Widening global variability in grassland biomass since the 1980s

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Abstract: Global change is associated with variable shifts in the annual production of aboveground plant biomass, suggesting localized sensitivities with unclear causal origins. Combining remotely sensed NDVI data since the 1980s with contemporary field data from 84 grasslands on six continents, we demonstrate a widening divergence in site-level biomass ranging from +51% to -34% globally. Biomass generally increased in warmer, wetter and species-rich sites with longer growing seasons while declining in species-poor arid areas. Phenological changes were widespread, revealing substantive transitions in grassland seasonal cycling. Grazing, nitrogen deposition, and plant invasion were prevalent in some regions but did not predict overall trends. Grasslands are undergoing sizable changes in production, with implications for food security, biodiversity, and carbon storage especially in arid regions where declines are accelerating.

Main Text

Shifting annual production of aboveground peak biomass by vascular plants (hereafter ‘biomass’) has been observed worldwide in response to global environmental change[1-5]. These shifts differ in magnitude and direction including positive responses (i.e., ‘winners and losers’[6]) suggesting localized sensitivities that have been difficult to simultaneously measure and test[7-11]. Given the importance of biomass to humanity for food and fuel and the likelihood of intensifying consumption going forward, there is an urgent need to assess its vulnerability to global change especially in areas where yield declines could intensify[12,13].

Analyses to date on biomass shifts[13-15] have mostly relied on remotely sensed data that can be prone to estimation bias and an inability to discern underlying fine-scale drivers[9-16]. This is problematic because plant biomass often varies with combinations of coarse- and fine-scale factors whose interactions can be expressed uniquely by location, even when vegetation structure and climate may seem similar[8,16]. For example, anthropogenic nitrogen (N) deposition and plant invasion can sometimes dramatically increase biomass especially with warming[17-19] yet some global regions are largely unaffected by one or both factors.

To date, hypothesized drivers of biomass variability have emphasized combinations of climate change, phenological shifts, N deposition, or local-scale biotic interactions. Climate impacts on biomass can vary based on regional differences in the magnitude of temperature change relative to historic baselines (e.g., greater warming at higher latitudes), shifts in seasonality within and across years (e.g., longer, hotter summers), the magnitude of temperature change relative to the tolerance thresholds of local taxa, and interactions between temperature and precipitation including whether warming sites become wetter or more arid[20,21]. Phenologically, shifts in the timing of seasonal growth can have variable impacts on plant biomass[8,9,15] - earlier emergence can increase biomass if plants are biologically active for longer periods or reduce it by accelerating seasonal cycling such that growing seasons shorten[22]. The impacts of anthropogenic N deposition on plant biomass and diversity sometimes exceed those of climate and vary by proximity to centers of industry and agriculture[19]. Nitrogen deposition often interacts strongly with climate, given linkages among moisture availability, growing period, and N demand by plants[19.23]. Finally, a multitude of biotic factors can affect biomass differently by location, including among-site variation in plant species richness[24], the diversity of plant traits[25], levels of plant invasion[17], and over-grazing[26,27]. Given these diverse and often scale-dependent drivers of biomass change, it is unsurprising that their effects have been difficult to disentangle. Doing so will require a global-level systematic assessment of biomass regulation both within and among continents[28,29].

Here, we link long-term remotely sensed NDVI data with more contemporary plot data from 84 grasslands on six continents to test drivers of biomass variability in response to global change. These grasslands span a latitudinal gradient from -52° to +78° (four within tropical latitudes), and capture ~1.6% of the world's total non-woody vascular flora including ~5% of all Poaceae and ~3% of Cyperaceae (Table S1). Seventy percent of our sites are arid (PET>annual rainfall – Table S1) matching the ratio of arid-to-mesic grasslands globally[30], with the highest number of sites in North America (41 sites), followed by Europe (17) Australia (13), South America (6), Africa (4), and Asia (3) (Fig. S1). We classify "grasslands" as low-statured non-forested plant communities. Functionally, grasslands occupy a climatically and edaphically determined tension zone between forest and desert[29-31], regulated by climate seasonality, extreme weather, fire, and human-managed and natural grazing with its total area covering ~53 million km^2 globally (excluding Antarctica and Greenland). These regulating processes are associated with variability in grassland production, especially relating to climate[32-34]. These same processes are being fundamentally re-shaped by global environmental change, resulting in grasslands becoming a bellwether of resilience (or vulnerability) to anthropogenic transformation including shifts in biomass.

Our remotely sensed data track changes in annual peak biomass from as early as 1986 based on Landsat-derived peak NDVI. Our primary analyses focused on identifying drivers of change in peak NDVI using temporal factors measured during the same interval (1986-2020). These included changes in the timing of three NDVI-based phenophases that can affect peak biomass: vegetation emergence (i.e., start-of-season spectral greening), senescence (i.e., end-of-season spectral browning), and growing season length (duration from greening to browning), as well as inter-annual and inter-seasonal changes in temperature, precipitation, and potential evapotranspiration (PET)[35]. We also tested NDVI trends in relation to site-level baseline factors calculated from different durations including mean annual precipitation (MAP) and mean annual temperature (MAT) based on hourly modelled temperature data from 1970-2020, and site aridity (the ratio of annual PET: precipitation - 1970-2020). Other baseline factors were anthropogenic N deposition based on modelled data from 2014-2016[36], the number of plant species per site based on the net total of all species detected in the first five years of sampling starting as early as 2007, the percentage of exotic taxa found in each site-level species pool over five years of sampling[29], grazing impacts by large mammals determined using offtake comparisons with exclosures at a subset of 46 grasslands, and composite community-level measures of plant traits for the species present at each site[37]. Using annually sampled aboveground biomass of plants (i.e., combined live, litter, and non-vascular) starting as early as 2007, we examined the accuracy of satellite-derived NDVI for predicting grassland biomass, given that there can be estimation biases relating to latitude, elevation, or species richness[9,16]. Analytically, we tested drivers of remotely sensed peak grassland NDVI by evaluating a series of regression and multivariate models that isolate localized differences based on our various explanatory factors (Table 1).

Results and Discussion

We observed a four-fold divergence in the slope of change in annual NDVI-estimated biomass over the past several decades (Fig. 1). This amounted to biomass shifts ranging from a maximum gain of 51% to a 34% decline (Figs. 1, S1). Overall, 56% of sites increased significantly, especially in the Arctic, the Pacific Northwest of North America, and western Europe. Other sites from both hemispheres declined, all of which were arid, including grasslands in Australia, Argentina, and parts of central and southwestern North America especially California. 36% of grasslands showed no significant shift in biomass, regardless of phenological change, warming, altered precipitation, N deposition, or plant invasion. Such geographically variable long-term changes in non-woody NDVI-estimated grassland biomass, including both sizeable increases[14,38-42] and declines even within the same continent (Figs. S1. S2), are consistent with previous observations especially from the Arctic[9,10,15]. We report this variability to be a global phenomenon affecting many grasslands.

We found that variability in shifting NDVI-estimated biomass was primarily explained by increases in growing season length, especially in combination with warming (Figs. 2, S2, S3; Table 1). Between the late 1980s and the late 2010s, growing seasons increased by an average of nine days (<u>1986-90</u>: $\bar{x}$ = 157 days [SE = 3]; <u>2016-20</u>: $\bar{x}$ = 166 days [SE = 2]). In total, 87% of sites had significant changes in the timing of the onset of greening, the onset of browning, and/or the length of the growing season since 1986 (e.g. Fig S4), indicating that many grasslands globally are undergoing substantive shifts in seasonal cycling. Longer growing seasons have been implicated as a warming response in grasslands and some cropping systems, and a causal factor of increased biomass based on the assumption that plants are active for longer periods[22]. Conversely, advancing greening, elevated production, or moisture limitation in arid environments can sometimes accelerate leaf physiological processes relating to photosynthesis that, in turn, shorten the growing season by triggering earlier senescence[22,23]. In total, 39% of sites had both earlier emergence and delayed senescence thereby creating longer growing seasons (Fig. S4) – it was these grasslands with the longest growing seasons that tended in experience that largest increases in NDVI-estimated biomass. However, many other sites responded differently such that there was no consistent global relationship between changes to the timing of emergence and senescence (i.e., starting earlier does not predict the timing of senescence: $F_{1,83} = 0.95$, $p = 0.33$; Fig. S4). For example, 19% of sites with earlier emergence in spring experienced earlier spectral browning thereby shortening the growing season, which has been observed previously in arid areas[23] and parts of the Arctic[45,46] including sites analyzed in this study. In total, variability in the connection between shifting phenology and changes in peak biomass reinforce that there can be powerful global trends in grassland responses to environmental change (e.g., longer growing seasons at many sites), but also localized and divergent outcomes sometimes regulated by different factors.

All sites showed temperature increases since the mid-1980s (i.e., all 84 temporal slopes for temperature were positive - Fig. S5, S6). However, the impacts of warming on growing season length were not universal, instead depending on the distinction between sites with the highest temperature increases but relatively low MATs (e.g., the

Arctic, Patagonia, and the alpine steppes of the Mongolian and Tibetan Plateaus) versus those with the highest MATs but less overall warming (e.g., arid grasslands of Australia, southwestern North America, Africa, and South America). (Figs. S2-S6). The former were more often in the Northern Hemisphere, in line with observations that global warming to date has been more pronounced north of the equator (i.e., interhemispheric temperature asymmetry[47]) (Figs. 3, S6). These sites with the highest warming also tended to be characterized by both high MAP and large increases in annual rainfall - the wettest sites generally are becoming both wetter and warmer. This is consistent with the ability of warmer air to support more moisture, as has been observed with increasing snowfall in a warming Arctic[45]. Conversely, sites with higher baseline MATs, less warming, and reduced NDVI were all arid grasslands that tended to undergo a shortening of growing season length, usually relating to an earlier onset of spectral browning in summer (Figs. S6, S7). Not all arid sites experienced declining biomass - only 32% of 59 arid sites had negative temporal slopes in NDVI even though 58% of all sites had less precipitation, increases in PET, or both (Figs. S1, S6, S7).

Our observed warming trends were more seasonal than annual, especially in the spring and summer months – this contributed to the tight connection between growing season length and temperature (Fig. S2). We examined changes to seasonal and annual temperatures by site from 1986, which is near the beginning of Landsat data collection while also capturing the onset of accelerating contemporary planetary warming that continues to the present day[34,45]. In testing the magnitude of seasonal and annual changes, we found that seasonal changes were more prevalent with 37% of sites having significantly warmer spring temperatures and 47% having warmer summers (e.g., Fig. S8). In contrast, only a subset of sites had significant increases in annual warming despite all slopes being positive. This decoupling of frequent seasonal warming from less common significant annual warming suggests an intensification of within-year inter-seasonal differences as has been reported previously in grasslands, with periods of increasing temperature in some seasons being muted or offset by cooling at other times of the year[6,48]. For example, we observed cooling spring temperatures in numerous mid-latitude grasslands of central North America and western Europe (Fig. S8) – many of these sites had increasing NDVI.

We also saw significant influences of species richness on changes in peak NDVI, although always interacting with phenology or climate (Table 1). Among sites with lengthening growing seasons or warming temperatures, species-rich grasslands generally displayed greater increases in NDVI than species-poor sites (Table 1; Figs. S2, S9). Conversely, for grasslands with shortened growing seasons or less warming (e.g., high MAT sites from the Southern Hemisphere and California), those with below-average richness were predicted to show reduced or less pronounced NDVI increases. These outcomes imply some form of context-dependent functional complementarity, which would be consistent with the intertwined causal factors known to regulate diversity and biomass in grasslands[49-51]. They also reveal an absence of any independent relationship of richness (Fig. 2, S9), and indeed sites with the highest numbers of species (e.g., the African Serengeti) did not necessarily demonstrate increasing NDVI. Such complexities on how richness affects biomass are illustrated when considering the numbers of invasive grassland plants at our sites. Invasion is sometimes linked with large increases in community-level biomass and site-level richness[52], yet we observed the opposite responses - invaded grasslands were more likely to have declining biomass and fewer species. This likely reflects climatic factors – most invaded sites were in arid regions where biomass trends since the 1980s were non-significant or negative. It also likely reflects lower numbers of species – sites dominated by invasive plants had significantly fewer plant taxa ($F_{1,63} = 9.2$, $P = 0.004$).

Several of our non-temporal hypothesized factors had no detectable effects on changes to grassland NDVI despite often having sizable impacts on biomass at some sites (Table 1). Sites with high levels of N deposition, especially in eastern North America, higher elevation areas of western Europe, and areas of China (Fig. 3), did not show significant changes in NDVI despite the well-described impacts of anthropogenic N increasing grassland biomass[19]. Similarly, there was a lack of detectable association between sites with high grazing offtake and changes to NDVI (Table S2). As with N deposition, grazing can significant affect grassland biomass[26] and indeed some of our grasslands have substantive differences in biomass between grazed and fenced areas including mesic grasslands of the Northern Hemisphere (sheep meadows in the UK, reindeer barrens in Finland) and arid regions of Australia[53,54]. However, variation in levels of offtake estimated by our exclosures were unable to predict the likelihood of NDVI change relative to the global-scale impacts of phenology, climate, or species richness (Table S2). Finally, we also failed to detect associations between site-level biomass change and variability in community-wide aggregate measures of plant size (e.g., leaf area index [LAI], height) or foliar nutrients despite a wider spectrum of resource-foraging strategies in plants sometimes being connected to higher biomass[37] (Table S3). Of particular note in our study was a lack of association between biomass change and LAI. Remotely estimated LAI is often used to model plant production given the strong connection between canopy density, light capture, and biomass[55,56]. However, we observed no predictive relationship between community-level LAI and long-term shifts in NDVI despite 90-fold differences in canopy density ranging from sparse arid grasslands of Australia and the American southwest to dense high-elevation mesic grasslands of the European Alps (Table S3).

Combined, the prevalence of grasslands with trends towards higher site-level biomass created a net 13.6% increase among our 84 sites since the 1980s (Fig. 1; $F_{1,83} = 91.6$, $p < 0.0001$). Longer-term increases in biomass were also detected using our field-measured data (Figs. 4, S10), and aligned with other reports of increasing overall plant biomass with global environmental change[38-42]. That being said, this magnitude of increase could be viewed with caution. In total, 61 of our 84 sites occur in the Northern Hemisphere, especially North America and Europe, where increases in precipitation and biomass are known to be especially pronounced[43,44]. Furthermore, there is evidence of a threshold of ~500 mm per year in precipitation below which sensitivity to climatic variability intensifies[44]. Although most of our sites are arid (PET>MAP), their annual precipitation averages 790 mm (SE = 43) with only 25% falling below 500 mm. We tested the potential impacts of these factors on the subset of sites that are arid or have MAP levels < 500 mm, and still observed net increases in biomass (arid sites: +12.2% [SE 2.6%]; MAP < 500 mm: +15.6% [SE 5.7%]). Nonetheless, we might still anticipate that mean site-level increases in biomass would be lower if more of our sites occurred in areas where declining precipitation is especially pronounced.

Biomass variability is not unexpected in grasslands, given its regulation by combinations of factors whose relative importance can change by locale including supply rates of limiting nutrients, grazing pressure, and whether warming increases or suppresses plant growth depending on precipitation[31-34]. Indeed, localized responses in biomass depending on whether warming sites are getting wetter or drier also occurs in annual crops[6], which is unsurprising given that large percentages of the world's croplands were once grassland[11,57]. Additionally, previous work on global-scale shifts in

NDVI-derived estimates of biomass, including in grasslands, has demonstrated both increases and decreases since the 1980s without a consistently clear mechanistic understanding given the challenges of testing fine-scale processes[1,2,14,58]. Here, we consolidate the disparate findings of previous work by showing that localized differences emerge because the dominant regulatory processes appear to vary widely. These findings are evident even though our results likely underestimate the full extent of shifting grassland biomass with global change since the 1980s. For example, we do not account for increased biomass caused by the invasion of trees and high-statured shrubs into grassland – an increasingly prevalent phenomenon[9,59]. We also did not account for shifts in root biomass, with root:shoot ratios at 2:1 or more in grasslands[60]. Finally, there may be an influence of rising atmospheric CO_2 on biomass, although global trends in CO_2 – a ~20% increase since the 1980s – tend to be expressed similarly by region[61].

Our analyses integrated remotely sensed and field measured levels of annual peak grassland biomass, demonstrating a strong positive relationship despite a ten-fold difference in species richness among sites and a hundred-fold difference in standing biomass. This indicates that NDVI can capture overall trends in aboveground standing biomass at our sites. Nonetheless, there was widening predictive error as NDVI exceeded 0.6 (Fig. 4). NDVI has been previously shown to accurately predict aboveground plant biomass in uncultivated grasslands[62]. Indeed, we found similar trends of an overall mean biomass increase among our 84 sites for both NDVI and plot-level biomass (Fig. S10). However, NDVI can be prone to estimation bias with increasing spatial scale, across years, at higher latitudes, and with increasing canopy density and structure[8,55,63] – factors that can characterize some of our data. A fundamental practical question for using NDVI is whether the ability to predict biomass can be improved with widely available ancillary data such as latitude and climate, or whether improvement requires detailed field calibration that may be impossible[16]. Our field data gave us a unique opportunity to test drivers of unexplained variation including fine-scale biotic factors (see Methods), revealing two primary sources of bias: high latitude and low elevation. Adding these widely available data to our models improved the predictive accuracy of NDVI for ground measured biomass by 21% (Table S4). Estimation bias at high latitude for NDVI is especially common, relating to methodological and biophysical factors including the potential underestimation of non-photosynthetically active vegetation (which we sampled)[9]. Although our fit between NDVI and aboveground biomass remained strong at higher latitudes, our work supports the need for caution when extrapolating trends in phenological change including the timing and magnitude of peak biomass. The same caution appears to apply to extrapolating connections among remotely sensed estimates of biomass and species richness[16,64], as we also detected a smaller but significant estimation bias between NDVI and field biomass as the numbers of species site^{-1} increased (Table S4).

Our work describes a substantial divergence of peak biomass by location within many grasslands globally. These results were obtained from non-cultivated permanent-cover grassland, a habitat type under long-standing and intensifying conversion pressure[55,65]. Despite grassland losses exceeding 99% in some regions[66], uncultivated areas still cover ~25% of Earth's terrestrial surface, store ~25% of its carbon, and support thousands of obligate flora and fauna[67]. Many of the global-scale ecological benefits of uncultivated grassland center on the annual production of biomass, including litter inputs that contribute to soil C cycling, providing forage for much of the world's remaining megafauna and half of all domesticated livestock, and regulating fire cycling given that grasslands account for most of Earth's annual burning[67]. Our documentation of shifts in the direction and magnitude of biomass in our grasslands suggests that there will be far-ranging implications for the planet moving forward, which will be experienced differently by location.

Methods

Study area and experimental design

Our study sites span a latitudinal gradient from Patagonia (-52°) to the high Arctic of Norway (+78°) and range in elevation from 0 m to 4241 m, with wide differences in potential evapotranspiration (0.79 – 6.49 mm day^{-1}), atmospheric N deposition (66.9 to 2162.1 mg N m^{-2} year^{-1}), and long-term (1970-2020) mean annual precipitation (MAP: 192 to 2224 mm) and mean annual temperature (MAT: -7.5 to 27.2°C) (Fig. S11, Table S1). There is wide variation in the total number of species per site ("species richness"), ranging from 13 to 176 species, summed together for all non-treated control plots based on five years of sampling in case there were cryptic taxa not visible in some years. Percent exotic flora ranges from 0 to 100% of all species per site (Table S1) with multiple species occurring at sites within both their ancestral and non-native ranges[68]. There were 421 non-native plant taxa in total, but with twenty of the 84 sites having no exotic species (all sites in Europe, Asia, and Africa). Levels of grazer offtake at the 46 sites with exclosures range from none to ~85% of total annual plot-level biomass[53,54]. We classify "grasslands" as low-statured non-forested plant communities, including treed savanna, prairie, planted permanent-cover pasture, montane meadows, and arctic-alpine tundra. Our sites cover a wide range of "Whittaker biomes" defined by the ratio of MAP to MAT (Fig S1). They also have some degree of geographic clustering, with an average minimum distance globally of 379.3 km (range: 1 to 3,087 km). This means that several sites have identical estimates of N-deposition given the spatial resolution of those data (2° × 2.5°). Our ratio of arid-to-mesic grasslands (71%:29% - Table S1) matches the global ratio[30] but the continental distribution of our sites is not proportional to the global range of grasslands. Almost half of our sites are from North America even though its continental coverage of grassland is only 13% globally. Australia and South America have similar ratios between number of our sites versus their global coverage (14:13%; 10:9% respectively), while Asia and Africa are under-represented (Fig. S1). For our invaded sites, there could be a concern that our data misrepresent invasion impacts on NDVI change because of the gap between the start of the remote sensing data (mid-1980s) and the field sampling (2007). Although we cannot definitively eliminate this possibility (e.g., an uninvaded site becoming heavily invaded after 1986), the odds are low as all sites occur in regions of the world with long legacies of invasion dating back a century or more[68]. Our study began with 127 sites but was ultimately reduced to 84 based on screening for extreme outliers, poor image resolution especially due to cloud cover, and confounding site factors such as tree cover (see below).

Our analyses combined NDVI calculated from Landsat images starting no earlier than 1986, climate data including PET[35], modelled N deposition data[36], and field data collected from 84 grassland sites from the Nutrient Network (NutNet), a globally distributed experiment[29]. All NDVI satellite data were extracted from unmodified areas adjacent to plots associated with NutNet (Fig. S12). All NutNet plot data were collected by local site scientists, starting in 2007 or later depending on when the site joined the network. Field sampling occurred within thirty permanently marked 5 x 5 m plots laid out in a grid (Fig S12). We used data from the year prior to the application of any experimental treatment (i.e., “Year 0” pre-treatment data, when all plots were unmodified) and from subsequent years (Years 1, 2, etc.) in the subset of plots that were untreated (i.e., all data in this study only come from unmodified control plots). Plot data were collected annually at peak biomass and included total aboveground biomass, clipped to ground level from two 10 cm x 100 cm strips within a larger 5 m x 5 m plot, with the clipping locations differing each year[29]. Clipped biomass was sorted to live, non-vascular, and litter, and then dried to a constant mass at 60° C and weighed. Differentiating biomass into live vascular, live non-vascular, and litter is one of several important novelties of our study, given the NDVI estimations of standing plant biomass can sometimes be insensitive to, or biased by, the latter two factors. Indeed, 53% of all Nutnet grasslands globally have been found to support non-vascular plant growth, with standing biomass as high as 635 g m^{-2} (Virtanen et al. submitted).

Our 84 sites captured a wide variation in the relative abundance of major functional groups, including graminoids (e.g., grasses and sedges), forbs, and, to a lesser degree and mostly in the Arctic, low-statured woody plants, lichens, and bryophytes. There was a wide range in the percentage of non-native flora per site. Many sites in Europe, Africa, and Asia had few or no non-natives, while some grasslands in North America, South America, and Australia were >90% exotic taxa[68]. Species composition data were used to calculate two measures of community-level trait variation, functional diversity (FD) and community weighted mean (CWM)[37]. FD, an estimate of trait variability, relates to degrees of trait converge or divergence within plots based on Rao's index of quadratic entropy. CWM (also referred to as FI[37]), an estimate of trait averages, is based on the community weighted mean for each trait in each plot. Trait data were compiled from TRY (public version), AusTraits (version1.1.0), BIEN (version 1.2.5), and NutNet (leaf traits), for six continuous traits (height, leaf surface area (LAI), specific leaf area (SLA – the ratio of leaf area to leaf mass), leaf N, leaf P, leaf C), that have relatively high coverage for species recorded in NutNet (93, 95, 87, 91, 86, 75, 81% for each trait, respectively). For species that do not have trait values, we used the mean values from their genus (see Table S3)

The only Nutnet treatment data were for grazer offtake, derived from fenced but unfertilized plots[53,54]. Grazing effects were expressed as the log response ratio of differences in clipped biomass between control plots in fenced and unfenced areas at a subset of 46 sites (the remaining 38 sites did not have exclosures). Typically, there were three fenced plots per site, and the fences were ~2.3 m tall with the lower 90 cm being 1 cm steel mesh and the upper portion surrounded by strands of barbless wire[29]. These grazing offtake data were calculated only in the first year after the exclosures were constructed (Year 1), given that longer-term exclosure effects can be confounded by shifts in plant species richness and relative abundance[51]. Levels of grazer offtake ranged from very low or nil with some sites lacking detectable grazing, to very high especially in parts of Australia, Africa, and western Europe (e.g., sheep grazing in Lancaster UK, domesticated reindeer grazing in Kilpisjarvi, Finland)[53,54].

For our analyses, we used single composite (non-temporal) site-level measures of species richness, exotic cover, traits, and grazing for each site – this allowed us to test, for example, whether background levels of site richness and invasion were associated with 36-year shifts in NDVI-estimated production.

NDVI measurements and phenological dates

We used images from Landsat missions 4, 5, 7, and 8, to calculate the normalized difference vegetation index (NDVI) at each site starting as far back as 1986 (depending on image quality) and extending annually to 2020 at a resolution of 30 m in an unmodified circular area selected near the Nutnet plots (Fig. S12). In these plots, we extracted a series of phenological NDVI measures within each growing season, modified from Buitenwerf et al.[8] given that we only targeted a single vegetation type (i.e., grasslands): off-season ‘trough’ when plants are inactive, start-of-season “emergence”, peak NDVI, end-of-season “senescence”, and “growing season length” derived from the number of days from emergence to senescence each year (Fig. S13). Elsewhere, NDVI has been used to detect trends in phenology and related biomass responses[9,16], including in grasslands where it has been shown to strongly align with live biomass[62]. Our work supports this significant relationship, albeit with increasing variation beyond NDVI values of 0.6 (Fig. 4). We conducted a series of analyses to identify sources of error for NDVI including tests for influences by outliers, the influences of regional-scale factors relating to latitude and elevation, and local-scale factors including non-vascular flora (described below – Table S4). We removed two sites that failed uniformity tests when conducting linear fits between annual peak NDVI and time, based on comparisons with a Theil-Sen median regressor and trend-filtering using a Mann-Kendall Trend Test – both were sparsely vegetated sites of the Icelandic tundra and arid grassland of central North America.

Location of the circular “NDVI plots” was done visually using Google Earth images. We located a central point in an area adjacent to the NutNet experiment, given that the Nutnet plots are readily detectable from the images (Fig. S12). This adjacent area was selected to contain vegetation identical to the vegetation within the experiment, in consultation with each Nutnet site PI. It was positioned at least 50 m from the closet NutNet plot to avoid the influence of any experimental treatments associated with the NutNet manipulations, while leveraging the site-specific vegetation and soil information derived from the experiment. There is always potential risk of positioning error using Google Earth – a global analysis of high-resolution Google Earth imagery has estimated an overall horizontal geo-registration accuracy of 39.7 m RMSE with an accuracy of 24 m RMSE in some countries[69] and subsequent studies demonstrate improved horizontal accuracy of 10.5 m RMSE[70]. We explicitly tested RSME error for eight of our sites, contrasting plot-level coordinate data generated using a hand-held

GPS at each of 30 plots per site versus coordinate data for those same 30 locations generated from Google Earth engine (Fig. S12, Table S5). Our calculated RSME error was always <5 m (Table S5).

In each circular plot per site, we extracted reflectance data from within a circular buffer within 30 m around this point (Fig. S12). This was done using images from top-of-atmosphere (TOA) reflectance collections in Google Earth Engine. The images were taken between 1982 and 2020, although the specific date ranges and sampling frequency varies at each site. All of our analyses using remote sensed data that start no earlier than 1986 as site data prior to this was found to be too sporadic (Fig. S13). In all cases, the spatial resolution of each image is 30 m. We used all available images from both Tier 1 and Tier 2 quality, which were aggregated and processed using Google Earth Engine. Tier 2 data were essential for obtaining images taken during the snow-covered “trough” portion of the year. The horizontal geo-registration accuracy of Tier 1 scenes is ≦ 12-meter root mean square error (RMSE) whereas the Tier 2 accuracy is > 12 m RMSE[71]. Landsat Collection 1 was used, although Collection 2 is the only collection currently available for download but both collections have the same published geo-registration accuracies[71]. For each image, we calculated NDVI using the corresponding near-infra red and red bands 4 and 3 for Landsat 4, 5, and 6, and bands 5 and 4 for Landsat 8. We also extracted information about image quality (BQA band) containing statistics from the image data and post-processing information[69]. BQA values were used to filter images to exclude any pixels that had a high likelihood of including clouds or cloud shadows. Using manual inspection, we included only pixels associated with clear, cloud-free imagery (Landsat 4, 5, and 7 BQA = 672, 680, 676, 680, 684; Landsat 8 BQA = 2720) or imagery over snow (Landsat 4, 5, and 7 BQA = 1696, 1700, 1704, 1708; Landsat 8 BQA = 3744). We discarded images where resolution was uncertain (e.g., clouds versus snow - <0.5% of all images).

We screened our initial pool of sites, reducing the final number of sites to 84 (Table S1). Exclusion of sites typically occurred for sites lacking (i) Nutnet field data for at least three years (ii) extreme outliers for one or data factors, whose origins could not be determined, or (iii) those for which only a minimal amount NDVI phenological data could be extracted. Reasons for the latter include poor satellite coverage by location (especially problematic for Landsat data from the early 1980s), persistent cloud cover (preventing fitting a trend), or for sites that rarely or never crossed an identifiable "greened-up" threshold in multiple years. In cases where established Nutnet plots could not be located on Google Earth (e.g., Fig S12) or any other issues inhibiting image processing (e.g., canopy cover by trees), we reached out to site PIs for guidance.

Once the time series of NDVI values was obtained for each site, we extracted key phenological and growing season information by post-processing the data in R version 3.6.1 (Fig. S13). First, we smoothed the data to reduce error by fitting cubic splines to the NDVI data at each site, and then determined the average date where NDVI was the lowest across all years ("trough date"). Then we created site-specific "growing season windows" consisting of 545 days (365 + 2*90). This window started 90 days before the trough date in each year, and then 365 days following the trough date plus an extra 90-day buffer at the end. We processed all dates initially as radians, which allowed flexibility in defining growing seasons particularly for sites with Mediterranean climates (e.g., California, western Australia) or located in the southern hemisphere where the period of vegetation activity spans multiple calendar years (e.g., green-up can be November of year x, senescence in April of year x + 1).

From our growing season windows for each site*year combination, we weighted data points so that the maximum NDVI value in each growing season window had a weight of 1, while all other points had a weight of 0.5, to better preserve the NDVI trends at sites with rapid green-ups and short growing seasons. We used a smoothing parameter (spar) of 0.5 to preserve these trends. From these annual cubic splines, we extracted green-up and senescence dates as the first and last dates, respectively, that NDVI was above a 50% NDVI range threshold (green threshold) according to the equation:

$$\text{Threshold} = \left(0.5\times\left(\overline{MaximumNDVI} - \overline{MinimumNDVI}\right)\right) + \overline{MinimumNDVI}$$

where the average maximum and minimum NDVI values were calculated across all years at each site. This green threshold allowed for flexibility to include sites with different minimum NDVI values (e.g., sites which become snow-covered and sites which do not) as well as different maximum NDVI values. In using a threshold, we were also able to ensure that a green-up or senescence date was biologically comparable across all years (indicating the same NDVI).

In all cases of fitting cubic splines, we forced a minimum NDVI value of 0 (if measured NDVI was < 0, we re-assigned the value to 0), as our smoothing and post-processing was dependent on consistency during the growing season troughs when data were typically sparse. During the growing season troughs, band quality information often indicated that pixels were cloud covered when visual analysis of images revealed snow cover (both cloud and snow cover containing water). We excluded pixels indicating cloud cover in this analysis. To overcome sparse data points during these periods in Tier 1 datasets we additionally used Tier 2 data. Given that data from both tiers were required and the radiometric calibration was top-of-atmosphere reflectance, alternative variations of NDVI that adjust for noise due to soil brightness and atmospheric light scattering, such as the enhanced vegetation index (EVI)[72,73], were not employed - indices with numerical constants can be inconsistent due to atmospheric noise[69]. Furthermore, snow cover decreases NDVI values but increases EVI values[70] and such sensitivity would confound the phenological analysis.

We approximated the relationship between NDVI and plot level aboveground biomass using sites with at least 3 years of harvested biomass and corresponding annual peak NDVI data from the same site (Figs. 4, S10). A log-transformed model provided the best fit between NDVI and average plot biomass site^{-1} year^{-1}, which we used to translate NDVI to an average biomass across all sites from 1986 to 2020.

Climate and N-deposition trends

Monthly long-term temperature (MAT) and precipitation (MAP) averages per site were obtained from the WorldClim database, from 1970-2020. MAT and MAP served to describe baseline levels of temperature and precipitation among sites. To determine annual deviations in temperature and precipitation from baseline MAP and MAT, we calculated a monthly time series for temperature and precipitation during the study period (1986-2020), with data obtained at the site level using the Climatic Research Unit (CRU) time-series (TS) version 4.03 data[35]. These annual deviations were calculated as slopes of change over time. Estimates of potential evapotranspiration (PET) were also obtained from the CRU time series[35], which calculates PET using mean, maximum, and minimum monthly temperatures, vapor pressure, and cloud cover (1970-2020).

Given predictions of increased interannual seasonal variability in climate, with the potential to affect phenology and peak biomass, we calculated slopes of 36-year trends in temperature and precipitation seasonality at each site. We targeted these calculations for two phenophases: (i) green-up based on a two-month window around the date of typical site-specific green-up date (the typical month of green-up, plus one month before), and (ii) maximum NDVI as a five-month window around the date of typical site-specific maximum NDVI (the typical month of NDVI max, plus two months before and after). These seasonal calculations allowed us to test more detailed climatic drivers of phenological change, which may not be detected by overall annual trends including the possibility of warmer springs, warmer and drier summers, and even seasonal cooling as is sometimes observed (e.g., Fig. S8)[48].

Atmospheric nitrogen (N) deposition was estimated for each of the sites using the GEOS-Chem Chemical Transport Model[36]. The model estimates wet and dry deposition of inorganic N using models of atmospheric chemistry together with meteorological data and emissions data. Outputs are at a 2° × 2.5° resolution averaged across the years 2014, 2015, and 2016. Although the N deposition model uses metrological data, there were weak and non-significant correlations between precipitation and estimates of N deposition ($r^2 = 0.009$).

Analysis

Our primary analysis tested drivers of change in maximum NDVI over the period starting from 1986 to 2020, based on site-specific slopes of biomass change over time (Fig. 1). We used a multi-model selection approach to evaluate the relative importance of variables associated with our four interacting hypotheses: (i) changes in climate including temperature, precipitation, and PET, (ii) changes in phenology including the timing of emergence, the timing of senescence, and growing season length, (iii) levels of atmospheric N deposition, and (iv) biotic factors of species richness, grazing intensity, traits, and exotic (non-native) species. We simplified our analytical models by removing factors that were tightly correlated, using principal coordinate analysis (e.g., Figs. S2, S3). For example, we found that overall changes in temperature and precipitation (the 36-year temporal trends based on slope) were tightly correlated with seasonal changes in spring and summer temperature and precipitation – we thus used the former in our models. Similarly, sites differed widely in changes to emergence and senescence over time, but we excluded both for our main models as their effects were significantly captured by trends in growing season length – sites that started earlier often had longer growing seasons, as did sites that senesced later (although only 39% of sites had both earlier emergence and later senescence – see Main Text).

Accordingly, we built a maximal linear model in R[74] that assessed the response of site-level biomass slopes (change in NDVI from as early as 1986 to 2020, depending on the site – Fig. 1) to all independent effects and pairwise interactions of a subset of factors: latitude, elevation, N deposition, species richness, growing season length, aridity, percent exotic species, overall annual temperature slope (warming since 1986), and overall annual precipitation slope (changes in precipitation since 1986). We included grazing in a separate model for these factors, for the 46 sites that had exclosures (Table. S2). All of these variables included in the final maximal model had low collinearity, as indicated by assessment of variance inflation factors[75]. These factors also met assumptions of normality (or were log transformed to aid this – e.g., N deposition), and were standardized to a mean of zero and standard deviation of 0.5 using the ‘arm’ package[76], as required for model comparison[77]. Further we adjusted our regression models using the inverse of the standard error of the slope from each site, so as to down-weight parameters estimated with larger error (e.g., Seabloom et al.[78]). We evaluated the fit of subsets of this model using the MuMIn package[74] and conducted a model averaging procedure for all candidate models within two AIC of the best model.

We present the full averages of parameter estimates from our final model (e.g., Tables 1, S2)[75-77].

Data and materials availability: Data and coding associated with this study are freely available from the Environmental Data Initiative.

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Tables

Table 1. Major factors associated with changing mean in peak NDVI in 84 grasslands 1986-2020. The table shows all variables highlighted to be significant drivers of changing NDVI (bold) and the remaining non-significant variables that were retained in the model selection process. Hypothesized factors that are not listed (e.g., N deposition) were not detected as influential, even non-significantly, during model selection.

Parameter	Estimate	Standard Error	Z-Score	P-value
Intercept	0.0018	0.0002	11.48	**<0.0001**
Growing season length (GSL)	0.0021	0.0003	6.13	**<0.0001**
GSL*temperature change	-0.0037	0.0008	4.5	**<0.0001**
Aridity*temperature change	-0.0024	0.0007	3.14	**0.002**
Temperature change	0.0010	0.0004	2.50	**0.013**
GSL*species richness	0.0018	0.0008	2.38	**0.018**
Temperature change*species richness	0.0020	0.0009	2.17	**0.03**
Aridity	-0.0007	0.0003	2.14	**0.033**
Species richness	-0.0004	0.0003	1.27	0.2
% exotic species	-0.0002	0.0003	0.54	0.59
Aridity*species richness	0.0003	0.0007	0.41	0.68
Precipitation change	0.0001	0.0002	0.33	0.74
Precipitation change*temperature change	-0.0002	0.0007	0.31	0.76
Elevation	0.00000	0.0002	0.25	0.80

Figure Captions

Fig. 1. Temporal change in mean peak NDVI*. Fitted trend lines for 84 grasslands, with the red dashed line indicating no temporal change. The open circles are the peak NDVI measures for each grassland over time (n=2,856). In total, 56% of sites have significant positive increases while 5% have significant declines, resulting in a four-fold difference in mean peak NDVI change. Given the wide spread of points and the risk of outlier bias, our fitted trends derive from a linear model using a Theil-Sen median regressor. Plotted trendlines were obtained from this model and filtered based on p-values from a Mann-Kendall Trend Test (see Methods).*

Fig. 2. Relationship between changes in major explanatory factors and maximum NDVI. (A) The figure emphasizes the significant impact of changes in growing season – shortening (left) or lengthening (right) - on shifts in grassland biomass declines (bottom) or increases (top) estimated with remote-sensed NDVI ($F_{1,83}$ = 31.8; p <0.0001)). There

are also significant relationships between (B) increasing NDVI and the slope of temperature increase by site ($F_{1,83} = 6.6$; $p=0.012$; note: all sites warmed) and (C) increasing NDVI and the slope of changes in annual precipitation ($F_{1,83} =5.3$; $p=0.023$). For species richness (D), there was no univariate impact on changing NDVI ($F_{1,83} = 0.34$; $p = 0.56$), although it interacted significantly with growing season length and warming (Table 1, Fig. S9). The inserted dashed lines in Figs. 2A-C indicate areas of no net change. All tests are linear regressions among the 84 sites of this study.

Fig. 3. Global maps showing variation among sites in (A) shifting average annual temperature, (B) average annual precipitation, (C) growing season length for 1986-2020, and (D) levels of atmospheric N deposition modelled for 2014-2016. *Data for temperature and precipitation came from CRU[35]. The largest temperature increases are mostly in the northern hemisphere – southern hemisphere sites have higher mean annual temperatures, but lower levels of warming since the 1980s. Growing season length were derived by site and over time based on differences between remotely sensed spectral greening and spectral browning each year. Atmospheric nitrogen (N) deposition was estimated using the GEOS-Chem Chemical Transport Model[36], which estimates wet and dry deposition of inorganic N using models of atmospheric chemistry together with meteorological data and emissions data – these N data have a 2° × 2.5° resolution.*

Fig. 4. Relationship between annual remotely sensed maximum NDVI and annual live aboveground biomass. *The best-fit curvilinear regression line ($F_{2,410} = 72.7$; $p < 0.0001$) derives from sites with three or more years of live biomass, with the red shaded area (confidence curves for the fitted line) showing how estimation bias begins to widen*

as annual maximum NDVI becomes higher (especially > 0.6). Analysis of the residuals indicates that this bias is strongly affected by higher latitude and lower elevation, with a contribution also from species richness (see Methods; Table S4).

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