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SPECIAL TOPIC: COORDINATED APPROACHES TO GLOBAL CHANGE RESEARCH

Global environmental change and the nature of aboveground net primary productivity responses: insights from long-term experiments

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Abstract Many global change drivers chronically alter resource availability in terrestrial ecosystems. Such resource alterations are known to affect aboveground net primary production (ANPP) in the short term; however, it is unknown if patterns of response change through time. We examined the magnitude, direction, and pattern of ANPP responses to a wide range of global change drivers by compiling 73 datasets from long-term (>5 years) experiments that varied by ecosystem type, length of manipulation, and the type of manipulation. Chronic resource alterations resulted in a significant change in ANPP irrespective of ecosystem type, the length of the experiment, and the resource manipulated. However, the pattern of ecosystem response over time varied with ecosystem type and manipulation length. Continuous directional responses were the most common pattern observed in herbaceous-dominated ecosystems. Continuous directional responses also were frequently observed in longer-term experiments (>11 years) and were, in some cases, accompanied by large shifts in community composition. In contrast, stepped responses were common in forests and other ecosystems (salt marshes and dry valleys) and with nutrient manipulations. Our results suggest that the response of ANPP to chronic resource manipulations can be quite variable; however, responses persist once they occur, as few transient responses were observed. Shifts in plant community composition over time could be important determinants of patterns of terrestrial ecosystem sensitivity, but comparative, long-term studies are required to understand how and why ecosystems differ in their sensitivity to chronic resource alterations.

Keywords Aboveground productivity · Hierarchical response framework (HRF) · Long-Term Ecological Research (LTER) Network · Nutrient addition · Precipitation manipulation

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Introduction

The scale, scope, and pace of change occurring in ecological systems today and forecast for the future are by all accounts unprecedented in human history (Vitousek et al. 1997; Lubchenco 1998; Sala et al. 2000; Smith et al. 2009). Indeed, we may have already exceeded key thresholds of climate change, biodiversity loss, and increased nitrogen (N) availability with regard to future ecosystem functioning for some systems (Rockström et al. 2009). Collectively, the global scale of these changes means that all ecosystems are, and will continue to be, impacted to some extent by global change drivers, leading to alterations of multiple ecosystem services (Foley et al. 2005; Schröter et al. 2005; IPCC 2013).

In general, global environmental changes can chronically alter resource levels either directly (e.g., increased atmospheric N deposition, elevated atmospheric CO_2 concentrations, increased precipitation variability) or indirectly (e.g., via warming, changes in biodiversity; Smith et al. 2009). The hierarchical response framework (HRF) was developed with the realization that species interactions, community dynamics, and ecosystem processes are now being driven by these chronic resource alterations, irrespective of natural or anthropogenic disturbance regimes (Smith et al. 2009). In this framework, mechanisms underlying an ecosystem response (e.g., either positive or negative changes in productivity, net ecosystem exchange, or nutrient cycling) are proposed to be hierarchical, ranging from the initial and relatively rapid responses of individuals (physiological plasticity) with potential shifts in the genetic composition of populations, to eventual alterations in species abundances (community re-ordering), and finally species turnover (immigration and loss) as resources continue to change over time (Smith et al. 2009). An assumption of the HRF is that large changes in ecosystem processes will be driven by altered species interactions that ultimately lead to changes in community composition (e.g., Jentsch et al. 2011; Jin and Goulden 2013).

A prediction of the HRF is that ecosystem responses to chronic resource alterations will be lagged and nonlinear over time (Fig. 1) because of the variable rates at which processes (physiological, species re-ordering, and species turnover) driving ecosystem response operate and the inherent nonlinearity in population dynamics. For example, physiological responses to changes in resources are typically immediate, leading to rapid ecosystem responses (e.g., Mendelssohn and Morris 2000; Wang et al. 2012; Sistla et al. 2013), whereas species re-ordering takes longer to occur as altered competitive interactions become manifest and resources accumulate enough to exceed the physiological limits for some species (e.g., Hautier et al. 2009; Isbell et al. 2013). The expectation is that ecosystem responses driven by species re-ordering or turnover should be larger than those driven by physiological responses, and thus, given that the former is expected to take longer than the latter, the resultant response trajectory over time should be lagged and nonlinear (Fig. 1). Alternatively, ecosystem responses over time may be gradual or linear if the magnitude or rate of change is similar for physiological, community re-ordering, and species turnover processes. Regardless of whether ecosystem responses are linear or nonlinear, and lagged or not, a prediction of the HRF is that there will be continuous directional change over time in response to chronically changing resource levels associated with global change drivers.

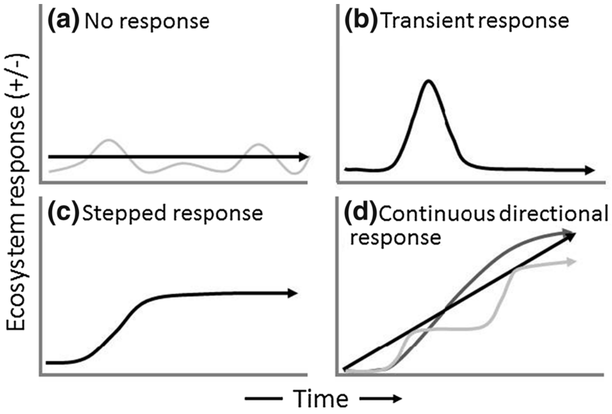

Fig. 1 Hypothesized terrestrial ecosystem responses (either positive or negative) to chronic resource alterations over time: **a** no (or idiosyncratic) response; discontinuous (**b** transient or **c** stepped); and **d** continuous directional, either linear (*black line*), nonlinear (*dark gray line*), or including multiple stepped responses (*light gray*) as a result of different processes (physiological, species reordering, species turnover) driving the response at different time frames (modified from Smith et al. 2009). For the latter, discontinuous stepped responses (**c**) can turn into directional responses over time, particularly if there are extended lags in response (*light gray line* in **d**). Note that the early lags in response depicted for (**b**–**d**) may not necessarily occur, particularly if rapid physiological responses drive initial ecosystem response

An alternative outcome is that ecosystem responses, even to chronic resource changes, could be discontinuous over time, as a result of transient or stepped ecosystem

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responses (Fig. 1). In these cases, other factors may constrain ecosystem response, such as the longevity of species in the community (i.e., an ecosystem dominated by long-lived species, such as in forests, may respond only minimally during the short time frames of many studies), or whether the regional species pool includes species adapted to the changing conditions or other resources limit ecosystem response (Shaver et al. 2000; Huxman et al. 2004; Luo et al. 2004; Ricklefs 2004; Ladwig et al. 2012). Finally, an ecosystem may exhibit no change over time (or an idiosyncratic response), even when resource levels are altered (Fig. 1). This category of response could emerge for a number of reasons. For example, the resource being altered may be nonlimiting (LeBauer and Treseder 2008). Alternatively, interactions among multiple drivers may result in no net change (Shaw et al. 2002; Reich 2009; Leuzinger et al. 2011; Morgan et al. 2011), or the lack of change over time could be due to other attributes of the community, such as high diversity, dominance, and compensatory responses among species or functional traits (Allan et al. 2011; Hallett et al. 2014; Mariotte et al. 2013; Jung et al. 2014).

While much is known about how alterations in resources affect ecosystem responses (Rustad et al. 2001; Worm et al. 2002; LeBauer and Treseder 2008; Wu et al. 2011), far less is known about how ecosystems differ in the magnitude and pattern of responses over time. This is, in part, due to the scarcity of long-term studies that manipulate resources chronically, i.e., on a yearly or more frequent basis, and because many resource manipulation studies are conducted in herbaceous ecosystems (e.g., Suding et al. 2005; LeBauer and Treseder 2008). Long-term studies in a wide range of ecosystems are critical for assessing differential ecosystem sensitivity and determining how ecosystem responses may change over time. With the maturation of long-term ecological research programs globally (e.g., the International Long-Term Ecological Research (ILTER) Network) and greater emphasis on extending experiments beyond the short term (i.e., typical 3-year funding cycle), such long-term studies are now becoming increasingly available (Knapp et al. 2012b).

Here, we conducted a meta-level analysis of long-term datasets (ranging from 6 to >20 yrs in duration) from 73 individual experiments conducted within 36 different communities (e.g., forest, grassland, wetland). For each of these experiments, resources have been altered annually or more frequently, either directly (i.e., via nutrient additions) or indirectly (i.e., via warming, disturbances or changes in biotic structure), and responses in aboveground net primary productivity (ANPP) were estimated each year (Table 1). These experiments represented unique combinations of ecosystem type, manipulation length and type of manipulation. We focused on ANPP because it is widely regarded as an integrated measure of ecosystem function in terrestrial ecosystems (McNaughton et al. 1989), and it readily scales across methods and ecosystem types (Fahey and Knapp 2007). Given that one of our goals was to assess patterns of ANPP response over time (Fig. 1), we restricted our analysis to those experiments where annual measures of ANPP were available for 5 or more years. To analyze these data, we used effect sizes to assess the magnitude and direction of response of ANPP to experimentally induced changes in several key resources. We also determined if these ANPP responses varied with the length of the experiment, ecosystem type, or the type of resource manipulated. In addition, we tested for the four types of ANPP response patterns expected over time with chronically changing resources (Fig. 1). Based on this analysis, we determined the frequency of occurrence of the four types of response patterns, and examined whether their frequency of occurrences differed with ecosystem type, length of manipulation, or the type of manipulation. Finally, for a subset of experiments in which plant community data were available, we determined if significant ANPP responses were correlated with changes in community composition over time, a key prediction of the HRF.

Materials and methods

To assess the sensitivity and patterns of ANPP response in terrestrial plant communities (including salt marsh), datasets were compiled from experiments that chronically manipulated at least one resource over time (i.e., on a yearly or more frequent basis) either (1) directly by adding nutrients, increasing CO_2, or altering precipitation, or (2) indirectly through warming or by altering biotic structure via grazing, fire, species removals, or biodiversity manipulations. These datasets were identified through a survey of the 26 Long-Term Ecological Research (LTER) sites in the US (Knapp et al. 2012b) and through personal communication with investigators at other well-known long-term research sites. The 73 datasets included in our data synthesis comprised 36 different plant communities at 13 sites (Table 1). These were selected based on the type of manipulation (direct or indirect resource alteration), the length of the experimental manipulation (i.e., >5 years), and whether ANPP was measured as a response variable. In all but two cases (resource removal via pumping water out of salt marsh or preventing rainfall in forest), direct manipulations of resources occurred via additions. Where an experiment imposed multiple levels of the same treatment, only the highest level was used in this analysis in order to capture the greatest change in resource availability over time.

For each type of ecosystem, ANPP was estimated using standard methods (Fahey and Knapp 2007, Table 1), and although these methods may differ between ecosystem

Table 1 Summary of long-term experiments included in the study

Site	Ecosystem type	No. of community types	Experiment length	Chronic resource manipulation				References
				Water	Nutrients	CO_2	Other	
Ascutney	Forest	1	14	–	3N	–	–	Aber et al. (1998)
Arctic LTER	Herbaceous	2	14	–	10N,5P	–	–	Gough and Hobbie (2003)
			11	–	10N, 5P	–	–	Hobbie et al. (2005)
Cedar Creek LTER	Herbaceous	2	10	–	4N	550 ppm	Biodiversity	Reich (2009)
		4	26	–	40N	–	–	Tilman (1987)
Bonanza Creek LTER	Forest	6	19	Precip. removal	14N, 3C	–	–	Yarie and Van Cleve (1996)
Duke FACE	Forest	1	12	–	11N	550 ppm	–	Oren et al. (2001)
Harvard Forest LTER	Forest	2	19	–	15N; 5N, 7S	–	–	Aber and Magill (2004)
Kellogg Biological Station	Herbaceous	1	19	–	12N	–	–	Foster and Gross (1998)
Konza Prairie LTER	Herbaceous	1	22	–	10N, 3P	–	Mowing, burning	Kitchen et al. (2009)
		2	17	Water addition	–	–	–	Collins et al. (2012)
		1	8	–	10N, 10P	–	–	Avolio et al. (2014)
McMurdo Dry Valley LTER	Other (dry valley)	3	10	Water addition	–	–	Temperature	Simmons et al. (2009)
North Inlet	Other (salt marsh)	2	25	–	30N, 15P	–	–	Sundareshwar et al. (2003)
Plum Island Ecosystem LTER	Other (salt marsh)	1	10	–	15N, 7.5P	–	–	Morris et al. (2013)
Sevilleta LTER	Herbaceous	1	6	–	10N	–	–	Ladwig et al. (2012)
		2	12	–	–	–	Herbivore removal	Báez et al. 2006
Virginia Coastal LTER	Other (salt marsh)	5	11	Pumped, border	–	–	–	

For each experiment, single or multiple resources were directly (nutrients, CO_2, water) or indirectly (temperature, other—biotic) manipulated on an annual or more frequent basis. The experiments encompassed three ecosystem types (forest, herbaceous-dominated, or other—coastal salt marsh and Antarctic dry valleys) and 36 community types, and ranged in duration from 6 to 26 years

Nutrients: *N* nitrogen (g m^{-2}; mol m^{-2} for salt marsh), *P* phosphorus (g m^{-2}; mol m^{-2} for salt marsh), *C* carbon (kg m^{-2}), *S* sulfur (g m^{-2})

types (e.g., forest vs. grassland), they provide comparable estimates of ANPP (Fahey and Knapp 2007). At herbaceous sites, ANPP was generally estimated as current year's aboveground growth harvested at ground level at the time of peak biomass. One exception was ANPP at the Sevilleta LTER, which was estimated using allometric equations (Muldavin et al. 2008). Aboveground productivity was generally estimated at forested sites as litterfall plus increases in basal area. At the McMurdo LTER dry valley site, ANPP was measured as the concentration of chlorophyll *a* (chla) in surface soils. In addition, 13 primarily herbaceous communities representing six experiments from five sites also had associated long-term plant species composition data collected concurrently with ANPP.

We used the test statistic, Hedges' *d*, to assess the magnitude and directionality of ANPP responses to chronic resource manipulations and to determine how these may differ with ecosystem type (forest, herbaceous-dominated, other: salt marsh and Antarctic dry valleys), length of manipulation (short: 6–10 yrs, mid: 11–20 yrs, and long: >20 yrs), and type of manipulation (nutrients: N, P, C, and CO_2; climate: water, temperature; biotic: biodiversity manipulation, disturbance, herbivore removal; Table 1). For each of the 73 datasets, we averaged ANPP over time for the treatment (ANPP_{trt}) and control (ANPP_{ctl}) plots to determine ANPP effects using the following equation (Hedges and Olkin 1985):

$$d_{\text{ANPP}} = \frac{(\text{ANPP}_{\text{trt}} - \text{ANPP}_{\text{ctl}})}{\sqrt{\frac{(n_{\text{trt}}-1)s^2_{\text{trt}}+(n_{\text{ctl}}-1)s^2_{\text{ctl}}}{n_{\text{trt}}+n_{\text{ctl}}-2}}} J,$$

where $J = 1 - \frac{3}{4(n_{\text{trt}}+n_{\text{ctl}}-2)-1}$ to correct for small sample sizes.

Following Preisser et al. (2005), we calculated the mean Hedges' *d* across experiments in two ways. First, we calculated the absolute value of Hedges' *d* to remove the confounding influence of directionality of the response from our evaluation of magnitude (Preisser et al. 2005). The second measure took into account effect direction; Hedges' *d* was allowed to be either positive or negative for individual experiments. Because our data were non-normal, we report 95 % confidence intervals derived from bootstrapping (MetaWin 2.1). Effect sizes were interpreted to be significant (either positive or negative) if the 95 % bootstrap CIs excluded zero and did not overlap between groups.

We used repeated measures ANOVAs (rmANOVAs) to classify the ANPP response to the experimental treatments into one of four hypothesized response types (Fig. 1). These rmANOVAs were performed separately for each of the 73 individual datasets, with the absolute difference in ANPP between the mean of the treatment and the control for each year (hereafter, "absolute ANPP difference") as the response variable, treatment as a fixed effect, and year as a repeated effect. Given the potential for both positive and negative ANPP responses over time to resource manipulations, these responses could cancel each other out, effectively resulting in no long-term response. Thus, we used the absolute ANPP difference to detect patterns of change in ANPP response over time. Based on the rmANOVAs, the 73 experiments were classified into four response types: (1) no response—year effect only, (2) transient response—year effect and year × treatment interaction, (3) stepped response—year and treatment effects, with no interaction, and (4) directional (continuous) response—treatment effect and year × treatment interaction.

For the 13 experiments with plant community data collected concurrently with ANPP, plant community dissimilarity was calculated between the treatment and control plots using Bray–Curtis distance matrices. Plant community dissimilarity was then regressed against the absolute ANPP difference for each experiment to determine whether the change in ANPP was related to changes in community dissimilarity over time.

Repeated measures ANOVAs and regression analyses were performed using SAS version 9.3, and significance was set at $P \leq 0.05$.

Results

For the 73 datasets included in our analysis, absolute d_{ANPP} across all experiments was significantly different from zero, with the largest ANPP effects in forest ecosystems (Fig. 2). However, the direction of the effects differed with ecosystem type; forests generally had negative ANPP effects, while herbaceous ecosystems responded positively to chronic resource alterations (Fig. 2b). When combined, there was no overall ANPP effect when the relative Hedges' *d* (with directionality) was calculated. The direction of ANPP effects also differed with manipulation length, with mid-duration ANPP effects usually negative, and short- (6–10 yrs) and long-duration (>20 yrs) effects positive (Fig. 2b). Given the difference in the direction of ANPP effects between ecosystem types, we examined ANPP responses for each ecosystem type separately. This revealed that the mid-duration negative effects were driven by the large number of forest studies with negative ANPP effects, while the herbaceous studies with positive ANPP responses were primarily either short- or long-duration manipulations (Fig. 3). Similarly, the lack of ANPP responses to nutrient manipulations overall (Fig. 2b) was driven by opposing responses of forest (negative d_{ANPP}) vs. herbaceous (negative d_{ANPP}) ecosystems.

All four predicted patterns of ANPP response over time (i.e., no response, transient, stepped, or directional) to chronic manipulations in resources were observed for the 73 datasets analyzed (Fig. 4, Table S1 of the Electronic supplementary material, ESM). Across all ecosystem types, the most frequent response (47.9 % of the datasets) was no significant change in the absolute ANPP difference over time (i.e., no treatment effect, or year × treatment interaction; Fig. 5). The next most common pattern was a stepped response (i.e., significant treatment and year effects; 31.5 % of the datasets), followed by a directional response (i.e., significant treatment and year × treatment effects; 15.1 % of the datasets). Transient responses were the least common (i.e., significant year effect and year × treatment interaction; 5 % of the datasets). The frequency of responses for the four categories differed with ecosystem type; forests and other (salt marshes and dry valleys) ecosystems tended to exhibit either no response (59.2 % of 27 and 52.6 % of 19 datasets, respectively) or a stepped response (40.7 % of 27 and 31.6 % of 19 datasets, respectively). In contrast, directional responses were most common for herbaceous ecosystems (33.3 % of 27 datasets, Fig. 5), though stepped and no-effect responses were frequent as well (25.9

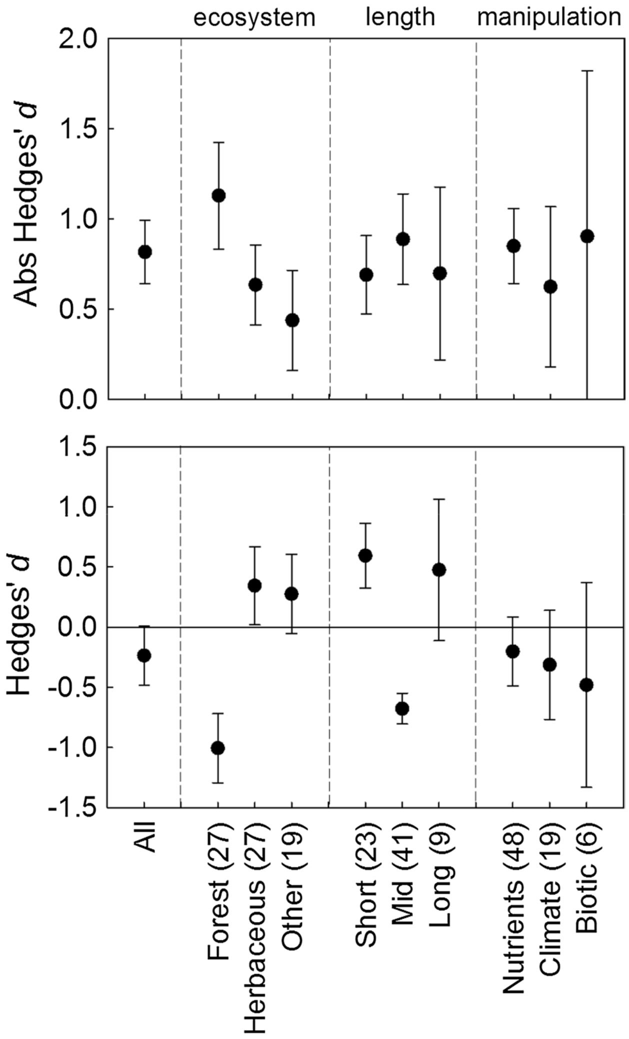

Fig. 2 Aboveground net primary production (ANPP) responses to chronic resource alterations, expressed as **a** absolute Hedges' *d* (d_{ANPP} multiplied by 1 if positive and −1 if negative) or **b** relative Hedges' *d*. Mean absolute and relative Hedges' *d* was calculated across all 73 datasets (*All*) and by ecosystem type (*ecosystem*; *Other* = salt marsh and dry valleys), experiment length (*length*; *Short* = 6–10 years, *Mid* = 11–20 years, *Long* = >20 years), and manipulation type (*manipulation*; see Table 1 for details). Shown are 95 % bootstrapped confidence intervals. Effect sizes are significant if the 95 % confidence intervals do not overlap with zero and between categories. *Numbers in parentheses* are the number of datasets in each category

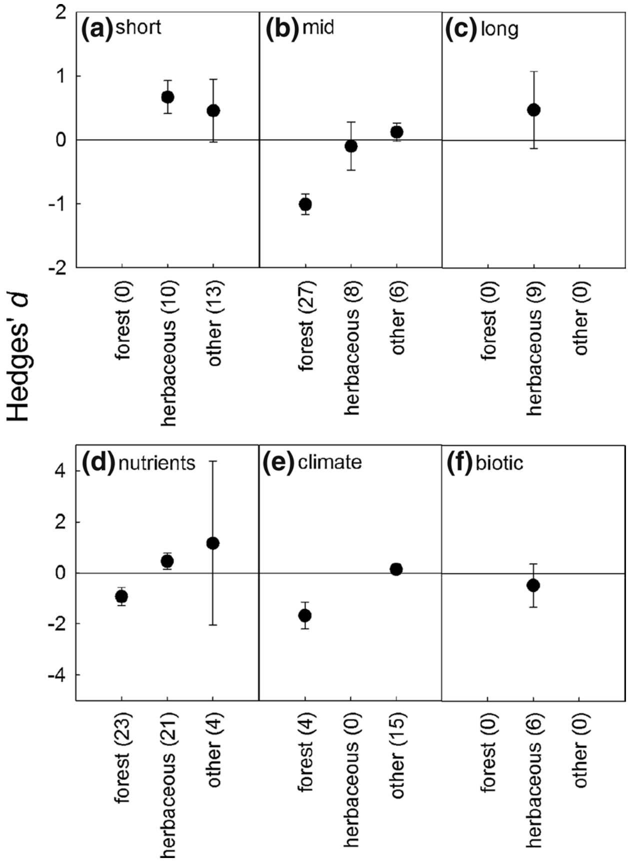

Fig. 3 Aboveground net primary production (ANPP) responses, expressed as relative Hedges' *d* (see Fig. 2), separated by ecosystem type and (*top*) length of experiment [**a** *short* (6–10 years), **b** *mid* (11–20 years), and **c** *long* (>20 years) experiment lengths] and (*bottom*) type of manipulation [**d** *nutrients*, **e** *climate*, and **f** *biotic*]. *Numbers in parentheses* are the number of datasets in each category

and 29.6 % out of 27 datasets, respectively). The length of the chronic resource manipulation also appeared to affect patterns of ANPP response, with no effect observed more often with short-term (<10 years) manipulations (43.5 % of 23 datasets), while directional change was most evident in long-term (>20 years) manipulations (55.6 % of 9 datasets). Length of experiment had little effect on stepped and transient patterns (34.1 % of 44 vs. 33.3 % of 9 datasets; Fig. 5). Finally, the type of manipulation affected the pattern of ANPP response, with climate manipulations (water and temperature) generally having no effect (63.2 % of 19 datasets), and nutrient manipulations generally having no effect or a stepped response (39.6 and 35.4 % of 48 datasets, respectively; Fig. 5).

In cases where ANPP responses to chronic resource alterations were significant over time, we assessed whether the response was driven by changes in the plant community, a key prediction of the HRF. Plant community data were available for only 13 datasets (9 directional, 2 stepped, 2 no effect). For those experiments, plant community dissimilarity was significantly and positively correlated with ANPP response for only two datasets (Table S2 of the ESM). In the case of moist-acidic tundra (ARC), community dissimilarity increased over time as the absolute ANPP difference increased over time, suggesting that community change was a primary driver of directional ecosystem response with chronic changes in N and P (Fig. 6a). Similarly, water removal (via pumping) in a salt marsh (VCR) resulted in a

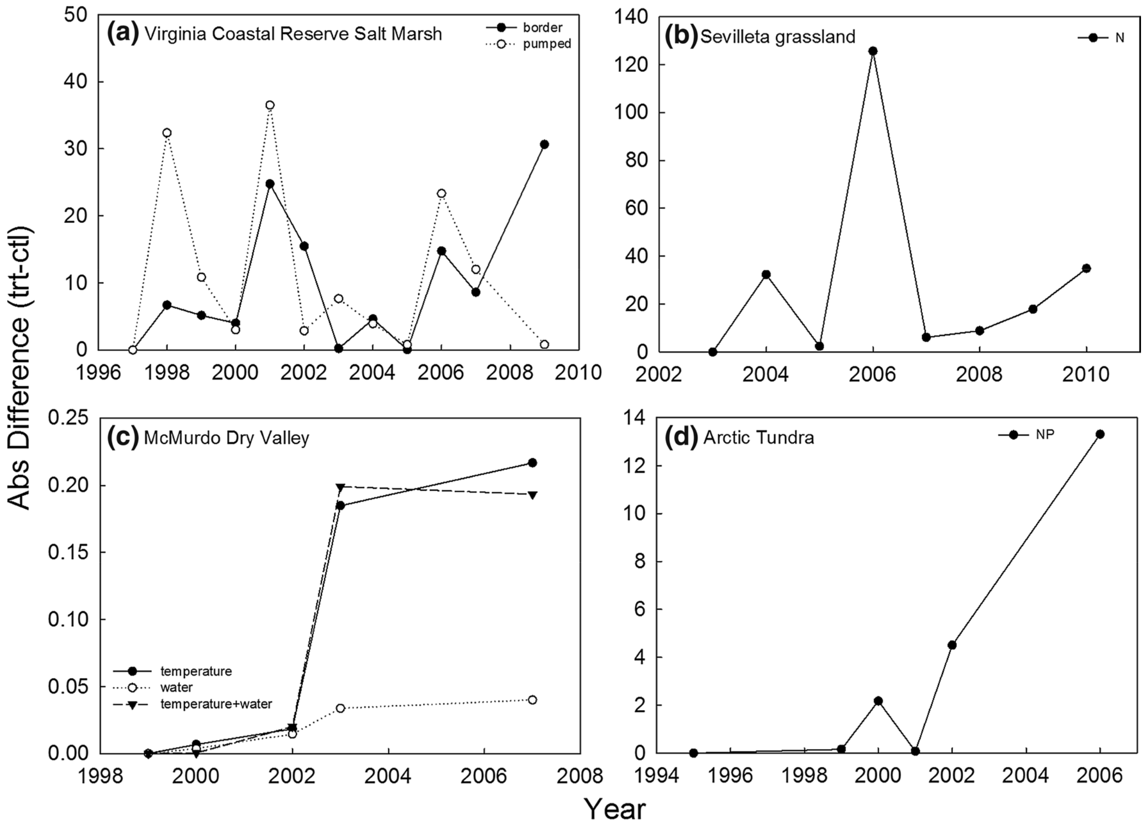

Fig. 4 Four examples of the types of aboveground net primary production (ANPP) responses [expressed as the absolute ANPP difference between treatment (*trt*) and control (*ctl*); see text] to chronic resource alterations: **a** no response (significant year effect), **b** transient response (significant year and year × treatment effects), **c** stepped response (significant year and treatment effects), and **d** directional response (significant treatment and year × treatment effects, see Table S1 of the ESM)

change in ANPP that tracked increases in community dissimilarity (Fig. 6b).

Discussion

The goals of this study were to assess how chronic resource alterations affected (1) the magnitude and direction of ANPP response as influenced by ecosystem type, duration of resource manipulation, and the type of resource manipulated, and (2) the pattern of temporal response (e.g., directional, stepped, transient) as predicted by the HRF (Fig. 1). We also determined if changes in plant community composition were associated with changes in ANPP over time, consistent with the prediction that community change is an important driver of ecosystem response to chronic resource alterations (Smith et al. 2009).

We found that ANPP responses (absolute d_{ANPP}) to chronic manipulations in resources (either direct or indirect) averaged over time were significant (i.e., different from zero), but that responses varied with ecosystem type; the largest ANPP effects occurred in forests (Fig. 2). Similarly, the directionality (relative d_{ANPP}) of ANPP responses varied with ecosystem type, with forests exhibiting significant negative ANPP responses and herbaceous ecosystems significant positive ANPP responses (Fig. 2). These contrasting ANPP responses resulted in no overall ANPP effect based on relative d_{ANPP}, which contrasts with the significant ANPP effects observed when using absolute Hedges' *d*. Absolute ANPP response (absolute d_{ANPP}) did not differ significantly with length or type of manipulation, although the 95 % confidence interval did not overlap with zero in any of the cases. However, once directionality was taken into account (relative d_{ANPP}), ANPP responses were negative and significant for mid-duration (11–20 yr) manipulations, positive and significant for short-duration (6–10 yrs) experiments, and not significant for long-duration (>20 yr) manipulations. Some of this variation can be explained by the fact that most of the mid-duration manipulations were in forests (Fig. 3), whereas there were no short- or long-duration manipulations in forests. Further, there were relatively few studies >20 yrs in duration (Figs. 2, 3). This emphasizes the need for global change manipulations that extend well beyond the typical duration

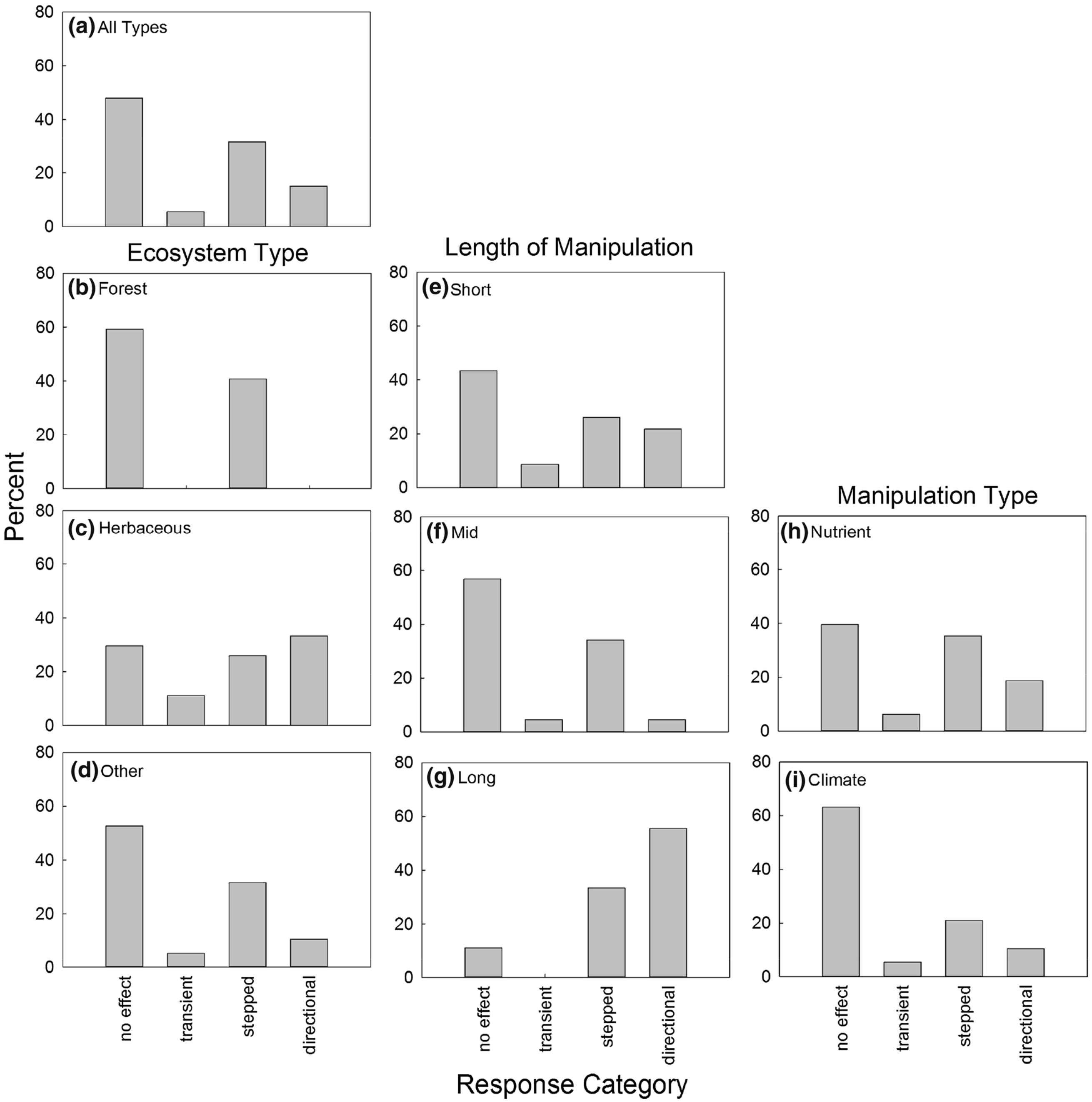

Fig. 5 Proportions of different types of ANPP responses over time to chronic alterations in resources. Four categories of response were identified, based on rmANOVAs (Table S1 of the ESM). Shown are the response frequencies for (*left*) ecosystem type [**a** all, **b** forests, **c** herbaceous, and **d** other (salt marshes, dry valleys)], (*middle*) length of experiment [**e** short (6–10 years), **f** mid (11–20 years), and **g** long (>20 years) experiment lengths], and (*right*) type of manipulation [**h** nutrients and **i** climate]

of ecological experiments, even those considered to be long-term (i.e., >10 yrs, Knapp et al. 2012b), particularly in forest ecosystems.

Similar to length of manipulation, there was a significant ANPP response to nutrient and climate manipulations based on absolute d_{ANPP}, but no significant effects were detected with relative d_{ANPP} (Fig. 2). These opposing patterns arose as a result of forests exhibiting negative responses to nutrient and climate manipulations but herbaceous and other ecosystems exhibiting positive responses (Fig. 3). Long-term biotic manipulations were few in number, making it difficult to detect significant effects for these types of experiments. Yet, such experiments are needed given that biotic alterations, such as those arising via

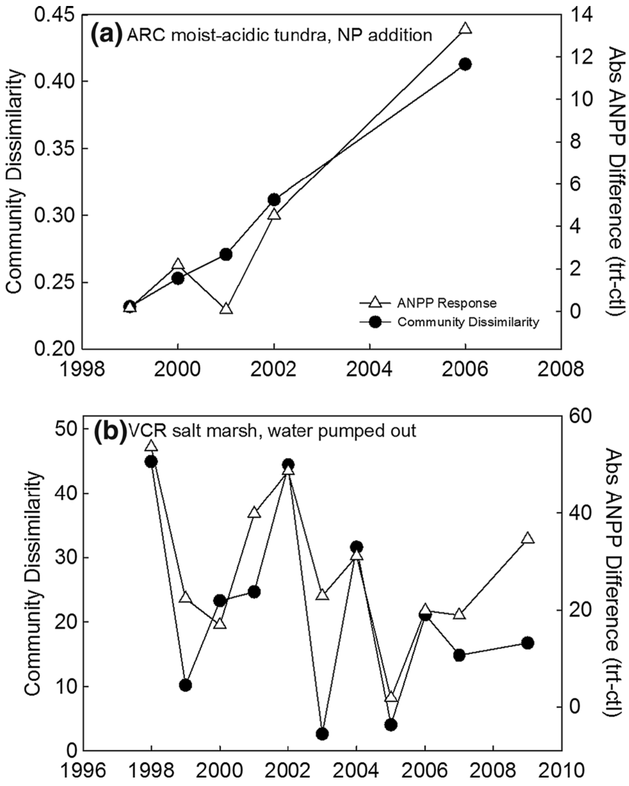

Fig. 6 The two community types—**a** moist-acidic tundra and **b** coastal salt marsh—that displayed a significant relationship between the response in ANPP to chronic alterations in resources (calculated as the absolute ANPP difference, see Fig. 4) and plant community dissimilarity between control and treatment plots (Table S2 of the ESM)

long-term changes in biodiversity and disturbance regimes, are an important aspect of global environmental change and a potentially important indirect driver of chronic resource alterations (Vitousek et al. 1997; Smith et al. 2009).

The contrasting ANPP effect patterns observed with our analysis show how the use of absolute vs. relative Hedges' *d* can lead to very different conclusions concerning how chronic resource alterations impact ecosystems. When combining response data from multiple drivers that may result in different directionality in ANPP effects (i.e., nutrients increase ANPP whereas water deficits or warming decrease ANPP) or ecosystems or communities that may exhibit opposing responses, we recommend that both absolute and relative Hedges' *d* metrics be used. This would allow for the assessment of how direction of effects influences conclusions concerning overall effect sizes.

In addition to examining mean ANPP effects, we also assessed how the absolute difference in ANPP response varied over time. The primary pattern of ANPP response over time (~48 % of the experiments) was that of no treatment effect or an idiosyncratic response (Fig. 4), suggesting that many communities are resistant to changes in functioning over time as resources are altered (Vittoz et al. 2009). This contrasts with the significant mean ANPP effect we detected, and suggests that while ANPP responds to resource alterations when averaged over time, this does not necessarily provide information on the temporal pattern of response. This is an important distinction given that most meta-analyses focus on mean effect sizes and not patterns of effects over time. The lack of ANPP response over time is surprising given that many of the experiments included in our study directly increased resource availability via nutrient additions (Table 1). However, many grassland ecosystems, for example, do show mechanisms of resistance to perturbations (Vittoz et al. 2009; Hallett et al. 2014). Alternatively, the lack of response could have been due to limited power in detecting change over time, particularly for the shorter-term experiments. Clearly, additional long-term (>10 yr) resource manipulation experiments are needed to determine how chronic resource alterations affect dynamics, stability and trajectories of change across a range of ecosystems.

When significant effects of chronic resource alterations occurred (52 % of the experiments), the pattern of ANPP response over time was quite variable. Contrary to predictions of the HRF, continuous directional responses were relatively uncommon across all community and ecosystem types (15 %). Instead, stepped responses were the most common pattern observed (32 %), which suggests that a resource-driven shift to some alternative state may have altered ecosystem function (e.g., Fig. 4c). State changes are increasingly becoming recognized as an important potential outcome of global change drivers, and this response is consistent with theory (Carpenter 2001; Scheffer et al. 2001; Barnosky et al. 2012). Alternatively, it may be that these stepped responses may emerge as nonlinear continuous responses if given enough time (Fig. 1). Finally, although several recent papers have argued that transient ecosystem responses may be a common outcome of resource manipulations (Luo et al. 2001; Leuzinger et al. 2011), we found transient responses to be relatively rare (see also Clark and Tilman 2010). This suggests that greater confidence may be placed in significant ANPP responses observed in shorter-term studies.

Although a stepped response was the most frequent pattern across all ecosystem types, this pattern differed when ecosystem types were examined separately (Fig. 4). For temperate forests and other ecosystems (salt marshes, Antarctic dry valleys), a stepped pattern of response was most frequently observed, with no occurrence of directional or transient responses for forests, and an infrequent occurrence of these patterns for salt marsh and dry valley ecosystems (11 and 5 %, respectively). The HRF predicts that differences among ecosystems in their patterns of response may, in part, be due to the longevity of dominant plant species in the ecosystem. For example, the stepped responses for many of the forest ecosystems studied here could represent a portion of a longer-term continuous change pattern of response (Fig. 1d), with much of the pattern driven by physiological responses, as species turnover times often exceed the time frames of many experiments (Chave et al. 2008; Runkle 2013). In contrast, directional change in herbaceous ecosystems may occur more rapidly due to relatively high turnover rates of herbaceous plant species (Gross et al. 2000; Collins et al. 2008). Indeed, a continuous directional response was the most frequent pattern observed for herbaceous ecosystems. Thus, species longevity could be an important determinant of how ecosystems respond to global environmental change (Cleland et al. 2012).

In addition to differences in ecosystem attributes (e.g., longevity of dominant species), the HRF predicts that the availability of limiting resources also may, in part, determine the rate and magnitude of response over time to chronic resource alterations. Factors that may influence the availability of limiting resources, and thus the variation in the pattern of ecosystem response observed, are the magnitude, direction (addition or removal), and intensity of resource manipulation. Furthermore, it may take an extended period of time for a chronic resource manipulation to alter resource availability to the extent that species tolerances are exceeded or an ecosystem crosses a resource threshold, as in the case of N saturation (Aber et al. 1998). Indeed, we found that the greatest frequency of stepped and directional responses occurred with the longer-term (>11 years) manipulations of resources, particularly those >20 years, suggesting that an increase in resource availability may have influenced the patterns of ecosystem response observed (Fig. 5). Unfortunately, these long-term experiments were primarily limited to herbaceous communities. Finally, the type of resource manipulation could also affect the pattern of ANPP response over time, with resources that have a potential to accumulate (i.e., N and P) more likely to result in directional or stepped response patterns (e.g., Clark and Tilman 2008). Although the primary response to either nutrient or climate manipulation was no effect (40 and 63 %, respectively), stepped and directional responses were more common with long-term nutrient manipulations (35 and 19 %) than climate manipulations (21 and 11 %, Fig. 5). Although an important aspect of resource availability is the standing amount (pool size) of a particular resource in an ecosystem prior to the resource manipulation, this information was not available for our analysis.

While our results suggest that patterns of ANPP responses to chronic resource alterations over the long term can be quite variable, determining the mechanisms that underlie these variations in response patterns over time requires further study along with a consideration of additional response variables. For example, Jentsch et al. (2011) showed that recurrent drought did not affect ANPP but did increase complementary plant–plant interactions, and reduced soil respiration, microbial biomass, and decomposition rate. To permit a broader range of potential mechanisms to be tested, comparable data that are complementary to ANPP responses should be collected. For example, with responses in plant community composition measured concurrent with ANPP, we can test whether species re-ordering within plant communities is related to patterns of ANPP response, a prediction of the HRF. For our analysis, these complementary data were available for only a small subset of the experiments that exhibited directional responses, and were not available for experiments with stepped responses. Of these, we found a significant correlation between community dissimilarity (a measure of change in community composition) and ANPP response in only two cases—a coastal salt marsh community and arctic tundra (Fig. 6; Table S2 of the ESM). This correlation emerged with both chronic resource addition and removal; however, additional studies that are designed to test this and other mechanisms underlying ecosystem response more rigorously are clearly needed.

Our analysis was based on the perspective that most global change drivers lead to alterations in key resources over time (Worm et al. 2002; Suding et al. 2005; Reich et al. 2006), and these are expected to affect community structure and ecosystem processes, particularly when resources are limiting (Fridley 2002; Stevens et al. 2004; Elser et al. 2007). Changes in the plant community and ANPP are expected to occur in tandem as a result of the strong linkage and feedback between community dynamics and ecosystem function (Cardinale et al. 2012; Hooper et al. 2012). Results from our synthesis are consistent with individual studies that have shown that some communities and ecosystems can be quite responsive to changes in resources (Parmesan and Yohe 2003; Adams et al. 2009; Halpern et al. 2008; Tilman et al. 2012), while others appear to be surprisingly resistant (Vittoz et al. 2009; Hudson and Henry 2010, Collins et al. 2012) or show only transient or variable responses over time (Luo et al. 2001; Cherwin and Knapp 2012) with minimal changes in community composition and structure (Collins et al. 2012; Knapp et al. 2012a). Our results also point to the need to expand our understanding of a broader suite of ecosystem responses (e.g., belowground NPP, NPP, net ecosystem exchange, soil CO_2 flux, etc.) to global environmental change. Improved understanding will require that we conduct studies in which resources and/or global change drivers are manipulated individually and in combination over very long time frames, yet few funding sources exist to support long-term research globally. Nevertheless, experiments that simultaneously manipulate multiple resources over the long term across a broad range of ecosystem types are urgently needed. Such experiments should measure ecosystem responses at multiple hierarchical levels to better understand patterns, mechanisms and consequences of chronic resource alterations. Such highly coordinated comparative research is essential for understanding how and why ecosystems may differ in their sensitivities over time to chronic resource alterations associated with global environmental change.

Author contribution statement MDS conceived the study and wrote the manuscript. KJL analyzed the data and developed the figures. AKK, KJL, and SLC contributed to writing the manuscript. KLG, JEB, SDF, LG, RJM, JTM, LER, and JY participated in the working group that led to this manuscript and contributed long-term datasets.

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