

Resource-enhancing global changes drive a whole-ecosystem shift to faster cycling but decrease diversity

ANU ESKELINEN ^{1,2,3,8} KELLY GRAVUER ⁴ W STANLEY HARPOLE ^{1,2,5} SUSAN HARRISON ⁶
RISTO VIRTANEN ³ AND YANN HAUTIER ⁷

¹Department of Physiological Diversity, Helmholtz Centre for Environmental Research - UFZ, Leipzig, Germany

²German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

³Department of Ecology and Genetics, University of Oulu, Oulu, Finland

⁴Graduate Group in Ecology, Department of Plant Sciences, University of California - Davis, Davis, California 95616 USA

⁵Institute of Biology, Martin Luther University Halle-Wittenberg, Halle, Germany

⁶Department of Environmental Science and Policy, University of California, Davis, California 95616 USA

⁷Ecology and Biodiversity Group, Department of Biology, Utrecht University, Utrecht, The Netherlands

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Abstract. Many global changes take the form of resource enhancements that have potential to transform multiple aspects of ecosystems from slower to faster cycling, including a suite of both above- and belowground variables. We developed a novel analytic approach to measure integrated ecosystem responses to resource-enhancing global changes, and how such whole ecosystem slow-to-fast transitions are linked to diversity and exotic invasions in real-world ecosystems. We asked how 5-yr experimental rainfall and nutrient enhancements in a natural grassland system affected 16 ecosystem functions, pools, and stoichiometry variables considered to indicate slow vs. fast cycling. We combined these metrics into a novel index we termed “slow-fast multifunctionality” and assessed its relationship to plant community diversity and exotic plant dominance. Nutrient and rainfall addition interacted to affect average slow-fast multifunctionality. Nutrient addition alone pushed the system toward faster cycling, but this effect weakened with the joint addition of rainfall and nutrients. Variables associated with soil nutrient pools and cycling most strongly contributed to this antagonistic interaction. Nutrient and water addition together, respectively, had additive or synergistic effects on plant trait composition and productivity, demonstrating divergence of above- and belowground ecosystem responses. Our novel metric of faster cycling was strongly associated with decreased plant species richness and increased exotic species dominance. These results demonstrate the breadth of interacting community and ecosystem changes that ensue when resource limitation is relaxed.

Key words: climate change; ecological multifunctionality; exotics; multiple global changes; native diversity; nutrient enrichment; slow transition; fast transition; whole-ecosystem shift.

INTRODUCTION

There is substantial evidence that anthropogenic global changes can modify plant community productivity, diversity, and trait composition in natural ecosystems (Stevens et al. 2004, Bobbink et al. 2010, Harrison et al. 2015, Alstad et al. 2016, Franklin et al. 2016). These shifts in aboveground communities are likely to modify multiple ecosystem functions and processes simultaneously and alter linkages between above- and belowground subsystems (Wardle et al. 2004, De Deyn et al. 2008). As plant community biomass is the carbon source for belowground soil organisms, shifts in productivity (i.e., resource quantity) can alter soil carbon inputs and

cycling (Aerts and Chapin 2000, De Deyn et al. 2008). Similarly, changes in plant trait composition (i.e., resource quality), especially those related to the leaf economics spectrum from acquisitive to conservative traits (Wright et al. 2004, Reich 2014), can affect litter quality, decomposition rates, and nutrient pools and cycling (Cornwell et al. 2008, De Deyn et al. 2008, Makkonen et al. 2012, Lee et al. 2017). An important ramification of these changes in belowground functions, pools and properties is that they have the potential to feed back on aboveground communities and ultimately lead to whole-ecosystem transitions (Wardle 2016).

Many ecosystem-level transitions can be described as shifts along a gradient from infertile, slow-cycling systems to fertile, fast-cycling systems (Aerts and Chapin 2000, Wardle et al. 2004, Bardgett and Wardle 2010). Global changes that increase limiting resources for plant and microbial growth (e.g., increased precipitation and

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⁸E-mail: anu.eskelinen@idiv.de

nutrient enrichment) are expected to engender transitions along this gradient. If resource-enhancing global changes lead to higher primary productivity and dominance of plants with fast-growing, nutrient-acquisitive traits (e.g., low tissue C:N ratio, high specific leaf area (SLA), and tall stature; Dwyer et al. 2014, Eskelinen and Harrison 2015, Fridley et al. 2016, Kaarlejärvi et al. 2017), they could increase belowground inputs of nitrogen and labile C via litter and root exudates (Aerts and Chapin 2000, De Deyn et al. 2008, Bardgett et al. 2005, Baxendale et al. 2014). Higher soil resource levels can yield faster nutrient and carbon cycling by supporting greater abundances of soil microbes, as well as higher relative abundances of taxa with fast growth rates and metabolic capabilities that promote faster element cycling (Fierer et al. 2007, Amend et al. 2016, Gravuer and Eskelinen 2017). Faster turnover of materials and higher nutrient pools should further favor fast-growing plants (Suding et al. 2008) and drive an overall ecosystem transition from slow to fast cycling (Wardle et al. 2004).

Ecosystem transitions from the “slow cycling” to the “fast cycling” state (Wardle et al. 2004), promoted by anthropogenic resource inputs, can threaten biodiversity because they promote high dominance in plant communities by fast-growing species and may eliminate many slower-growing native species (Suttle et al. 2007, Borer et al. 2014, Eskelinen and Harrison 2015, Harpole et al. 2016). At present, there is no analytic framework designed specifically to measure transitions of ecosystems from slow to fast cycling under resource-enhancing global changes. Because ecosystem functions and community properties often exhibit tradeoffs, relying on the knowledge of single variable responses to global changes is likely to give a biased or limited picture of overall ecosystem shifts (Byrnes et al. 2014, Manning et al. 2018). It is therefore critical to take an integrated approach to studying whole-ecosystem shifts, one in which all of the variables considered in the fast-slow framework, including functions, pools, and stoichiometry both above and belowground, are considered simultaneously.

In the vast literature asking whether higher levels of biodiversity give rise to increased ecosystem functioning, the standard metrics of high ecosystem function (e.g., high levels of biomass, productivity, or nutrient cycling) have generally been attributes of fast-cycling systems (Hooper et al. 2005, van der Ploeg 2019), even though in nature, fast-cycling systems are often associated with low diversity and/or high levels of exotic species dominance. In recent years, a more nuanced view of the value of biodiversity is that it leads to higher levels of multifunctionality, or tendency of ecosystems to support at least adequate levels of multiple different ecosystem functions (Isbell et al. 2011, Maestre et al. 2012, Soliveres et al. 2016, Fanin et al. 2018, Hautier et al. 2018, Manning et al. 2018, Meyer et al. 2018). Multifunctionality is commonly measured by a now widely used metric that integrates multiple ecosystem processes and

properties into a single value and takes into account the tradeoffs among these variables (Hooper et al. 2005, Byrnes et al. 2014, Manning et al. 2018). Here we adapt this multifunctionality metric to an alternative context where, rather than variation in biodiversity being the driver, resource-enhancing global changes are the drivers of shifts in ecosystem function.

Our new metric, which we call “slow-fast multifunctionality,” uses an a priori theory-driven classification of variables according to the slow-fast framework and enables tests about whether shifts along this gradient lead consistently in the “fast” direction. Our metric integrates above- and belowground systems and uses ecosystem measures of functions (rates), pools (states), and stoichiometry (quality), i.e., plant trait composition and productivity, plant and litter quality, and pools and functions related to soil nutrient and carbon cycling. We used a 5-yr factorial rainfall and nutrient addition experiment in a grassland system to test how this concept may relate to global change factors and plant diversity. We asked (1) Do resource enhancements drive whole-ecosystem transitions along a gradient from slower to faster cycling? And (2) are these transitions associated with reduced plant species richness and increased exotic dominance? We measured 16 relevant ecosystem variables representing functions, pools and stoichiometry from above- and belowground systems (Table 1; Aerts and Chapin 2000, Wardle et al. 2004, Bardgett and Wardle 2010). Based on the ecological function and role of different variables used in the index, we classified these 16 variables into five ecologically based groups (Table 1) and calculated slow-fast multifunctionality. We used interactive structural equation modeling (SEM) to disentangle the direct and indirect relationships between experimental resource additions, slow-fast multifunctionality, and species richness and exotic species dominance in the plant community.

METHODS

Study system and experimental design

Our experimental site of $\sim 500 \times 1000$ m (12-ha area) is located in a heterogeneous grassland system in the Inner North Coast Range of California (38°52' N, 122°26' W), at the University of California McLaughlin Reserve. The climate is Mediterranean, with mean annual temperatures of 8°C in January and 25°C in July. The mean annual rainfall is 62 cm and falls mainly in October–April. The soils and vegetation in the grassland system vary depending on soil depth and the underlying bedrock material: nutrient-poor soils supporting low-productivity grassland vegetation prevail on shallow rocky slopes of serpentine rocks, while more productive grassland vegetation occurs on deeper, more nutrient-rich serpentine soils on slopes and valley bottoms and on nutrient-rich soils derived from sedimentary rocks. At our experimental site, these soil types are interspersed

TABLE 1. Ecological grouping of different above- and belowground variables, the expectation of whether high value should indicate fast- or slow-cycling system based on the slow-fast cycling framework of Wardle et al. (2004) and other literature, and the value (normal or sign-reversed) of each variable that was used in the calculation of the slow-fast multifunctionality index.

Category/ecological grouping and variable	Expectation based on slow-fast cycling framework (Wardle et al. 2004)	Other supporting references	Value
Productivity			
Live and litter biomass	Higher value indicates faster cycling system. Higher productivity means higher C stored in aboveground biomass.	De Deyn et al. (2008)	1
Plant trait composition			
CWM C:N	High value indicates slower cycling system. Higher C:N ratio indicates conservative resource use and slow growth. High CWM C:N indicates dominance of plants with resource conservative strategy.	Wright et al. (2004), Reich (2014)	-1
CWM height	High value indicates faster cycling system. Tall stature indicates high competitive ability for light under resource-rich conditions. High CWM height indicates dominance of plants with tall stature.	De la Riva et al. (2016), Eskelinen and Harrison (2015), Kaarlejärvi et al. (2017)	1
CWM SLA	High value indicates faster cycling system. Higher value indicates rapid resource use and fast growth under resource-rich conditions. High CWM SLA indicates dominance of plants with resource acquisitive strategy.	Wright et al. (2004), Reich (2014)	1
Plant and litter quality			
Plant tissue C:N (from experimental plots)	High plant tissue C:N indicates slower cycling system. High tissue C:N indicates N-poor, low-quality, plant material.	Lee et al. (2017), Cornwell et al. (2008)	-1
Litter C:N (from experimental plots)	High litter C:N indicates slower cycling system. High litter C:N indicates N-poor, low-quality litter.	Lee et al. (2017), Cornwell et al. (2008)	-1
Soil C pools			
DOC	High value indicates faster cycling system. Fast-growing plants produce more labile C, e.g., via root exudates.	De Deyn et al. (2008)	1
Soil organic matter	High value indicates slower cycling system. Slow-cycling systems accumulate organic matter in the soil because of slow decomposition and low-quality C input. In fast-cycling systems organic matter can also be on lower level because root exudates stimulate microbial activity and decomposition of more stable carbon pools.	De Deyn et al. (2008)	-1
Microbial biomass C	High value indicates faster cycling system. Availability of labile C sources should stimulate microbial biomass growth.	Bardgett et al. (2005), Cotrufo et al. (2013), de Vries and Caruso (2016)	1
Soil nutrient pools and cycling			
Litter decomposition rate	High value indicates faster cycling system. Initial decomposition rate should be higher in fast-cycling systems due to high-quality litter and root exudates that stimulate microbial activity.	De Deyn et al. (2008), Cornwell et al. (2008), Santiago (2007), Hobbie (2015)	1
Mineralization rate	High value indicates faster cycling system. Mineralization rates should be higher in fast-cycling systems due to greater amounts of high-quality litter.	De Deyn et al. (2008), Cornwell et al. (2008), Santiago (2007), Hobbie (2015)	1
Nitrification rate	High value indicates faster cycling system. Nitrification rate should be higher in fast-cycling systems due to greater availability of ammonium.	De Deyn et al. (2008), Cornwell et al. (2008), Santiago (2007), Hobbie (2015), Laughlin (2011)	1
Microbial biomass N	High value indicates faster cycling system. As noted above, availability of labile C sources should stimulate microbial biomass growth. Microbial N generally increases in proportion to microbial C in upland.	Cleveland and Liptzin (2007), Hartman and Richardson (2013)	1
Soil NH ₄ concentration	High value indicates faster cycling system. There should be positive link between plant and soil nutrients. Fertile systems are often characterized by greater nutrient concentrations.	Hobbie (2015), Lee et al. (2017), Eskelinen et al. (2009)	1
Soil NO ₃ concentration	High value indicates faster cycling system. There should be positive link between plant and soil nutrients. Fertile systems are often characterized by greater nutrient concentrations.	Hobbie (2015), Lee et al. (2017), Eskelinen et al. (2009)	1

TABLE 1 (Continued)

Category/ecological grouping and variable	Expectation based on slow-fast cycling framework (Wardle et al. 2004)	Other supporting references	Value
Soil P	High value indicates faster cycling system. There should be positive link between plant and soil nutrients. Fertile systems are often characterized by greater nutrient concentrations.	Hobbie (2015), Eskelinen et al. (2009)	1
Soil K	High value indicates faster cycling system. There should be positive link between plant and soil nutrients. Fertile systems are often characterized by greater nutrient concentrations.	Hobbie (2015), Eskelinen et al. (2009)	1

Notes: To calculate the slow-fast multifunctionality index, each variable was first assigned a normal or sign-reversed value. Then the values were standardized to a common scale ranging from 0 to 1 to remove differences in measurement scales and units. Finally, average slow-fast multifunctionality was calculated as the mean of all above- and belowground standardized ecosystem variables. CWM, community-weighted mean.

over short distances and form a mosaic of annual grassland vegetation varying in productivity, species and trait composition (Eskelinen and Harrison 2015). Vegetation is a mixture of native and exotic annual species, exotic annuals being more abundant in more productive parts of the grassland system.

To manipulate rainfall and nutrients, we established a watering and fertilization experiment in which none watering lines brought water to 131, 2 × 2 m, experimental plots across sites of varying soils, productivity and species composition. To cope with this heterogeneous vegetation, we had 30–35 replicates per treatment combination, the slightly varying plot number resulting from when a heavy vehicle drove over some plots. We randomly assigned plots to factorial treatments of (1) fertilization with slow-release granular NPK (10-10-10) with micronutrients (Lilly Miller Ultra Green, Lilly Miller Brands, Walnut Creek, CA, USA) adding a total of 10 g N/m², 10 g P/m², and 10 g K/m² per year applied in three equal doses in November, February, and March; (2) addition of 2.5 cm of harvested rainwater applied weekly for eight consecutive weeks over a 12-h period at night (to reduce evapotranspiration), increasing average annual rainfall by approximately 18%. Sprinkler heads were placed in the center of the plots, 50 cm above soil surface and sprayed in a 3-m radius (Mini Rotor Drip Emitters, Olson Irrigation, Santee, CA, USA). This treatment was based on previous work in Californian grasslands (Suttle et al. 2007) and aimed to mimic future climate predictions for California (National Assessment Synthesis Team 2000); it began in March or April each year when rainfall had ceased for at least a week and none was forecast. The nutrient addition treatment was chosen to match the Nutrient Network protocol (Borer et al. 2014b) and to relax nutrient limitation as broadly as possible. N levels corresponded with the upper range of atmospheric nitrogen deposition values in California (Schlesinger et al. 1982, Fenn et al. 2003). Other nutrients, including P and K, are also present in nutrient deposition (Schlesinger et al. 1982, Newman 1995); however, their concentrations are probably lower than used

in our experiment. Both treatments were repeated yearly from 2010 to 2014.

Sampling and analyses of ecosystem variables and species richness

Productivity.—To measure aboveground productivity, we collected live and litter biomass from 25 × 25 cm subplots within each experimental plot in June 2014, dried these samples at 60°C for 72 h and weighed them. Because most plants in the communities are annuals, total aboveground biomass is a measure of annual net primary productivity.

Plant trait composition.—To assess trait composition, we first visually estimated cover for all plant species in 1 × 1 m subplots within each plot in 2014. We repeated the sampling three times (in April, June, and August) to capture peak cover for early, middle and late flowering species, and used the highest value for each species. All plots were surveyed by the same experienced person. For all species, we then measured SLA (leaf area in mm²/g dry mass), foliar C:N, and plant height, which are widely documented to be associated with the leaf economics spectrum and competitive ability for light, fertile and infertile systems, and water and nutrient manipulations (Wright et al. 2004, Dwyer et al. 2014, Reich 2014, Eskelinen and Harrison 2015, Kaarlejärvi et al. 2017). Trait data were measured from 10 individuals per species in the study area outside the experimental plots and representing control conditions, according to standard protocols (Pérez-Harguindeguy et al. 2013). We calculated community-weighted mean (CWM) trait values for each trait in each plot by multiplying each species' relative abundance (cover) in 2014 by its mean trait value, and summed across all species to form a single trait value per plot.

Species richness and exotic cover.—Species richness was recorded as the number of species in the 1 × 1 m plots where cover was sampled in 2014. For exotic cover, we

pooled the cover of all exotic species recorded in the plots in 2014.

Plant and litter quality.—To quantify plant and litter tissue qualities as influenced by watering and fertilization, we analyzed percent C and N in live biomass samples collected in 2014 and in litter samples collected in 2012. Litter samples were collected in an earlier year because they were later used to assess litter decomposition rate. Total C and N were measured using combustion coupled with thermal conductivity/IR detection (LECO FP-528, LECO Corporation, St. Joseph, MI, USA and TruSpec CN Analyzers, St. Joseph, MI, USA.) at the UC Davis Analytical Laboratory.

Soil C pools.—To assess soil C pools, we analyzed dissolved organic carbon (DOC), total soil organic matter, and microbial biomass C. In spring 2013, three 7.5-cm deep soil cores per plot were collected, composited, and stored at 4°C for less than 48 h before analyses. DOC was measured before and after a 5-d chloroform fumigation via extraction with 0.5 mol/L K_2SO_4 and analysis on a Shimadzu TOC-V CSH (Shimadzu Scientific Instruments, Columbia, MD, USA). To calculate microbial biomass carbon, the difference in DOC between initial and post-fumigation extracts was divided by 0.45 (Jenkinson et al. 2004). Organic matter was measured on another subsample via loss on ignition by A&L Western Laboratory (Modesto, California, USA).

Soil nutrient pools and cycling.—To assess soil nutrient pools and cycling, we measured litter decomposition rate, potential net N mineralization and nitrification rates, and concentrations of microbial biomass N, extractable soil ammonium (NH_4^+ -N), nitrate (NO_3^- -N), P, and K. To determine litter decomposition rate, we placed 3 g air-dried litter, collected in the fall 2012, into 10×10 cm nylon fiber bags and placed the litter bags on the soil surface in the same plots from which the litter had been collected. The bags were collected 9 months later and the remaining litter weighed to determine mass loss. Litter decomposition rate was calculated as $100 \times \text{final/initial}$ litter mass. Soil potential net N mineralization and nitrification rates were assessed in 2013 using an aerobic laboratory incubation (Hart et al. 1994). At the same time as initial 0.5 mol/L K_2SO_4 extractions, another subsample of field-moist soil was incubated in the dark at 22°C for 7 d and then similarly extracted. Extracts were stored at -20°C until colorimetric analysis for NH_4^+ -N and NO_3^- -N (Kempers and Kok 1989, Doane and Horwath 2003). Net N mineralization was calculated as the difference between post-incubation and initial NH_4^+ -N + NO_3^- -N and net nitrification as the difference between post-incubation and initial NO_3^- -N. Soil P was measured via sodium bicarbonate (Olsen) extraction and soil K was measured via ammonium acetate extraction by A&L Western Laboratory. In May 2014, we collected another set of soil samples that were analyzed for NH_4^+ -N and NO_3^- -N

concentrations using flow injection analysis at UC Davis Analytical laboratory. These were used in the calculation of slow-fast multifunctionality.

Slow-fast multifunctionality framework

We developed a novel way to test the effects of rainfall addition and nutrient enrichment on ecosystem transitions along the slow-fast cycling gradient. We assigned each ecosystem variable (function, pool or stoichiometry) either a positive or negative value (i.e., used normal or sign-reversed values) depending on whether a high value of the variable indicated a fast- or slow-cycling system, respectively (Table 1). For example, we used sign-reversed values for soil organic matter because high values indicate a slow-cycling system, whereas we used positive values for microbial biomass C because high values indicate a fast-cycling system. Therefore, low values of soil organic matter but high values of microbial biomass C would increase the slow-fast multifunctionality index. Our expectations were based on the framework of Wardle et al. (2004) and other literature (Table 1), where infertile systems are driven by slow process rates and low nutrient pools and fertile systems by fast process rates and high nutrient pools. Our ecologically based approach thus avoided subjective decisions about the desirability of positive or negative values of each variable (Byrnes et al. 2014). This is because the directionality of each variable (i.e., whether higher values are linked to higher or lower functioning) is not determined by a subjective decision from human demand but instead stems from a system's ability to perform as slow or fast cycling. For example, decisions on directionality in past studies have often involved assumptions that high levels of pools and functions are desirable, perhaps stemming from human demand for certain ecosystem services (Manning et al. 2018); however, these subjective assignments may not foster an understanding of the functioning of natural ecological systems. Instead, by linking functions to the slow-fast cycling, our approach does not take a human perspective on directionality, as directionality is determined by the nature of a functions performance along the slow-fast spectrum. Also, our metric intrinsically takes into account that not all functions can be maximized simultaneously (Allan et al. 2015, Meyer et al. 2018).

To calculate the slow-fast multifunctionality index, we standardized each variable (with normal or sign-reversed values assigned based on Wardle et al. 2004, see description above) to a 0–1 scale (Soliveres et al. 2016) to remove differences in measurement scales and units. We then calculated “average slow-fast multifunctionality” as the mean of all standardized variables. We used averaging rather than a threshold-based approach (Byrnes et al. 2014) because the latter was impossible for groups that had only a few variables (Table 1). This method is also intuitive, easy to understand and interpret and, up to now, the only multifunctionality metric with clear null expectations (for example that plant diversity and

multifunctionality are not related; Manning et al. 2018, Meyer et al. 2018). To decompose this average slow-fast multifunctionality into its major component parts, we recalculated the index for the following variable groups based on their ecological role: (1) productivity (live and litter mass), (2) plant trait composition (mean of three community-weighted mean traits), (3) plant and litter quality (mean C:N ratio from plants and litter), (4) soil carbon pools (mean of different soil C variables), and (5) soil nutrient pools and cycling (mean of different nutrient concentrations and functions related to nutrient cycling; see Table 1).

Statistical analyses

To analyze treatment effects on slow-fast multifunctionality (question 1), we fitted generalized linear mixed effects models (GLME) where the average slow-fast multifunctionality and its five components (productivity, plant trait composition, plant and litter quality, soil carbon pools, soil nutrient pools, and cycling), were each explained by watering, fertilization, and their interaction (fixed variables), with each response variable in its own model. Watering line was included as a random variable in all models. As our response variables were bounded between 0 and 1, we used binomial error structure. We corrected for overdispersion by including observation-level random effects (Elston et al. 2001).

To analyze how slow-fast multifunctionality was associated with diversity (question 2), we modeled bivariate relationships among average slow-fast multifunctionality, species richness, and exotic cover. We fitted generalized linear mixed effect regression models with either average slow-fast multifunctionality or slow-fast multifunctionality within each of the five ecological groups as the dependent variable, and species richness and exotic cover as independent variables. Watering line was included as a random variable and the models were corrected for overdispersion by adding a residual error as random variable in all models (Elston et al. 2001). Although we used regressions, we did not intend to imply causality.

To examine relationships between experimental treatments, species richness/exotic cover, and the five ecological slow-fast multifunctionality groups, and to investigate how much each of the five ecological groups contributed to the average slow-fast multifunctionality, we formulated a hypothetical model based on a priori knowledge and tested it using structural equation models (SEM) with a mixed effects error structure and watering line as a random effect. We included watering, fertilization and their interaction as categorical external predictors and included direct paths from these to species richness, exotic cover, and to the five ecological slow-fast multifunctionality groups. Relationships between species richness and exotic cover and ecological slow-fast multifunctionality groups were fitted as correlations. We also fitted causal paths from the five ecological slow-fast multifunctionality groups to the average slow-fast

multifunctionality. As the ecological groups could be correlated with each other, covariances between them were estimated. Note that there is no path between average multifunctionality and species richness/exotics because the five subgroups are a full decomposition of the variance in average multifunctionality.

All statistical analyses were carried out using R Statistical program version 3.5.1 (R Core Team 2018). We used the lme4 package for generalized linear mixed effects models (Pinheiro et al. 2018), the car package (Fox and Weisberg 2019) for *P* values and the piecewiseSEM package (Lefcheck 2016) for SEM.

RESULTS

Watering and fertilization interacted to affect the average slow-fast multifunctionality (Fig. 1a, Appendix S1: Table S1). Fertilization alone greatly increased the average slow-fast multifunctionality ($\chi^2 = 61.1$, $P < 0.0001$), i.e., it drove the grassland ecosystem toward faster cycling. However, fertilization and watering together pushed the system back toward slower cycling relative to fertilization alone (watering and fertilization interaction, $\chi^2 = 7.9$, $P = 0.0051$, Fig. 1a), although still faster than controls (Fig. 1a). Similar antagonistic interactions were seen in soil nutrient pools and cycling (Fig. 1b, $\chi^2 = 6.7$, $P = 0.0099$), soil C pools (Fig. 1c, $\chi^2 = 7.1$, $P = 0.0077$), and plant and litter quality (Fig. 1d, $\chi^2 = 9.4$, $P = 0.0022$). In contrast, aboveground plant community productivity and trait composition showed either synergistic or additive increases in fast-cycling characteristics in response to the joint treatment of watering and fertilization (watering and fertilization interaction, Fig. 1e, $\chi^2 = 5.3$, $P = 0.0218$, and Fig. 1f, $\chi^2 = 0.1$, $P = 0.8146$, respectively).

Transition of our grassland ecosystem toward faster cycling, i.e., higher values of the average slow-fast multifunctionality, was coupled with decreased plant species richness (Fig. 2a, $\chi^2 = 31.083$, $P < 0.0001$) and increased exotic cover (Fig. 2b, $\chi^2 = 51.022$, $P < 0.0001$).

The SEM model fitted our data well (Fisher's $C = 7.943$, $df = 8$, $P = 0.439$, $K = 27$, likelihood degrees of freedom (K), $n = 129$), and both reinforced the results from separate GLMM models and provided deeper insights on our data (Fig. 3). Fertilization alone exhibited a direct negative effect on species richness while at the same time it and watering increased exotics, productivity and the dominance of fast-growing plants. These were all negatively correlated with species richness, matching bivariate relationships (Fig. 2, Appendix S1: Fig. S1a, b), while productivity and dominance of fast-growing species were positively linked to abundance of exotics (Fig. 3).

Our SEM also revealed that high species richness was significantly positively associated with fast-cycling features of soil C pools (standardized path coefficient = 0.19, Fig. 3), although this relationship was not significant in the bivariate relationships (Appendix S1:

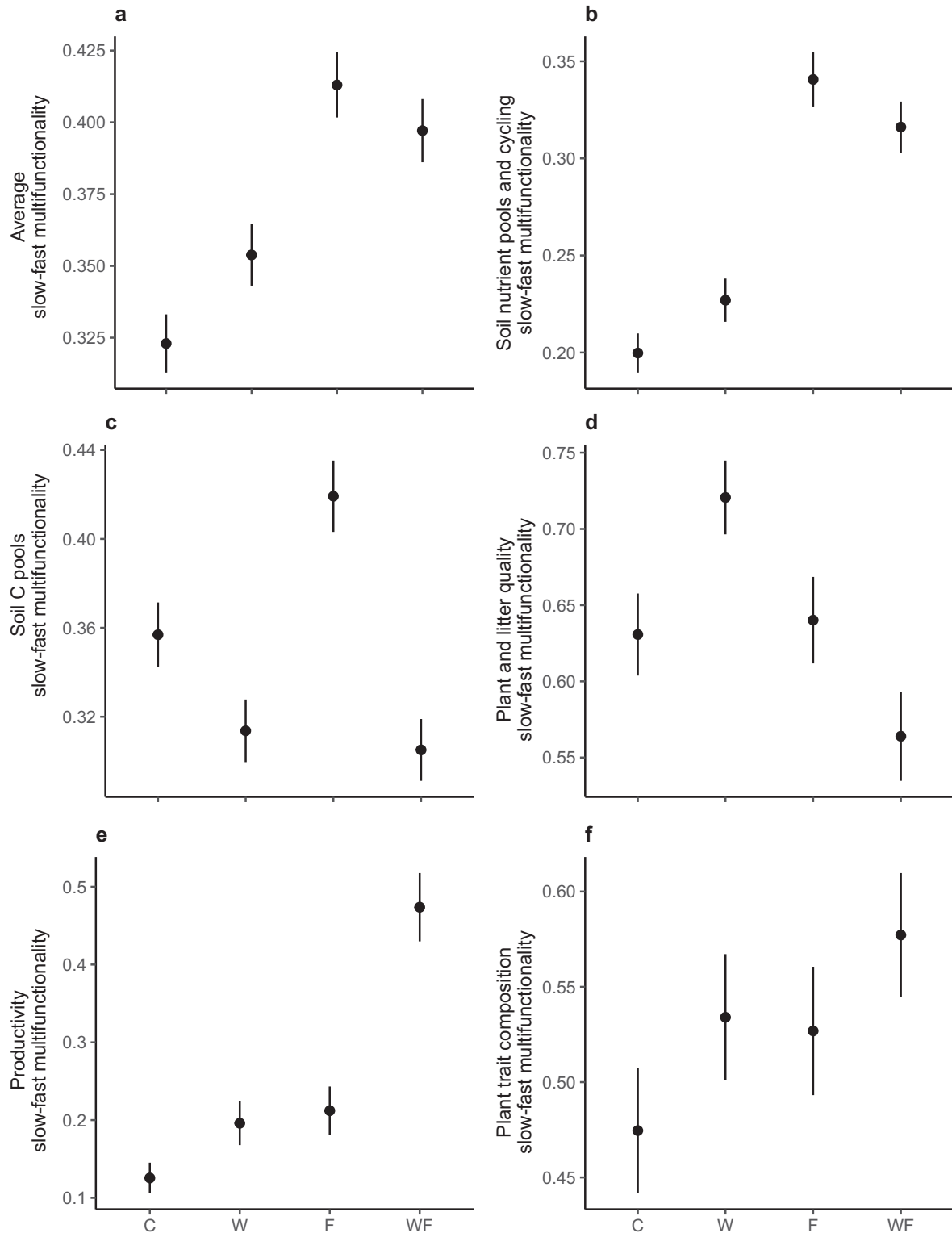


FIG. 1. Effects of watering and fertilization on (a) average slow-fast multifunctionality and on the five ecological slow-fast multifunctionality groups: (b) soil nutrient pools and cycling, (c) soil carbon pools, (d) plant and litter quality, (e) productivity, and (f) plant trait composition. Means and SEs are predictions from generalized linear mixed effects models with binomial error structure that were corrected for overdispersion. Higher values indicate increasing features of faster cycling systems. Note the different y-axis scales. C, control; W, watering; F, fertilization; WF, watering and fertilization.

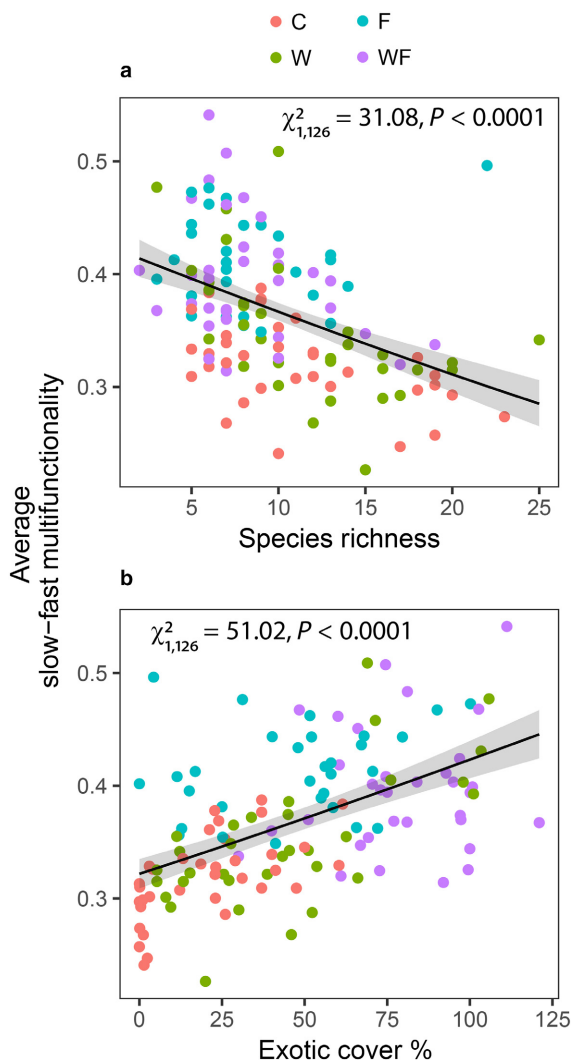


FIG. 2. Relationships between (a) average slow-fast multifunctionality and species richness and (b) average slow-fast multifunctionality and exotic cover in different treatment combinations. Fitted lines are from generalized linear mixed effects models with binomial error structure that were corrected for overdispersion. The gray areas indicate 95% confidence intervals. C, control; W, watering; F, fertilization; WF, watering and fertilization. [Color figure can be viewed at wileyonlinelibrary.com]

Fig. S1d). In contrast, there was no significant direct relationship between species richness and soil nutrient pools and cycling in our SEM model, despite a strong bivariate relationship between these variables (Fig. 3, Appendix S1: Fig. S1e), likely because the true causal pathways were via productivity and plant trait composition, which both correlated with soil nutrient pools and cycling (significant standardized path coefficient = 0.19 and 0.36, respectively, Appendix S1: Fig. S2). However, exotic cover was directly positively associated with fast-cycling features of nutrient pools and cycling (Fig. 3).

Fertilization also increased fast-cycling features of soil C pools and soil nutrient pools and cycling, the latter

effect being the strongest in the model (as indicated by the high value of standardized path coefficient = 0.83, Fig. 3). Nutrient pools and cycling also strongly contributed to the average slow-fast multifunctionality (standardized path coefficient = 0.67, Fig. 3).

DISCUSSION

Using a novel analytic framework designed to specifically measure transitions of ecosystems from slow to fast cycling, we demonstrate that resource-enhancing global changes can concordantly alter ecological functions, pools, and stoichiometry variables both above- and belowground, and result in a whole-ecosystem transition from slower to faster cycling in a natural grassland ecosystem. Importantly, we also demonstrate that this transition is associated with increased dominance by exotic species and loss of plant diversity in our system, suggesting that resource-enhancing global changes have the potential to simultaneously reduce diversity and alter ecosystem functioning.

Nutrient enrichment alone drove a shift of our grassland ecosystem as a whole from slower to faster cycling. It directly promoted fast-cycling features of plant trait composition, plant community productivity and soil C pools, and exhibited especially strong impacts on soil nutrient pools and cycling. This result is consistent with the faster process rates, larger nutrient pools, and greater productivity found in studies of nutrient addition effects on some single ecosystem variables (Mack et al. 2004, Knorr et al. 2005, Isbell et al. 2013a, Mueller et al. 2013, Leff et al. 2015). Our results extend these earlier findings by showing how nutrient addition enhances fast-cycling features of the whole grassland ecosystem, based on simultaneous shifts in 16 ecosystem functions, pools and stoichiometry variables, both above- and belowground, and as predicted by theory (Wardle et al. 2004). Our results were remarkably strong considering that they were applied across a soil-driven productivity gradient spanning 160–1,120 g/m^2 in aboveground plant biomass (Eskelinen and Harrison 2015), suggesting the applicability of our results to a wide range of grasslands. Overall, our findings underscore the pervasiveness of nutrient enrichment effects on whole grassland ecosystems, which may not be reversible unless a considerable amount of accumulated nutrients both above- and belowground is removed (Storkey et al. 2015, Tilman and Isbell 2015).

When nutrient addition was combined with rainfall addition, it pushed the grassland system back toward slower cycling and led to a partial divergence of above- and belowground responses. Rainfall addition diminished the positive effects of nutrients on labile soil C pools, and nutrient cycling and pools, although it enhanced the positive effects of nutrients on aboveground productivity and trait composition. Rainfall addition may have accelerated the leaching of nutrients and dissolved organic carbon, promoting fast but leaky nutrient cycling (see Appendix S1: Fig. S3, Ren et al.

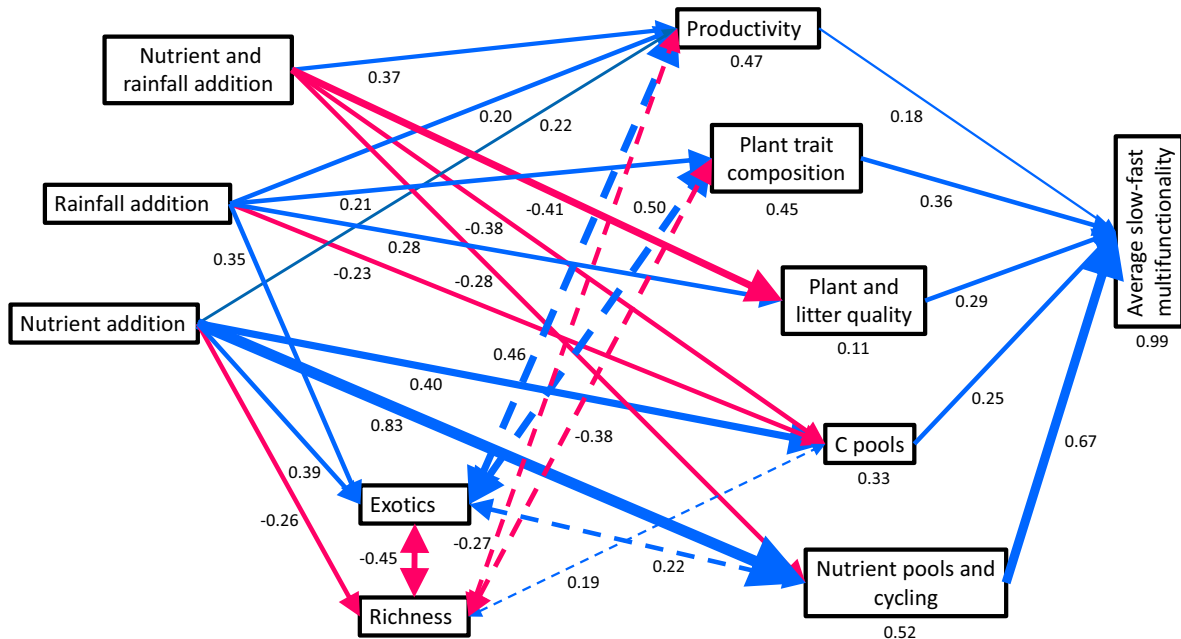


FIG. 3. Structural equation models exploring interactions among experimental treatments (watering and fertilization and their interaction), plant species richness/exotic cover, five ecological slow-fast multifunctionality groups, and average slow-fast multifunctionality. The SEM model fitted our data well (Fisher's $C = 7.943$, $df = 8$, $P = 0.439$, $K = 27$, likelihood degrees of freedom (K), $n = 129$). Boxes represent experimental treatments and measured response variables. A solid blue arrow from a treatment represents positive effect on the response variable, i.e., the treatment increases features of fast cycling, and a solid red arrow represents negative effect, i.e., the treatment increases features of slow cycling. Arrow from the joint treatment of watering and fertilization indicates significant interaction term, i.e., either synergistic (blue arrow) or antagonistic (red arrow) effect. Dashed blue arrows represent positive correlations and dashed red arrows represent negative correlations. Standardized path coefficients are given below each respective path/arrow. Conditional R^2 values (% based on a model with fixed and random effects) are given below each measured variable. Correlations between the five ecological slow-fast multifunctionality groups are not shown (even when significant) to simplify the figure (see Appendix S1: Fig. S2). Otherwise, only significant ($P < 0.05$) paths are shown in the figure. [Color figure can be viewed at wileyonlinelibrary.com]

2017). At the same time, the combination of water with nutrients may have allowed fast-growing plants to compete effectively against microbes for nitrogen (Kaye and Hart 1997, Moreau et al. 2015). Consequently, increased sequestration of nutrients in plant biomass under this combined treatment may have relaxed colimitation of plant growth by water and nutrients (Eskelinen and Harrison 2015), and thereby reduced the fast-cycling soil features. Overall, our results emphasize that the impacts of multiple global changes on multiple above- and belowground ecosystem properties and functions may deviate from those imposed by single factors (Eskelinen and Harrison 2015, Harpole et al. 2016).

Transformation from slower to faster cycling in our grassland system was accompanied by loss of plant diversity and invasion of exotic species. In line with many earlier studies, nutrient addition had a direct negative effect on plant species diversity (Huenneke et al. 1990, Clark and Tilman 2010, Isbell et al. 2013a, Borer et al. 2014, Eskelinen and Harrison 2015, Kaarlejärvi et al. 2017). However, in our study, diversity was also negatively correlated with the dominance of species with fast-growing traits (high SLA, tall stature) and high

community productivity that were both promoted by fertilization. These findings suggest that competitive exclusion by tall species capable of preempting light in nutrient enriched conditions (plant trait composition effects; Hautier et al. 2009) and other mechanisms, such as reduced niche dimensionality (i.e., direct effects of fertilization; Harpole et al. 2016) and increased litter (i.e., biomass effects; Clark and Tilman 2010), contributed to diversity loss under faster cycling. Loss of diversity and greater dominance of fast-growing species may make these communities vulnerable to future extreme events (Craven et al. 2018) and longer-term ecosystem eradication (Isbell et al. 2013b).

Exotic species cover exhibited positive response to nutrient addition and was associated with fast-cycling features of soil nutrient pools and cycling, as well as with fast-cycling plant community traits, high productivity, and low diversity, implying that exotics were to some extent responsible for many of the ecosystem changes in resource-enriched plots. In our grassland system, exotics are often taller and have higher SLA than natives. Our results are in line with earlier findings from studies investigating connections among exotics and individual

ecosystem properties/functions, in that exotics may modify nutrient cycling and budgets via their fast-growing traits, easily decomposable litter, accelerated microbial functioning (nitrification and N mineralization rates), and effects on microbial community composition (Ehrenfeld et al. 2001, Hawkes et al. 2005, Vilà et al. 2011, Lee et al. 2017). In addition, in our study nutrient addition directly positively affected many of the ecosystem variables, especially strongly soil nutrient pools and cycling, and these changes in the soil should have indirectly facilitated exotics. Our results add to the earlier findings by showing that exotics are linked to multiple interacting ecosystem variables simultaneously, and to a whole-ecosystem shift toward faster cycling. Increasing exotic dominance may thus lead to higher “multifunctionality” as defined by higher process rates (Ramus et al. 2017), but simultaneously lead to the erosion of diversity under enhanced rainfall and nutrients.

Although our results were dominated by the faster cycling and loss of diversity caused by resource addition, our SEM also identified a positive effect of species richness on fast-cycling features of soil C pools (i.e., high microbial biomass C and dissolved organic C concentrations, low soil organic matter). In more species-rich communities, even with less aboveground biomass (but possibly more root biomass), there may be more labile C released from roots as root exudates, thereby supporting greater microbial biomass (De Deyn et al. 2008, de Vries and Caruso 2016). In contrast, soil organic matter responded little to the treatments (Appendix S1: Fig. S3), suggesting that shifts in more stable C pools happen over longer timescales (Smith 2004).

In many multifunctionality studies, faster cycling and greater nutrient pools are considered to represent high ecosystem functioning (Maestre et al. 2012, Byrnes et al. 2014, Manning et al. 2018). Our results call for caution in equating faster cycling with high ecosystem functioning, to the extent that native diversity is also valued. Our results of whole-ecosystem transitions being linked to diversity loss are in line with those of Allan et al. (2015), who found that land-use intensification in grasslands increased agricultural productivity but was negatively associated with plant diversity. Inherently relatively low-productivity and slow-cycling systems may be especially vulnerable to any resource-enhancing global changes that accelerate process rates and may simultaneously erode native biodiversity. It is possible, however, that in extremely low-productivity systems, such as in arid ecosystems, greater availability of limiting resources could support both higher diversity and faster cycling, but this is yet untested.

Our novel slow-fast metric is based on a widely used theoretical framework by Wardle et al. (2004), integrates a whole-ecosystem approach with multifunctionality metrics (Byrnes et al. 2014, Manning et al. 2018), and uses an a priori theory-driven classification of variables representing above- and belowground functions, pools, and stoichiometry. We believe it may be of widespread

value in detecting larger ecosystem shifts that cover both above and below ground systems, as we found in analyzing the effects of resource enhancements (mimicking global changes) on a natural grassland ecosystem. Understanding such connections among ecosystem-level changes, biodiversity and exotic invasion is imperative for predicting the fates of natural ecosystems, for assessing how ecosystems changes will affect services valued by humans (Díaz et al. 2019), and for applying appropriate conservation actions in the Anthropocene.

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