and environmental autocorrelation (ac = ρ) on how microbial communities respond to a change in the environment. Environmental change was represented by an applied press disturbance of magnitude $pr = \Delta\bar{x}$, which alters the mean environmental condition in the time series. Each of the three factors was sampled from a uniform distribution: pr varied from 0.0 to 2.0, ac varied from −1.0 to 1.0 and sd varied from 0.0 to 2.0. A total of 4000 random combinations of pr, ac and sd were generated and used for simulations.

These simulations proceeded in three phases. During the first phase of the simulations, we constructed a community by randomly introducing species at an average rate of one per 100 days. New species niche optima were drawn from a normal distribution with zero mean and unit standard deviation, niche breadths from a log-normal distribution with log-mean zero and log-standard-deviation one. After the assembly phase, the model was simulated for an additional 1000 years without immigration. These extended periods of simulation were necessary to allow the community to reach a steady-state composition. Prior to the third phase, the output of the model was sampled over an additional 10-year pre-disturbance period. The environmental change was then applied (the mean environment shifted an amount prescribed by the variable pr). We then simulated for an additional 1000 years to allow the model to reach a new equilibrium. The recorded output was averaged over a final 10-year post-disturbance period. Throughout the simulations, species whose total active and dormant biomass fell below one-part-per-million were culled from the model on a daily basis.

Community-level function was in the form of soil resource use, where 100% resource use represented full acclimatisation. Because the effect of the environmental change was often approximately binomial (either 0 or 100% resource utilisation; Fig. 3), we fit a GLM to the results with resource utilisation greater than 50% as the dependent variable. In all cases, treatments were entered into the model as continuous ordered variables, not discrete contrasts. The GLM results are summarised in Table 3.

Table 3 Influence of environmental characteristics on the probability that resource utilisation is above 50%

Variable	Estimate	Standard error	*z*-value
Intercept	5.56	0.63	8.9
Environmental change (pr)	−7.44	0.79	−9.4
Environmental variation (sd)	−1.90	0.47	−4.1
Environmental autocorrelation (ac)	1.01	0.68	1.5
pr × sd	1.90	0.58	3.3
pr × ac	2.65	0.65	4.1
sd × ac	−2.18	0.38	−5.7

Estimates are regression coefficients from a binomial GLM.

MODEL RESULTS

Sensitivity

Model sensitivities are given in Table 2. Total resource input rate constant (I) had the largest impact as it controls the total resource and biomass accumulations. Maximum microbial uptake rate (r) and half-saturation coefficients (s) also showed high sensitivity across all pools. Active biomass loss rate (b) was sensitive for biomass pools. Interestingly, the shape parameters (u, v) of the dormancy switch were highly sensitive for both active and dormant biomass pools indicating that shifts in the propensity to switch between active and dormant states has a strong influence on biomass accumulation and distribution between active and dormant pools.

Interaction between historical fluctuations and abrupt environmental change

The magnitudes of the environmental change had strong influences on acclimatisation of resource use. When the size of the environmental shift was large, resource utilisation declined, indicating a collapse in the microbial community owing to poor fitness in the altered environment (Fig. 3). This collapse occurred despite the mechanisms supporting resilience we discuss in the following sections, suggesting a cautionary note with regard to abrupt environmental change: a sufficiently large perturbation can overwhelm both individual species physiological plasticity (here, niche breadth) and the capacity of the community to exhibit a compensatory response in which previously maladapted species flourish under the new environmental regime.

Interestingly, the relationship between historical environmental variation and resource utilisation was not monotonic, instead showing a strong unimodal 'humped' relationship in most cases and especially for intermediate levels of environmental change (Fig. 4). The mechanism underlying the collapse of the community at high environmental standard deviations is likely the strong inherent penalty (maximum growth trade-off) of being a generalist with broad physiological tolerance. Large environmental standard deviations should favour more plastic generalists, but their average fitness will still be small relative to specialists in a more constant environment. Collapse at low historical environmental variation is more puzzling. Clearly, a lack of historical environmental variability (sd = 0.0) resulted in communities that were more sensitive to an environmental change than those that experienced past environmental variation (Fig. 4). The result is a peaked response at intermediate levels of historical variation (Figs 3 and 4). The obvious explanation is that a lack of historical environmental variation leads to dominance by a single or

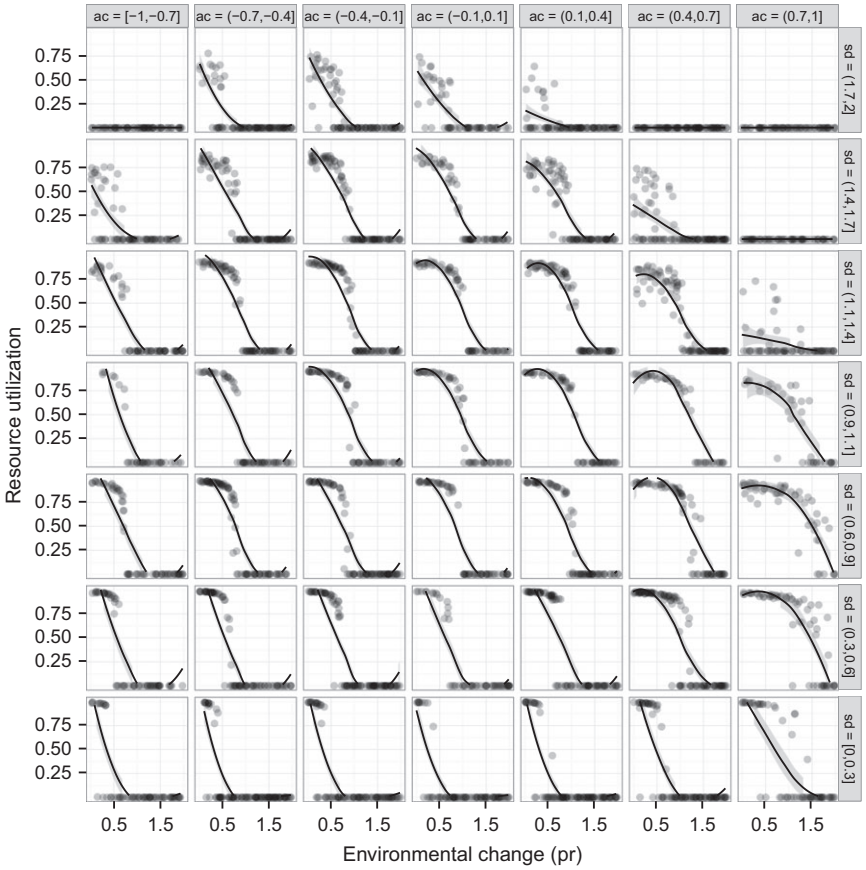

Figure 3 Resource utilisation fraction (0 = resource not utilised; 1 = full resource utilisation) as a function of environmental change (pr). Each row corresponds to a different historical environmental variation (sd) and each column to a different level of historical environmental autocorrelation (ac). The three treatments (pr, ac, sd) were each drawn from a uniform random distribution and then binned into the indicated intervals. The line is a loess fit through the points. The shaded region indicates standard errors of the loess curve. Points are plotted with 25% transparency such that isolated points appear grey and clusters of points appear in increasingly darker shades.

small number of specialist that cannot survive in the altered environment. The competitive exclusion of generalist and non-optimal specialists is roughly analogous to the evolutionary mechanism of local adaptation leading to specialisation on a narrow niche. This, in turn, may inhibit acclimatisation to new environments if specialisation limits evolutionary rescue.

Influence of environmental autocorrelation

Changes in the frequency of similarity in historical environments over time, that is environmental autocorrelation, also exhibited a unimodal response (Fig. 5), albeit not as consistently as did historical environmental variation. For environmental variation (sd) less than 1.0 and intermediate levels of environmental change, positive autocorrelation appears to impart greater resilience, perhaps because the greater long-term variation associated with strong autocorrelation may maintain a larger community of generalists. At higher levels of environmental variation (sd > 1.0) it appears that strong autocorrelation, whether positive or negative, reduces resilience. This again likely is a result of the greater long-term variation associated with strong positive and negative autocorrelation. The magnifying influence of autocorrelation on long-term environmental variation may have led to greater effective environmental variation and subsequent extinction (Fig. 4).

Influence of environmental variation on pre- and post-disturbance niches

Environment variation strongly influenced the niche properties of the assembled communities (Fig. 6). Community average niche breadth ($\bar{\sigma}$) in particular shows a strong positive relationship to environmental variation, clearly indicating that niche specialists were disadvantaged in the more variable scenarios. Community average niche optima ($\bar{\mu}$) conform to the mean environment pre-disturbance and increase in response to the post-disturbance increase in the environmental mean. The effect is most dramatic at intermediate environmental variability (sd $\approx$ 0.5) where many average community optima show strong tracking of environmental change owing to growth of more fit species and extinction of less fit species post-disturbance. Per-species average active and dormant biomass decreases with increasing environmental variation. (The distinct vertical structure of active pre-disturbance biomass is likely driven by cases where the community relaxed to a single species consuming all of the resource, two species sharing the resource, etc.) Average dormant biomass shows a

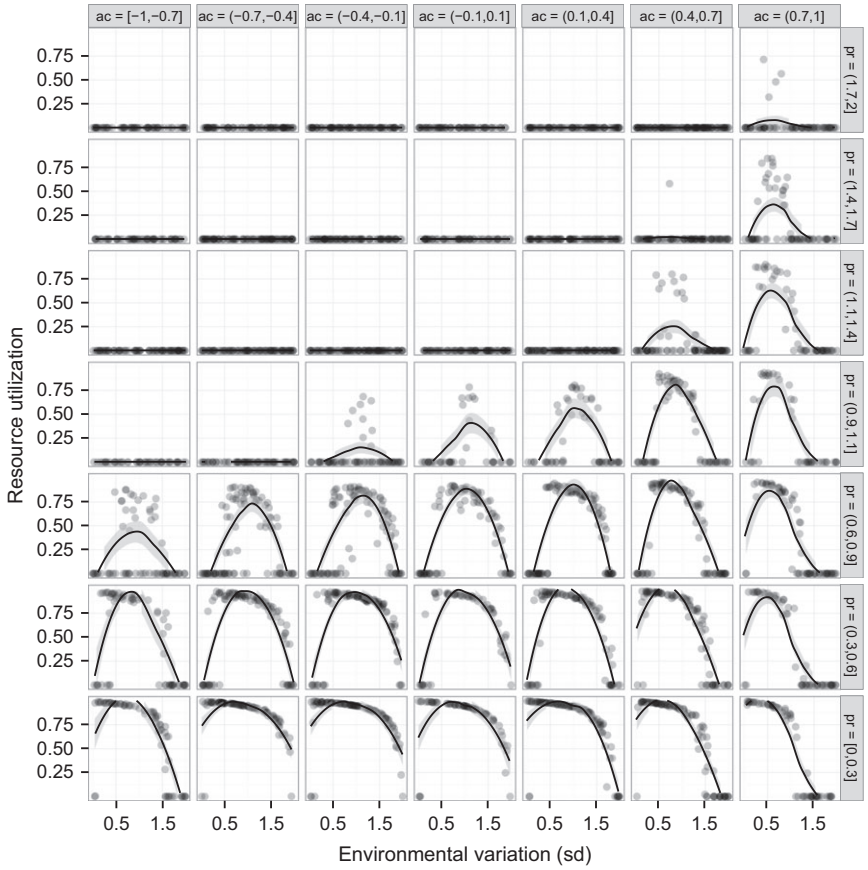

Figure 4 Resource utilisation fraction (0 = resource not utilised; 1 = full resource utilisation) as a function of historical environmental variation (sd). Each row corresponds to a different environmental change (pr) and each column to a different level of historical environmental autocorrelation (ac). The three treatments (pr, ac, sd) were each drawn from a uniform random distribution and then binned into the indicated intervals. The line is a loess fit through the points. The shaded region indicates standard errors of the loess curve. Points are plotted with 25% transparency such that isolated points appear grey and clusters of points appear in increasingly darker shades.

large increase post-disturbance indicating that this is a key mechanism for species persistence under environmental change. While average per-species active biomass declines with increasing environmental variation, total resource utilisation, the product of number of species, their fitnesses and biomasses, is maximised at intermediate environmental variation (Fig. 4).

DISCUSSION

Based on results of the simulations, acclimatisation responses can interact with legacies of previous environmental conditions to affect both microbial community function and composition in the face of climate change, making outcomes less predictable than if neither or only one factor was at play. Specifically, the degree of acclimatisation was highly dependent on how the balance of generalists and specialists shifted with the magnitude of the environmental change (pr), historical levels of environmental variation (sd) and historical patterns of autocorrelation (ac). Although we did not address all possible microbial response mechanisms, the dynamics captured here suggest a role for microbial mechanisms in driving local variability in soil functional responses to environmental change.

Intermediate levels of historical variation in particular had a strong influence on the resilience of communities (Fig. 6). This result can be explained by the maintenance of a large pool of moderately generalist species in the pre-disturbance species pool. The greater range of niche optima in the more diverse communities leads to a greater chance of a compensatory response to environmental change by pre-adapted species. Further increases in environmental variation generated still greater average niche breadth, but there is a tipping point where the negative influence of being a generalist begins to reduce species richness, range of niche optima, and overall resilience of the community. Although the specific details of this mechanism depend of course on the resource supply rate and metabolic maintenance costs, these results give strong support for an intermediate disturbance mechanism regulating species richness and community resilience to environmental change. These results are consistent with predictions of the intermediate disturbance hypothesis (Connell 1978). The primary difference between the mechanism operating here and most applications of the intermediate disturbance hypothesis is that our 'disturbances' operate symmetrically: there are no community-wide 'good' or 'bad' epochs. A directional fluctuation in the environment can either harm or benefit any given species dependent upon its assigned niche optimum and

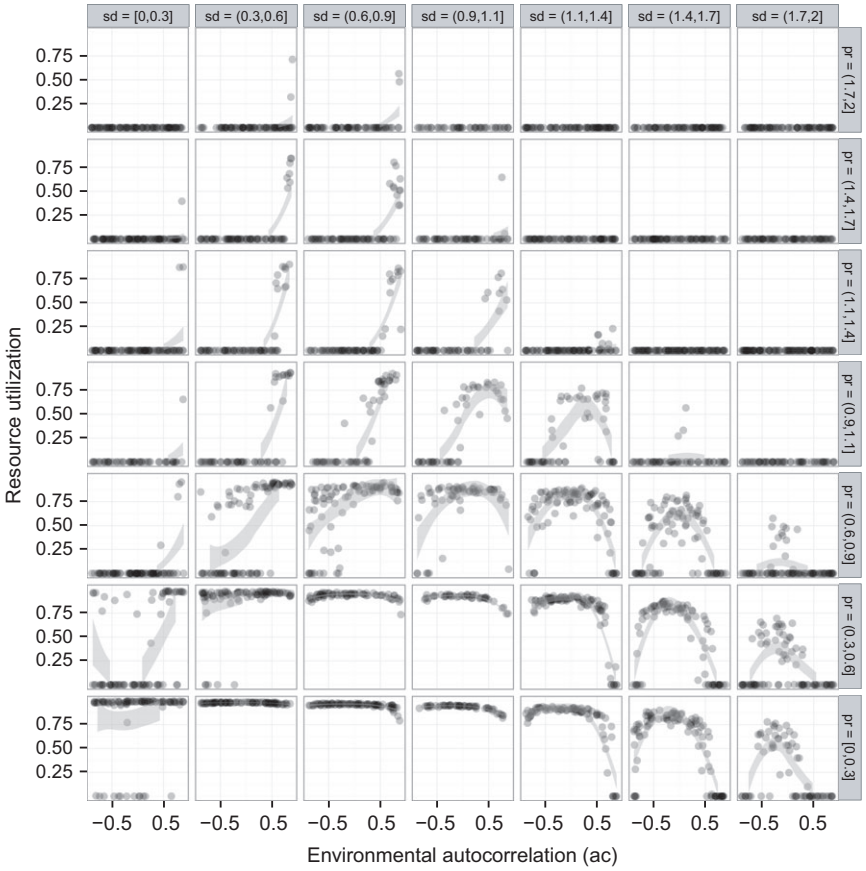

Figure 5 Resource utilisation fraction (0 = resource not utilised; 1 = full resource utilisation) as a function of historical environmental autocorrelation (ac). Each row corresponds to a different environmental change (pr) and each column to a different level of historical environmental variation (sd). The three treatments (pr, ac, sd) were each drawn from a uniform random distribution and then binned into the indicated intervals. The line is a loess fit through the points. The shaded region indicates standard errors of the loess curve. Points are plotted with 25% transparency such that isolated points appear grey and clusters of points appear in increasingly darker shades.

breadth. It remains to be determined whether this represents a fully stabilising versus equalising mechanism *sensu* Chesson (2000). Furthermore, in experimental settings the effects of disturbance on microbial abundance, composition and function do not consistently follow the intermediate disturbance pattern (reviewed in Griffiths & Philippot 2013) suggesting that a better understanding of detailed mechanism may be required to generalise this result.

By modelling individual responses to climate change, the simulation results establish a plausible scenario under which the magnitude and pattern of historical environmental variation influences the functioning of niche-based, competitively structured communities in response to a change in the environment. Depending on the degree of environmental change and the environmental history, both resilience and collapse could result from plasticity (environmental generalists) or adaptation (environmental specialists). Obviously soil microbial communities are far more complex and subject to additional positive feedbacks not incorporated in the current model. For example other ecosystem process models have incorporated microbial traits or functional groups explicitly related to resource use rather than the environment (e.g. Moorhead & Sinsabaugh 2006; Orwin *et al*. 2011; Allison 2012; Waring *et al*. 2013). Future models could incorporate simultaneous consideration of environmental and resource-based traits in the context of a changing environment, including feedbacks between the environment and resource pools. Nevertheless, more work will be required to determine the level of detail necessary to successfully model these effects at higher levels, such as longitudinal time series of responses to environmental change for soils from different environmental histories, accounting for both function and different taxa or functional groups.

Even the simple niche-based mechanisms addressed here resulted in complex patterns of resource use related to the previous environment that could scale up to microbe-driven local variability in ecosystem responses to environmental change. Such local variability might prevent extrapolation across sites or ecosystems without additional understanding of how specific local controls might be generalised. For example if acclimatisation of microbial resource use, such as decomposition of dissolved organic matter, depends on both the historical environment and the degree of environmental change, then there is likely to be a high degree of local variability in how ecosystem processes such as soil carbon cycling respond to climate. One relatively simple outcome of the current model was that microbial communities from more constant environments were more sensitive to environmental change, and did not acclimatise well. This paradoxically could imply that systems

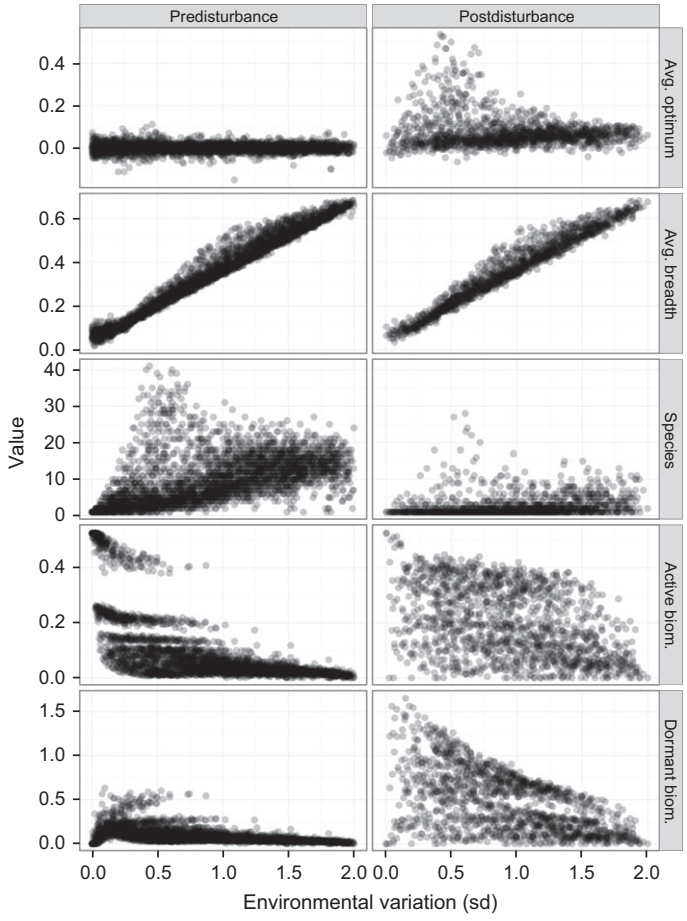

Figure 6 Influence of environmental variation on model outputs averaged over a 10-year period prior to and subsequent to an abrupt environmental change (pre- and post-disturbance respectively). Data are pooled over all values of environmental change (pr) and environmental autocorrelation (ac). Biomass is per-species average biomass, not total community biomass. Points are plotted with 25% transparency such that isolated points appear grey and clusters of points appear in increasingly darker shades.

with constant conditions, such as moisture availability, may be less resilient than those that experience harsher, more variable conditions, which are usually considered more fragile. Clearly under some conditions acclimatisation will occur, whereas under other conditions historical contingencies will cause soil microbes to function at a lower level than expected under climate change, with large consequences for the terrestrial carbon cycle. Empirical quantification of these relationships might allow for relatively simple modification to large-scale models.

Local variability in potential acclimatisation will be particularly relevant in situations where communities are dispersal-limited and composition is largely a function of local interactions (Büchi & Vuilleumier 2014). Absent a large influx of new variants that can thrive in the changed environment, mechanisms for resilience are limited to compensatory shifts in physiology or community composition, modelled here, or in rapid evolutionary change, which we did not address (Fig. 1). Both physiological and compositional changes have been documented and modelled for real-world soil microbial communities (e.g. Allison *et al*. 2010; Hawkes *et al*. 2011; Placella *et al*. 2012; Waring *et al*. 2013), but dispersal and rapid evolution remain poorly understood (e.g. Lindström & Langenheder 2012; Wilkinson *et al*. 2012; Adams *et al*. 2013).

Our current model is highly simplified to extract the essential features of a competitively structured community in a variable environment. However, future work could expand in a number of directions. A natural extension would be to consider a spectrum of potential resources, which would add opportunities for resource niche specialisation. Resource use also depends on other specific factors not addressed here, such as temperature, substrate quality and the annual time span of microbial activity (e.g. Xu *et al*. 2014). An additional consideration would be soil enzyme kinetics that feedback to the carbon pool as addressed in Allison *et al*. (2010) and Wang *et al*. (2013). A combination of modelling studies and experiments will be needed to improve our understanding of the links between microbial individuals and soil function.

Empirical tests of microbial responses to environmental change can further inform future predictive models that account for climate change. Manipulations that expose whole soils to new conditions can speak to aggregate functional responses (e.g. Bradford *et al*. 2010), but we can generally only infer that several mechanisms are likely operating simultaneously in the microbial community. However, as sequencing and isotope technologies continue to develop and their use becomes more widespread, it will be easier to distinguish microbial response mechanisms. Zaneveld *et al*. (2011) suggest that the combination of phylogenetic and genomic approaches can be used to reveal local adaptation in microbial communities. For *in situ* detection of both function and identity at the level of individual cells, nano-scale secondary ion mass spectrometry links high-resolution microscopy with isotopic analysis (Li *et al*. 2008). This is particularly powerful when combined with stable isotope probing to track specific functions (Pett-Ridge & Weber 2012). To examine how microbial response mechanisms vary by local environments, these methods could be applied to soils from environmental gradients that have been experimentally manipulated in common gardens or in the laboratory (Kreyling *et al*. 2014).

CONCLUSIONS AND FUTURE DIRECTIONS

Historical contingencies will act together with both ecological and evolutionary mechanisms in microbial responses to climate change and their impacts on soil processes. Future studies that aim to partition the relative importance of potential physiological, community and evolutionary response mechanisms, as well as their context-dependence, will aid in our understanding of how ecosystems will respond to climate change. In particular, ecosystem predictions could be improved by knowledge of how these mechanisms affect the time frame of and potential lags in acclimatisation, the relationship between historical environmental conditions (including environmental variability) and responses to new environmental conditions, and the relative importance of non-climatic, abiotic conditions, such as soil resources, vs. climatic factors in microbial responses. Such

mechanistic studies will enhance our understanding of basic microbial biology, and should be broadly applicable to microbial processes in soil. Given the potential for positive feedbacks to climate change from soil carbon pools that are double the size of current atmospheric pools (Schlesinger & Andrews 2000), these timely efforts have practical applications as well.

ACKNOWLEDGEMENTS

The authors thank Stephanie Kivlin, Melanie Mayes, Gangsheng Wang and three anonymous reviewers for comments on previous drafts of this manuscript. T. Keitt acknowledges support from the National Science Foundation (EF 1064901).

AUTHORSHIP

CH developed the conceptual ideas and TK performed the modelling. CH and TK jointly wrote the manuscript.

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Editor, Dr. Aimee Classen
Manuscript received 8 January 2015
First decision made 17 February 2015
Manuscript accepted 13 April 2015