

# Resilience and resistance of ecosystem functional response to a precipitation pulse in a semi-arid grassland

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## Summary

**1** In water-limited ecosystems, discrete precipitation events trigger brief but important episodes of biological activity. Differential responses of above- and below-ground biota to precipitation may constrain biogeochemical transformations at the ecosystem scale.

**2** We quantified short-term dynamics of whole ecosystem response to 39 mm irrigation events (precipitation pulses) during June 2002 and 2003 using plant physiological and ecosystem gas-exchange measurements as state variables in a principal components analysis (PCA). Experimental plots consisted of either native (*Heteropogon contortus* L.) or non-native (*Eragrostis lehmanniana* Nees) bunchgrasses planted in monoculture on two distinct geomorphic surfaces in a semi-arid grassland.

**3** For 15 days, treatments followed similar, non-linear trajectories through state variable space with measurement periods forming distinct clusters; PCA axes 1 and 2 combined to explain 80.7% of the variation during both 2002 and 2003.

**4** During both years, bunchgrass species interacted with soil type such that there was a reduction in ecosystem functional resistance in plots planted with the non-native bunchgrass species on the fine-textured clay geomorphic surface.

**5** System-level hysteresis, emerging as a result of independent responses of photosynthesis, respiration and evapotranspiration to precipitation, indicated the potential for alternative functional states.

**6** Quantifying the frequency and duration of ecosystem alternative functional states in response to individual precipitation events within a season will provide insights into the controls of species, soils and climate on ecosystem carbon and water cycles.

*Key-words:* carbon, hysteresis, net ecosystem exchange, PCA, Santa Rita Experimental Range

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## Introduction

The ability to quantify the temporal nature of complex dynamics in entire ecological systems has been a focal point in the development of the ecosystem concept in ecology (Lindeman 1942; Odum 1969; see also Golley 1993). However, assessing whole-system responses to dynamic biotic and abiotic processes remains difficult and the need to evaluate ecosystem function in response to annual and seasonal climate variability remains a

central focus (Weltzin *et al.* 2003). Assessing complex, whole-system responses will require a fundamental understanding of how the physiological mechanisms underlying ecosystem function operate over differing spatial and temporal scales.

In arid and semi-arid ecosystems, annual net primary productivity correlates strongly with total annual precipitation (Gutierrez & Whitford 1987; Huxman *et al.* 2004a). However, the precipitation arrives in discrete, episodic events (Noy-Meir 1973; Loik *et al.* 2004), suggesting that biophysical investigations should focus on the implications of such events (Weltzin & Tissue 2002; Reynolds *et al.* 2004). The variability of episodic resource input and the non-linear responses of individual plants

and soil microorganisms to inter- and intra-annual variation in rainfall all influence the magnitude and temporal dynamics of ecosystem response to precipitation (BassiriRad *et al.* 1999; Knapp *et al.* 2001; Schwinning & Ehleringer 2001; Knapp *et al.* 2002; Weltzin *et al.* 2003). Further, few studies have described the role of biotic (e.g. species composition) and abiotic (e.g. soils) conditions on ecosystem functional response to episodic resource availability (e.g. Huxman *et al.* 2004b; McLaren *et al.* 2004).

Ecosystem response to episodic moisture availability is partially limited by the ability of organisms to up-regulate metabolic processes (Huxman *et al.* 2004c). Soil microbiota may respond to changes in soil water potential within hours, while grasses respond in the order of hours to days (Sala & Laurenroth 1982; Schwinning *et al.* 2002). Patterns of biomass allocation, demographics or community structure resulting from periods of prior resource availability may also constrain biological activities following a rainfall pulse (Gulluscio *et al.* 1998; Flanagan *et al.* 2002; Emmerich 2003; Ogle & Reynolds 2004).

A modern perspective links the biotic community to ecosystem function in response to episodic resource availability; however, assessment of dynamic, complex ecosystem function on a meaningful time-scale is problematic. Quantifying ecosystem functional responses requires measuring the temporal dynamics of both above- and below-ground activity, along with several concurrent and interrelated ecosystem properties and processes (e.g. soil water status, plant water status and evapotranspiration). Beyond the logistical challenge of such an endeavour, a conceptual framework for the analysis is required. Recently, Beisner *et al.* (2003) summarized alternative stable state theory in community ecology. State variables such as species abundances, age class and population size, as well as any number of other descriptors, can be used to characterize communities. In time, these state variables describe the integrated response of a community to perturbation (Scheffer *et al.* 2001; Beisner *et al.* 2003). Traditionally, a simplified two-dimensional model of this idea has been illustrated with the 'ball-in-cup' model, whereby a stimulus (e.g. an environmental perturbation) or shifts in state variables themselves (e.g. stochastic change in species abundance) cause a community to move to a new stable state. This two-dimensional model describes alternative stable states as basins in a topological surface. Community resilience is then described as the characteristics of a basin that act to return a community to a reference state (Holling 1973; Gunderson 2000; Beisner *et al.* 2003). Resistance, a closely allied term to resilience, describes a system's tendency to remain in a reference state, despite perturbation (Chapin *et al.* 2002). In response to a stimulus or a change in state variables, the non-linear and irreversible trajectory of communities through state variable space, an emergent property of complex systems with alternative stable states (Beisner *et al.* 2003), is known as hysteresis.

Adopting the conceptual framework of resilience and resistance in community ecology provides a springboard to assess the complex, short-term dynamics of ecosystem functional characteristics in response to episodic resource availability. Instead of community metrics, ecosystem fluxes, such as net ecosystem exchange (balance of gross ecosystem photosynthetic and respiratory activity) and evapotranspiration, serve as state variables. Perturbations affecting such variables over hours and days are analogous to the effects of disturbance on plant community structure and composition over years and decades. In both cases, the trajectory and rate of change in response to perturbation depend on previous conditions and are potentially irreversible on relevant time-scales.

We do not suggest that a multivariate approach should replace traditional single-variable time-series analysis in the interpretation of ecosystem responses to precipitation pulses, but rather that it offers a complementary succinct illustration of system-level dynamics through time. The objectives of this research were to describe the influence of soil physical characteristics and warm-season bunchgrass species on ecosystem functional resilience and resistance in response to experimentally simulated pulses of precipitation and to document the potential for alternative functional states in response to soil wetting and subsequent drying, by examining whether the response of the simulated grassland system is hysteretic or not.

## Methods and analysis

Physiological and ecosystem-scale functional variables were measured during June 2002 and again during June 2003 on plots within the Santa Rita Experimental Range (SRER) rainfall manipulation experiment (31.78° N, 110.88° W; English *et al.* 2003) prior to and following a 39-mm irrigation pulse. Huxman *et al.* (2004b) provide detailed descriptions of the site, the experimental design and data collection and single-variable time-series analyses associated with the June 2002 irrigation pulse. Vegetation within these randomized 1.5 × 1.8 m plots consisted of monotypic stands of either a native (*Heteropogon contortus* L.) or a non-native (*Eragrostis lehmanniana* Nees) warm-season bunchgrass. These plots were planted in July of 2001 with seedling densities (18.6 plants m<sup>-2</sup>) typical of that observed in natural stands on the SRER. Each species treatment was replicated three times on two different soil types for a total of 12 plots. Soils were a loamy-sand developed on a Holocene alluvium and a clay developed on a Pleistocene surface. The clay was characterized by a well-developed argillic horizon approximately 30 cm below the soil surface (McAuliffe 1995). From the inception of the experiment in July 2001, all treatments received identical irrigation regimes that mimicked long-term (1970–2000) rainfall patterns in nearby (*c.* 15 km) Tumacacori, Arizona. Prior to the 2002 and 2003 irrigation pulses, treatment plots did not receive any

irrigation for 90 days, a condition simulating the fore-summer drought experienced in this region.

FIELD METHODS

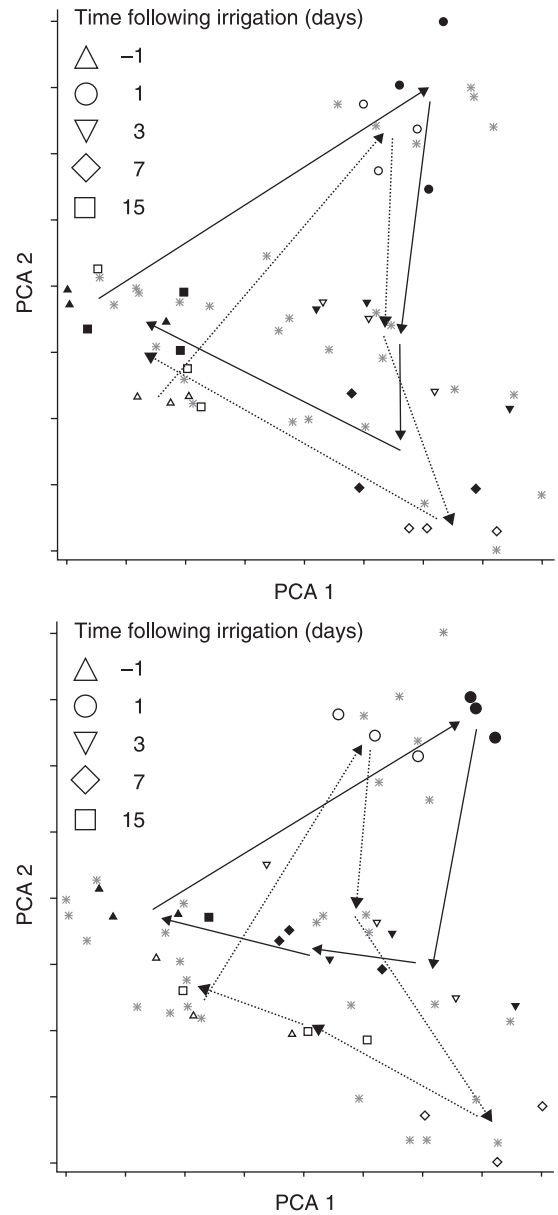
We monitored leaf level photosynthetic gas exchange with a portable photosynthesis system (LI-6400, Li-Cor Inc., Lincoln, NE, USA) targeting ambient environmental conditions at mid-morning on recent, fully expanded leaves prior to, and 1, 3, 7 and 15 days following irrigation. Soil CO<sub>2</sub> efflux throughout the experiment in each of the treatment plots was measured using a LI-6400 analyser and soil chamber (model 6400-09) on two collars per plot that were averaged prior to analysis. We measured the time course of whole-plot CO<sub>2</sub> and H<sub>2</sub>O exchange using a static chamber placed and sealed upon the plots with an open-path infrared gas exchange analyser (LI-7500, Li-Cor Inc.) located inside (see Arnone & Obrist 2003; Huxman *et al.* 2004b). A laptop computer recorded the transient changes in chamber water vapour and CO<sub>2</sub> concentrations. Whole plot measurements took approximately 90 seconds, over which time water vapour and CO<sub>2</sub> concentration changes had no significant effects on plant transpiration or canopy photosynthesis (Huxman *et al.* 2004b). The material used for chamber construction allows 92% of photosynthetically active radiation to pass into the plots, while allowing IR radiation to escape the chambers. Canopy temperature during an average measurement period increased by less than 0.2 °C. Data for net and gross ecosystem CO<sub>2</sub> exchange (NEE and GEE, respectively) and evapotranspiration were analysed according to Huxman *et al.* (2004b), and diurnal values were calculated using the spline-fit and integration function in SigmaPlot v7.0 (SPSS Inc., Chicago, IL, USA).

STATISTICAL ANALYSIS

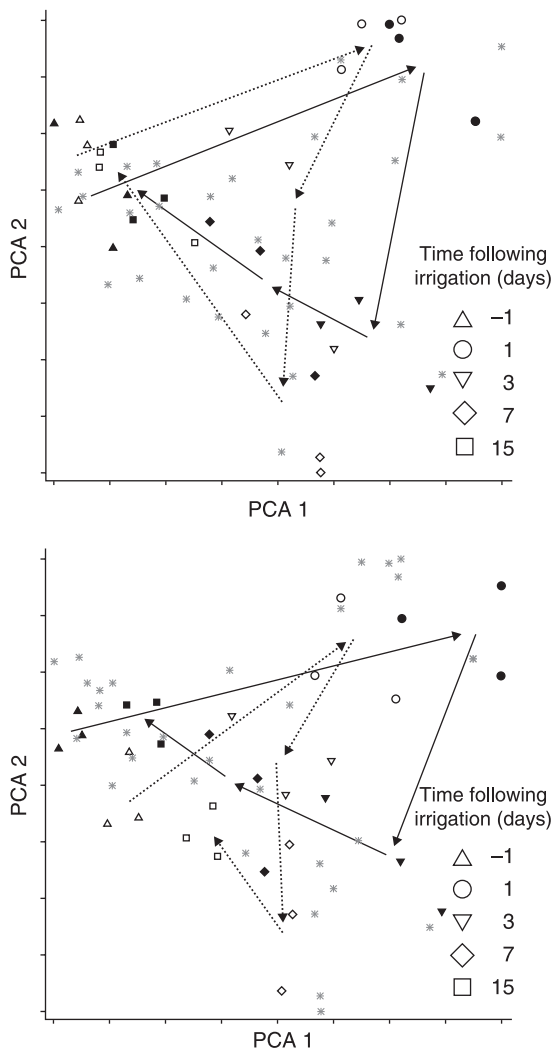
Data for response variables were assessed for normality and, if necessary, a log transformation was performed. Using PC-ORD (Version 4.25, McCune & Mefford 1999), we constructed a matrix of plot by response variables. Ordinations of the treatments were produced using principal components analysis (PCA) on the correlation coefficients of the cross products matrix. To characterize the influence of soil physical characteristics on ecosystem functional response, species treatments on both soil types were ordinated together. To quantify the magnitude of ecosystem response to perturbation, we used the distance matrix generated by PC-ORD to determine standardized, normalized Euclidean distances between plots. Statistical analyses of Euclidean distances were conducted to detect the influence of time, species and soil, along with their interactions, using a split-plot, repeated measures ANOVA design, followed by pairwise post-hoc testing for individual time and treatment combinations (JMP-IN Statistical Discovery Software Version 4.0, SAS Institute, Cary, NC, USA).

Results

PCA revealed that treatments followed similar trajectories through multivariate space following the pulse during both 2002 and 2003 (Figs 1 and 2). In both ordinations, the first two principal component axes contained more information than would be expected by chance



**Fig. 1** Principal components analysis of state-variables collected during June 2002 following a 39-mm irrigation event. Ordination with the first two principal component axes illustrates clustering according to time since irrigation, soil type and grass species. In the upper panel, plots on the loamy-sand soil are emphasized; clay plots are illustrated with (\*). In the lower panel, plots on the clay soil are emphasized; loamy-sand plots are illustrated with (\*). Open symbols represent native *H. contortus*; closed symbols represent non-native *E. lehmanniana*. Arrows are included as an interpretive aid describing differences in time. Dashed arrows represent the trajectory of native *H. contortus*; solid arrows represent non-native *E. lehmanniana*. PCA 1 most strongly correlates with maximum evapotranspiration rates (eigenvector = -0.48). PCA 2 most strongly correlates with daily net ecosystem exchange (eigenvector = 0.55).



**Fig. 2** Principal components analysis of state-variables collected during June 2003. Symbols as in Fig. 1. PCA 1 most strongly correlates with maximum evapotranspiration rates (eigenvector = -0.47). PCA 2 most strongly correlates with maximum net ecosystem exchange (eigenvector = 0.56).

alone (Johnson’s broken stick estimate, McCune & Grace 2002). In the case of the 2002 pulse experiment, the first two ordinal axes combined to explain 80.7% of the variation observed across treatments (axis 1 = 43.3%, axis 2 = 37.4%). Maximum evapotranspiration corre-

lated most strongly with principal components axis 1 and daily NEE correlated most strongly with principal components axis 2 (see Table 1). In the case of the 2003 pulse experiment, the first two ordinal axes again combined to explain 80.7% of the variation observed across treatments (axis 1 = 48.7%, axis 2 = 31.9%). Again maximum evapotranspiration correlated strongly with principal components axis 1 and maximum NEE correlated most strongly with principal components axis 2 (see Table 1).

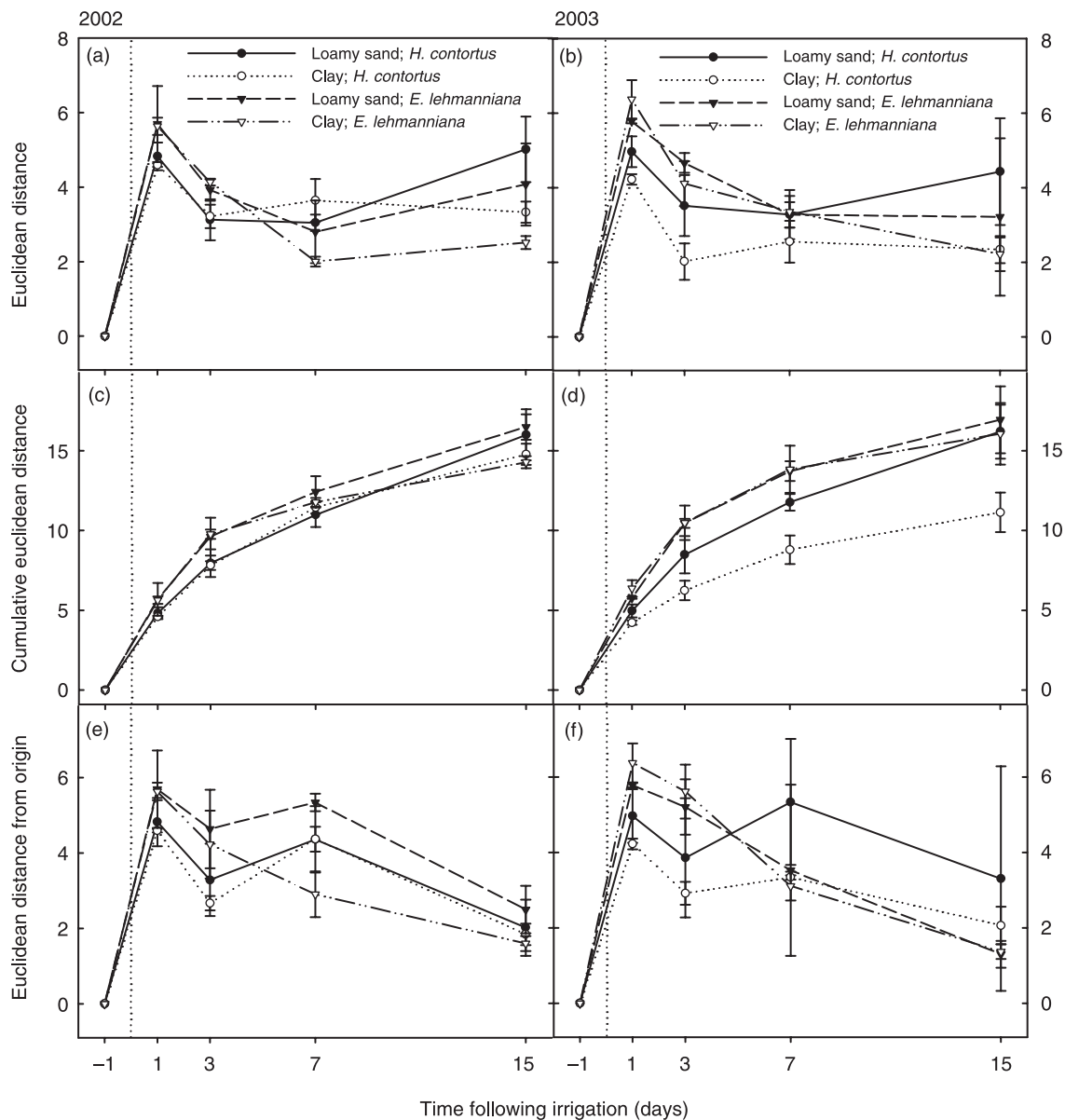
Ordinations from the two years closely resembled one another, with treatments from the same measurement period clustering together in the ordination to reflect similar suites of state variable values. Prior to watering, experimental treatments aligned with the first ordinal axis, their relative position illustrating the influence of soil type on water available to plants for transpiration. Following the pulse, plot shifts reflected a dramatic change in soil water potential and an increase in NEE.

By the third day following irrigation, the multivariate trajectory of plots shifted again, correlating with an increasing contribution of photosynthesis to ecosystem carbon balance (see Huxman *et al.* 2004b). Between day 3 and day 7 the treatments moved only slightly in multivariate space, indicating a period of relatively stable activity in both the above- and below-ground components of the ecosystem. However, by day 15 the treatments had nearly returned to their initial positions in multivariate space prior to watering.

To quantify the interaction between species and time on each soil surface we compared standardized, normalized Euclidean distances between points in time for different treatments during both years. During 2002, there was an interactive effect between species and time on the clay surface (split-plot, repeated measures ANOVA,  $F = 12.39$ , d.f. = 3,6,  $P < 0.005$ ) that was not observed on the loamy-sand surface ( $F = 1.43$ , d.f. = 3,6,  $P = 0.32$ ). During 2003, the interaction between species and time was similar on the two geomorphic surfaces, although less distinct on the clay soil (split-plot, repeated measures ANOVA,  $F = 3.28$ , d.f. = 3,6,  $P = 0.1$ ). Post-hoc *t*-tests revealed clear species differences in Euclidean distances between species treatments immediately following the 2002 and 2003 pulses on the clay soil

**Table 1** Eigenvectors of state variables

Process variable	Principal component axis		
	1 2002/2003	2 2002/2003	3 2002/2003
Maximum net ecosystem exchange	0.11/0.02	0.53/0.56	0.34/-0.48
Maximum evapotranspiration	-0.48/-0.47	0.09/-0.02	-0.22/0.17
Ecosystem respiration	-0.44/-0.47	0.29/0.21	-0.11/0.01
Gross ecosystem exchange	0.40/0.41	0.31/0.26	0.40/-0.38
Daily net ecosystem exchange	0.04/-0.34	0.55/0.43	-0.08/-0.18
Net photosynthesis	-0.12/-0.21	0.54/-0.42	0.11/-0.51
Leaf stomatal conductance	-0.31/-0.19	-0.23/-0.43	0.67/-0.54
Soil respiration	-0.46/-0.45	0.24/0.11	0.03/0.05



**Fig. 3** Several measures of distances travelled through multivariate space by species/soil treatments following a 39-mm irrigation event during June 2002 and 2003. Panels on the left illustrate 2002 data; those on the right illustrate 2003 data. Upper panels illustrate Euclidean distances between successive points in time (e.g. the distance between day 3 and day 7). Middle panels describe the cumulative Euclidean distance travelled at each point in time (e.g. day 7 values reflect the total Euclidean distance travelled since irrigation). Bottom panels describe the distance from the origin at each point in time for each soil/species treatment (e.g. Euclidean distance from the origin to day 7, not cumulative distance from the origin to day 7). Circles represent native *H. contortus*; triangles represent non-native *E. lehmanniana*. Open symbols represent experimental plots on the clay soils; closed symbols represent those on the loamy-sand soils.

(Student's *t*-test,  $t = 4.38$ , d.f. = 4,  $P = 0.012$ , and  $t = 4.01$ , d.f. = 4,  $P = 0.016$ ) (Fig. 3a,b). During both years, plots planted with the non-native bunchgrass on the clay soil surface moved farther in multivariate space, indicating decreased ecosystem functional resistance to perturbation compared with the native grass plots.

During both years, we observed differences between species in the cumulative Euclidean distance travelled on both soil types for the first four days following the precipitation pulse (Fig. 3c,d). During 2002, species differences in the cumulative distance travelled through state space disappear by day 8 on the clay soil, indicating an interaction between soil type and species during

the period of peak ecosystem activity following soil wetting. For up to a week following the precipitation pulse, non-native *E. lehmanniana* treatments moved farther through multivariate space than those planted with the native *H. contortus* on the loamy-sand soil. On the clay soil, species-mediated differences persisted for only up to 4 days following the precipitation pulse. During 2003, soil-mediated differences in cumulative Euclidean difference were again apparent. However, during 2003, plots of the native *H. contortus* on the clay soil moved substantially less through multivariate space than those planted on the loamy-sand. No such differences were observed in plots of the non-native

*E. lehmanniana* during 2003, suggesting the emergence of a species by soil–type interaction with regard to whole-system response to a precipitation pulse.

To illustrate the non-linearity of ecosystem response to the precipitation pulse and to quantify the return of the treatments to the pre-pulse reference state, we examined the distance from each treatment's initial position to positions throughout the measurement period (e.g. Euclidian distance from the origin to day 7, not cumulative distance from the origin to day 7) during both years. Species treatments on the loamy-sand soil, despite differences in absolute magnitude, responded similarly through time to pulses during 2002 and 2003 in this analysis (split-plot, repeated measures ANOVA,  $F = 0.56$ , d.f. = 3,6,  $P = 0.66$ , and  $F = 2.96$ , d.f. = 3,6,  $P = 0.11$ , respectively; see Fig. 3e,f), each species treatment possessing a second peak around day 7, coincident with positioning in the third quadrant of the ordination (Fig. 1). However, species treatments on the clay soil showed a different pattern from one another during both 2002 and 2003 (split-plot, repeated measures ANOVA,  $F = 5.94$ , d.f. = 3,6,  $P = 0.031$ , and  $F = 8.88$ , d.f. = 3,6,  $P = 0.012$ , respectively). During 2002, *H. contortus* treatments on the clay soil exhibited a second peak in Euclidean distance from its initial position around day 7 similar to the pattern of both species on the loamy-sand soil. In contrast, *E. lehmanniana* on the clay soil did not exhibit a second peak, instead illustrating a steady return to its pre-pulse position in multivariate space following the pulse (Fig. 3e). During 2003, *E. lehmanniana* treatments on both soil surfaces followed a similar pattern, which peaked on the first day after irrigation and declined steadily thereafter. During 2003, differences among native *H. contortus* plots appeared to drive the species–time observed interaction. A pronounced day 7 peak was not observed in plots of *H. contortus* on the clay soil, whose flattened response more closely resembled that of plots of *E. lehmanniana*. We predicted that proximity to the pre-pulse reference state on day 15 would reveal clear treatment-mediated differences in ecosystem functional resilience. However, there was no evidence for such treatment effects during either year.

To further quantify the non-linearity of treatment trajectories in response to soil wetting and drying we calculated the trajectory change of plots between day 1 and day 3 following the pulse during 2002 and 2003. A linear trajectory through multivariate space in response to soil wetting and subsequent drying would predict a 180-degree trajectory shift after day 1. Instead, the confidence intervals of the mean trajectory change after day 1 did not include 180 degrees during either 2002 or 2003 ( $140.7^\circ \pm 20.8$ ,  $n = 12$ ;  $135.7^\circ \pm 21.2$ ,  $n = 12$ , respectively), indicating that whole-system response to initial soil drying (day 1 to day 3) includes processes not affected by initial soil wetting. There is no evidence to suggest that this trajectory change after day 1 is affected by geomorphic surface or bunchgrass species (data not shown).

## Discussion

Multivariate trajectories of ecosystem functional response variables quantify how the non-linear temporal responses of below-ground microbial-mediated soil respiration and above-ground plant-mediated photosynthesis interact to govern ecosystem responses to soil moisture availability. The triangular trajectory of ecosystem functional response to soil wetting and subsequent drying was similar for all species and soil type combinations in multivariate space. However, species composition influenced the magnitude of the multivariate response as measured by Euclidean distances. Whole-ecosystem differences between species treatments reflect documented species-specific behaviour of respiratory and photosynthetic processes following soil wetting during this experiment (Huxman *et al.* 2004b). Across treatments, during both the 2002 and 2003 pulse experiments, ecosystem respiration and evapotranspiration peaked on the first day following irrigation while gross ecosystem exchange and stomatal conductance peaked on the seventh day following irrigation.

The non-linear trajectory of treatments in multivariate space in response to soil wetting and subsequent drying can be described as possessing hysteresis, one characteristic of complex systems possessing multiple, interacting subsystems (e.g. Scheffer *et al.* 2001). In micrometeorological settings (Gilmanov *et al.* 2003), leaf physiological studies (e.g. Tuzet *et al.* 2003) and stream nutrient-transport (Hatch *et al.* 1999), hysteresis has been demonstrated on diurnal time-scales. Hysteresis has been documented in forest-floor CO<sub>2</sub> efflux (Drewitt *et al.* 2002) at annual scales and in community composition shifts in response to climate and disturbance at decadal scales (e.g. Westoby *et al.* 1989; Sternberg 2001). Identifying ecosystem hysteresis and quantifying state variable trajectories will provide a way to assess and describe fluctuations in ecosystem function associated with variation in resource availability. In this case, hysteresis suggests the potential not for alternative community assemblages but instead for alternative functional states in ecosystems. Extending the concept of multivariate dynamics of whole ecosystems may allow for a more critical evaluation of the controls over biosphere/atmosphere carbon and water exchanges, especially in arid and semi-arid regions.

Our analysis of ecosystem response to a precipitation event was sensitive to differences in bunchgrass species; given the same perturbation (rainfall pulse), the initial response of the non-native bunchgrass plots was to move farther in multivariate space than the native bunchgrass systems on the clay soil (Fig. 3a,b). Greater functional response in the *E. lehmanniana* plots following soil wetting could be the result of differences in canopy architecture and litter abundance within the plots. *E. lehmanniana* canopies are less dense than those of *H. contortus*, and tend to have less plant litter that is dispersed in a more heterogeneous fashion, thereby allowing greater incoming radiation on the soil surface

(J. F. Weltzin, unpublished data). This study considered leaf-level and whole-canopy measures as state variables for analysis. At the scale of the individual plant, it is reasonable to suggest that structural, fine-root and leaf area adjustments during periods of episodic resource availability also contributed to ecosystem response. Future studies should investigate the specific mechanisms by which plant species, functional types and soils affect the initial response of ecosystem processes to episodic resource availability.

Persistent water limitation during periods of otherwise favourable metabolic conditions maintains a reference state of minimal biological activity in the semi-arid grassland of southern Arizona. With a large standing-crop biomass compared with soil microbial biomass, and access to deep pools of soil moisture, plants are responsible for low levels of ecosystem carbon and water exchange during extended dry periods. Immediately following a precipitation pulse, a new state, characterized by soil surface evaporation, the up-regulation of microbial metabolism and the physical displacement of soil CO<sub>2</sub> by infiltrating water, replaces the reference state (see Huxman *et al.* 2004b). Ecosystem response between day 1 and day 3, points in time where CO<sub>2</sub> efflux from soils and evaporation were dominant factors in ecosystem response, reflects this first alternative functional state. Day 7, a period characterized by high rates of biological activity in both the above- and below-ground components, reflects the relative abundance of water for both plants and microbes. This period, illustrated by the second peak in Euclidean distances from the origin in three of the four species/soil treatments during 2002 (Fig. 3e) and in native bunchgrass treatments during 2003 (Fig. 3f), can be considered to be an alternative functional state in this ecosystem. Following this period of mutually accessible water, the relative influence of plants in shaping ecosystem response grows, while the absolute magnitude of carbon and water exchange declines in response to increasing scarcity of soil water. By the last measurement period on day 15, the treatments are approaching their respective origins and a state of minimal biological activity (Fig. 2e,f).

Predicting pathways of energy and nutrient cycling has long been an objective of comparative ecosystem ecology (Lindeman 1942; Odum 1969; Noy-Meir 1973; see also Golley 1993). As an extension of the pulse-reserve model of production in water-limited ecosystems (Noy-Meir 1973; Reynolds *et al.* 2004), the concept of alternative ecosystem functional states acknowledges both the role of plant production and the dynamic contribution of soil heterotrophs to ecosystem carbon balance in response to precipitation pulses. Comparing alternative functional states (e.g. those in which fluxes are dominated by plant vs. microbial and abiotic mediated processes) in various pulse-driven ecosystems could yield novel insights into the complexities and relative influence of biotic (e.g. phenological differences amongst species or rooting depth differences amongst

functional types) and abiotic (e.g. soil texture and horizontal zonation) controls over canopy-scale ecosystem processes. By revealing the complex time course of plant, microbial and soil influences over ecosystem response to episodic resource availability, current predictive models of carbon and water exchange might be improved.

D'Odorico & Porporato (2004) described a bimodal system of soil moisture 'preferred states' potentially related to positive feedbacks on drought persistence in a temperate grassland system. Similarly, McLaren *et al.* (2004) experimentally observed dynamic seasonal patterns of biotic and abiotic controls over soil moisture heterogeneity associated with soil moisture abundance (i.e. moisture pulses) in a Northern Great Plains setting. Using the perspective of alternative functional states, the dynamic controls of plants and soil microbes on canopy-scale carbon and water exchange in response to precipitation pulses of different frequencies and magnitudes might be characterized. This experiment focused on the impact of a large precipitation pulse that resulted in the expression of two distinct, alternative functional states in addition to the pre-pulse state of minimal biological activity. A smaller precipitation pulse may only shallowly infiltrate the soil and persist as biologically available for a few days, enough time for the first alternative functional state (physical displacement of CO<sub>2</sub>, microbial metabolism and surface evaporation) to briefly dominate ecosystem carbon and water fluxes but precluding a second alternative functional state (the balance of microbial respiration and plant photosynthesis) from coming to dominate ecosystem response. Quantification of the seasonal frequency and duration of alternative functional states in a pulse-driven ecosystem could reveal intra- and inter-annual variation in influences of plant and microbial mediation of ecosystem processes in response to episodic resource availability and link short-term fluctuations in ecosystem function with more classical metrics of community assessment.

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