

Widening global variability in grassland biomass since the 1980s

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

221 **Main Text**

222 Shifting annual production of aboveground peak biomass by vascular plants
223 (hereafter 'biomass') has been observed worldwide in response to global environmental
224 change¹⁻⁵. These shifts differ in magnitude and direction including positive responses
225 (i.e., 'winners and losers'⁶) suggesting localized sensitivities that have been difficult to
226 simultaneously measure and test⁷⁻¹¹. Given the importance of biomass to humanity for
227 food and fuel and the likelihood of intensifying consumption going forward, there is an
228 urgent need to assess its vulnerability to global change especially in areas where yield
229 declines could intensify^{12,13}.

230 Analyses to date on biomass shifts¹³⁻¹⁵ have mostly relied on remotely sensed data
231 that can be prone to estimation bias and an inability to discern underlying fine-scale
232 drivers⁹⁻¹⁶. This is problematic because plant biomass often varies with combinations of
233 coarse- and fine-scale factors whose interactions can be expressed uniquely by
234 location, even when vegetation structure and climate may seem similar^{8,16}. For
235 example, anthropogenic nitrogen (N) deposition and plant invasion can sometimes
236 dramatically increase biomass especially with warming¹⁷⁻¹⁹ yet some global regions are
237 largely unaffected by one or both factors.

238 To date, hypothesized drivers of biomass variability have emphasized
239 combinations of climate change, phenological shifts, N deposition, or local-scale biotic
240 interactions. Climate impacts on biomass can vary based on regional differences in the
241 magnitude of temperature change relative to historic baselines (e.g., greater warming at
242 higher latitudes), shifts in seasonality within and across years (e.g., longer, hotter
243 summers), the magnitude of temperature change relative to the tolerance thresholds of
244 local taxa, and interactions between temperature and precipitation including whether
245 warming sites become wetter or more arid^{20,21}. Phenologically, shifts in the timing of

246 seasonal growth can have variable impacts on plant biomass^{8,9,15} - earlier emergence
247 can increase biomass if plants are biologically active for longer periods or reduce it by
248 accelerating seasonal cycling such that growing seasons shorten²². The impacts of
249 anthropogenic N deposition on plant biomass and diversity sometimes exceed those of
250 climate and vary by proximity to centers of industry and agriculture¹⁹. Nitrogen
251 deposition often interacts strongly with climate, given linkages among moisture
252 availability, growing period, and N demand by plants^{19,23}. Finally, a multitude of biotic
253 factors can affect biomass differently by location, including among-site variation in plant
254 species richness²⁴, the diversity of plant traits²⁵, levels of plant invasion¹⁷, and over-
255 grazing^{26,27}. Given these diverse and often scale-dependent drivers of biomass change,
256 it is unsurprising that their effects have been difficult to disentangle. Doing so will
257 require a global-level systematic assessment of biomass regulation both within and
258 among continents^{28,29}.

259 Here, we link long-term remotely sensed NDVI data with more contemporary plot
260 data from 84 grasslands on six continents to test drivers of biomass variability in
261 response to global change. These grasslands span a latitudinal gradient from -52° to
262 +78° (four within tropical latitudes), and capture ~1.6% of the world's total non-woody
263 vascular flora including ~5% of all Poaceae and ~3% of Cyperaceae (Table S1).
264 Seventy percent of our sites are arid (PET>annual rainfall – Table S1) matching the
265 ratio of arid-to-mesic grasslands globally³⁰, with the highest number of sites in North
266 America (41 sites), followed by Europe (17) Australia (13), South America (6), Africa (4),
267 and Asia (3) (Fig. S1). We classify “grasslands” as low-statured non-forested plant
268 communities. Functionally, grasslands occupy a climatically and edaphically determined
269 tension zone between forest and desert²⁹⁻³¹, regulated by climate seasonality, extreme
270 weather, fire, and human-managed and natural grazing with its total area covering ~53

271 million km² globally (excluding Antarctica and Greenland). These regulating processes
272 are associated with variability in grassland production, especially relating to climate³²⁻³⁴.
273 These same processes are being fundamentally re-shaped by global environmental
274 change, resulting in grasslands becoming a bellwether of resilience (or vulnerability) to
275 anthropogenic transformation including shifts in biomass.

276 Our remotely sensed data track changes in annual peak biomass from as early as
277 1986 based on Landsat-derived peak NDVI. Our primary analyses focused on
278 identifying drivers of change in peak NDVI using temporal factors measured during the
279 same interval (1986-2020). These included changes in the timing of three NDVI-based
280 phenophases that can affect peak biomass: vegetation emergence (i.e., start-of-season
281 spectral greening), senescence (i.e., end-of-season spectral browning), and growing
282 season length (duration from greening to browning), as well as inter-annual and inter-
283 seasonal changes in temperature, precipitation, and potential evapotranspiration
284 (PET)³⁵. We also tested NDVI trends in relation to site-level baseline factors calculated
285 from different durations including mean annual precipitation (MAP) and mean annual
286 temperature (MAT) based on hourly modelled temperature data from 1970-2020, and
287 site aridity (the ratio of annual PET: precipitation - 1970-2020). Other baseline factors
288 were anthropogenic N deposition based on modelled data from 2014-2016³⁶, the
289 number of plant species per site based on the net total of all species detected in the first
290 five years of sampling starting as early as 2007, the percentage of exotic taxa found in
291 each site-level species pool over five years of sampling²⁹, grazing impacts by large
292 mammals determined using offtake comparisons with exclosures at a subset of 46
293 grasslands, and composite community-level measures of plant traits for the species
294 present at each site³⁷. Using annually sampled aboveground biomass of plants (i.e.,
295 combined live, litter, and non-vascular) starting as early as 2007, we examined the

296 accuracy of satellite-derived NDVI for predicting grassland biomass, given that there
297 can be estimation biases relating to latitude, elevation, or species richness^{9,16}.
298 Analytically, we tested drivers of remotely sensed peak grassland NDVI by evaluating a
299 series of regression and multivariate models that isolate localized differences based on
300 our various explanatory factors (Table 1).

301 *Results and Discussion*

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

315 We found that variability in shifting NDVI-estimated biomass was primarily
316 explained by increases in growing season length, especially in combination with
317 warming (Figs. 2, S2, S3; Table 1). Between the late 1980s and the late 2010s, growing
318 seasons increased by an average of nine days (1986-90: \bar{x} = 157 days [SE = 3]; 2016-
319 20: \bar{x} = 166 days [SE = 2]). In total, 87% of sites had significant changes in the timing of
320 the onset of greening, the onset of browning, and/or the length of the growing season

321 since 1986 (e.g. Fig S4), indicating that many grasslands globally are undergoing
322 substantive shifts in seasonal cycling. Longer growing seasons have been implicated as
323 a warming response in grasslands and some cropping systems, and a causal factor of
324 increased biomass based on the assumption that plants are active for longer periods²².
325 Conversely, advancing greening, elevated production, or moisture limitation in arid
326 environments can sometimes accelerate leaf physiological processes relating to
327 photosynthesis that, in turn, shorten the growing season by triggering earlier
328 senescence^{22,23}. In total, 39% of sites had both earlier emergence and delayed
329 senescence thereby creating longer growing seasons (Fig. S4) – it was these
330 grasslands with the longest growing seasons that tended in experience that largest
331 increases in NDVI-estimated biomass. However, many other sites responded differently
332 such that there was no consistent global relationship between changes to the timing of
333 emergence and senescence (i.e., starting earlier does not predict the timing of
334 senescence: $F_{1,83} = 0.95$, $p = 0.33$; Fig. S4). For example, 19% of sites with earlier
335 emergence in spring experienced earlier spectral browning thereby shortening the
336 growing season, which has been observed previously in arid areas²³ and parts of the
337 Arctic^{45,46} including sites analyzed in this study. In total, variability in the connection
338 between shifting phenology and changes in peak biomass reinforce that there can be
339 powerful global trends in grassland responses to environmental change (e.g., longer
340 growing seasons at many sites), but also localized and divergent outcomes sometimes
341 regulated by different factors.

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

346 Arctic, Patagonia, and the alpine steppes of the Mongolian and Tibetan Plateaus)
347 versus those with the highest MATs but less overall warming (e.g., arid grasslands of
348 Australia, southwestern North America, Africa, and South America). (Figs. S2-S6). The
349 former were more often in the Northern Hemisphere, in line with observations that
350 global warming to date has been more pronounced north of the equator (i.e.,
351 interhemispheric temperature asymmetry⁴⁷) (Figs. 3, S6). These sites with the highest
352 warming also tended to be characterized by both high MAP and large increases in
353 annual rainfall - the wettest sites generally are becoming both wetter and warmer. This
354 is consistent with the ability of warmer air to support more moisture, as has been
355 observed with increasing snowfall in a warming Arctic⁴⁵. Conversely, sites with higher
356 baseline MATs, less warming, and reduced NDVI were all arid grasslands that tended to
357 undergo a shortening of growing season length, usually relating to an earlier onset of
358 spectral browning in summer (Figs. S6, S7). Not all arid sites experienced declining
359 biomass - only 32% of 59 arid sites had negative temporal slopes in NDVI even though
360 58% of all sites had less precipitation, increases in PET, or both (Figs. S1, S6, S7).

361 Our observed warming trends were more seasonal than annual, especially in the
362 spring and summer months – this contributed to the tight connection between growing
363 season length and temperature (Fig. S2). We examined changes to seasonal and
364 annual temperatures by site from 1986, which is near the beginning of Landsat data
365 collection while also capturing the onset of accelerating contemporary planetary
366 warming that continues to the present day^{34,45}. In testing the magnitude of seasonal and
367 annual changes, we found that seasonal changes were more prevalent with 37% of
368 sites having significantly warmer spring temperatures and 47% having warmer summers
369 (e.g., Fig. S8). In contrast, only a subset of sites had significant increases in annual
370 warming despite all slopes being positive. This decoupling of frequent seasonal

371 warming from less common significant annual warming suggests an intensification of
372 within-year inter-seasonal differences as has been reported previously in grasslands,
373 with periods of increasing temperature in some seasons being muted or offset by
374 cooling at other times of the year^{6,48}. For example, we observed cooling spring
375 temperatures in numerous mid-latitude grasslands of central North America and
376 western Europe (Fig. S8) – many of these sites had increasing NDVI.

377 We also saw significant influences of species richness on changes in peak NDVI,
378 although always interacting with phenology or climate (Table 1). Among sites with
379 lengthening growing seasons or warming temperatures, species-rich grasslands
380 generally displayed greater increases in NDVI than species-poor sites (Table 1; Figs.
381 S2, S9). Conversely, for grasslands with shortened growing seasons or less warming
382 (e.g., high MAT sites from the Southern Hemisphere and California), those with below-
383 average richness were predicted to show reduced or less pronounced NDVI increases.
384 These outcomes imply some form of context-dependent functional complementarity,
385 which would be consistent with the intertwined causal factors known to regulate
386 diversity and biomass in grasslands⁴⁹⁻⁵¹. They also reveal an absence of any
387 independent relationship of richness (Fig. 2, S9), and indeed sites with the highest
388 numbers of species (e.g., the African Serengeti) did not necessarily demonstrate
389 increasing NDVI. Such complexities on how richness affects biomass are illustrated
390 when considering the numbers of invasive grassland plants at our sites. Invasion is
391 sometimes linked with large increases in community-level biomass and site-level
392 richness⁵², yet we observed the opposite responses - invaded grasslands were more
393 likely to have declining biomass and fewer species. This likely reflects climatic factors –
394 most invaded sites were in arid regions where biomass trends since the 1980s were

395 non-significant or negative. It also likely reflects lower numbers of species – sites
396 dominated by invasive plants had significantly fewer plant taxa ($F_{1,63} = 9.2$, $P = 0.004$).

397 Several of our non-temporal hypothesized factors had no detectable effects on
398 changes to grassland NDVI despite often having sizable impacts on biomass at some
399 sites (Table 1). Sites with high levels of N deposition, especially in eastern North
400 America, higher elevation areas of western Europe, and areas of China (Fig. 3), did not
401 show significant changes in NDVI despite the well-described impacts of anthropogenic
402 N increasing grassland biomass¹⁹. Similarly, there was a lack of detectable association
403 between sites with high grazing offtake and changes to NDVI (Table S2). As with N
404 deposition, grazing can significantly affect grassland biomass²⁶ and indeed some of our
405 grasslands have substantive differences in biomass between grazed and fenced areas
406 including mesic grasslands of the Northern Hemisphere (sheep meadows in the UK,
407 reindeer barrens in Finland) and arid regions of Australia^{53,54}. However, variation in
408 levels of offtake estimated by our exclosures were unable to predict the likelihood of
409 NDVI change relative to the global-scale impacts of phenology, climate, or species
410 richness (Table S2). Finally, we also failed to detect associations between site-level
411 biomass change and variability in community-wide aggregate measures of plant size
412 (e.g., leaf area index [LAI], height) or foliar nutrients despite a wider spectrum of
413 resource-foraging strategies in plants sometimes being connected to higher biomass³⁷
414 (Table S3). Of particular note in our study was a lack of association between biomass
415 change and LAI. Remotely estimated LAI is often used to model plant production given
416 the strong connection between canopy density, light capture, and biomass^{55,56}.
417 However, we observed no predictive relationship between community-level LAI and
418 long-term shifts in NDVI despite 90-fold differences in canopy density ranging from

419 sparse arid grasslands of Australia and the American southwest to dense high-elevation
420 mesic grasslands of the European Alps (Table S3).

421 Combined, the prevalence of grasslands with trends towards higher site-level
422 biomass created a net 13.6% increase among our 84 sites since the 1980s (Fig. 1; $F_{1,83}$
423 = 91.6, $p < 0.0001$). Longer-term increases in biomass were also detected using our
424 field-measured data (Figs. 4, S10), and aligned with other reports of increasing overall
425 plant biomass with global environmental change³⁸⁻⁴². That being said, this magnitude of
426 increase could be viewed with caution. In total, 61 of our 84 sites occur in the Northern
427 Hemisphere, especially North America and Europe, where increases in precipitation and
428 biomass are known to be especially pronounced^{43,44}. Furthermore, there is evidence of
429 a threshold of ~500 mm per year in precipitation below which sensitivity to climatic
430 variability intensifies⁴⁴. Although most of our sites are arid ($PET > MAP$), their annual
431 precipitation averages 790 mm (SE = 43) with only 25% falling below 500 mm. We
432 tested the potential impacts of these factors on the subset of sites that are arid or have
433 MAP levels < 500 mm, and still observed net increases in biomass (arid sites: +12.2%
434 [SE 2.6%]; MAP < 500 mm: +15.6% [SE 5.7%]). Nonetheless, we might still anticipate
435 that mean site-level increases in biomass would be lower if more of our sites occurred in
436 areas where declining precipitation is especially pronounced.

437 Biomass variability is not unexpected in grasslands, given its regulation by
438 combinations of factors whose relative importance can change by locale including
439 supply rates of limiting nutrients, grazing pressure, and whether warming increases or
440 suppresses plant growth depending on precipitation³¹⁻³⁴. Indeed, localized responses in
441 biomass depending on whether warming sites are getting wetter or drier also occurs in
442 annual crops⁶, which is unsurprising given that large percentages of the world's
443 croplands were once grassland^{11,57}. Additionally, previous work on global-scale shifts in

444 NDVI-derived estimates of biomass, including in grasslands, has demonstrated both
445 increases and decreases since the 1980s without a consistently clear mechanistic
446 understanding given the challenges of testing fine-scale processes^{1,2,14,58}. Here, we
447 consolidate the disparate findings of previous work by showing that localized differences
448 emerge because the dominant regulatory processes appear to vary widely. These
449 findings are evident even though our results likely underestimate the full extent of
450 shifting grassland biomass with global change since the 1980s. For example, we do not
451 account for increased biomass caused by the invasion of trees and high-statured shrubs
452 into grassland – an increasingly prevalent phenomenon^{9,59}. We also did not account for
453 shifts in root biomass, with root:shoot ratios at 2:1 or more in grasslands⁶⁰. Finally, there
454 may be an influence of rising atmospheric CO₂ on biomass, although global trends in
455 CO₂ – a ~20% increase since the 1980s – tend to be expressed similarly by region⁶¹.

456 Our analyses integrated remotely sensed and field measured levels of annual
457 peak grassland biomass, demonstrating a strong positive relationship despite a ten-fold
458 difference in species richness among sites and a hundred-fold difference in standing
459 biomass. This indicates that NDVI can capture overall trends in aboveground standing
460 biomass at our sites. Nonetheless, there was widening predictive error as NDVI
461 exceeded 0.6 (Fig. 4). NDVI has been previously shown to accurately predict
462 aboveground plant biomass in uncultivated grasslands⁶². Indeed, we found similar
463 trends of an overall mean biomass increase among our 84 sites for both NDVI and plot-
464 level biomass (Fig. S10). However, NDVI can be prone to estimation bias with
465 increasing spatial scale, across years, at higher latitudes, and with increasing canopy
466 density and structure^{8,55,63} – factors that can characterize some of our data. A
467 fundamental practical question for using NDVI is whether the ability to predict biomass
468 can be improved with widely available ancillary data such as latitude and climate, or

469 whether improvement requires detailed field calibration that may be impossible¹⁶. Our
470 field data gave us a unique opportunity to test drivers of unexplained variation including
471 fine-scale biotic factors (see Methods), revealing two primary sources of bias: high
472 latitude and low elevation. Adding these widely available data to our models improved
473 the predictive accuracy of NDVI for ground measured biomass by 21% (Table S4).
474 Estimation bias at high latitude for NDVI is especially common, relating to
475 methodological and biophysical factors including the potential underestimation of non-
476 photosynthetically active vegetation (which we sampled)⁹. Although our fit between
477 NDVI and aboveground biomass remained strong at higher latitudes, our work supports
478 the need for caution when extrapolating trends in phenological change including the
479 timing and magnitude of peak biomass. The same caution appears to apply to
480 extrapolating connections among remotely sensed estimates of biomass and species
481 richness^{16,64}, as we also detected a smaller but significant estimation bias between
482 NDVI and field biomass as the numbers of species site⁻¹ increased (Table S4).

483 Our work describes a substantial divergence of peak biomass by location within
484 many grasslands globally. These results were obtained from non-cultivated permanent-
485 cover grassland, a habitat type under long-standing and intensifying conversion
486 pressure^{55,65}. Despite grassland losses exceeding 99% in some regions⁶⁶, uncultivated
487 areas still cover ~25% of Earth's terrestrial surface, store ~25% of its carbon, and
488 support thousands of obligate flora and fauna⁶⁷. Many of the global-scale ecological
489 benefits of uncultivated grassland center on the annual production of biomass, including
490 litter inputs that contribute to soil C cycling, providing forage for much of the world's
491 remaining megafauna and half of all domesticated livestock, and regulating fire cycling
492 given that grasslands account for most of Earth's annual burning⁶⁷. Our documentation
493 of shifts in the direction and magnitude of biomass in our grasslands suggests that there

494 will be far-ranging implications for the planet moving forward, which will be experienced
495 differently by location.

496 **Methods**

497 *Study area and experimental design*

498 Our study sites span a latitudinal gradient from Patagonia (-52°) to the high Arctic
499 of Norway (+78°) and range in elevation from 0 m to 4241 m, with wide differences
500 in potential evapotranspiration (0.79 – 6.49 mm day⁻¹), atmospheric N deposition (66.9
501 to 2162.1 mg N m⁻² year⁻¹), and long-term (1970-2020) mean annual precipitation (MAP:
502 192 to 2224 mm) and mean annual temperature (MAT: -7.5 to 27.2°C) (Fig. S11, Table
503 S1). There is wide variation in the total number of species per site (“species richness”),
504 ranging from 13 to 176 species, summed together for all non-treated control plots based
505 on five years of sampling in case there were cryptic taxa not visible in some years.
506 Percent exotic flora ranges from 0 to 100% of all species per site (Table S1) with
507 multiple species occurring at sites within both their ancestral and non-native ranges⁶⁸.
508 There were 421 non-native plant taxa in total, but with twenty of the 84 sites having no
509 exotic species (all sites in Europe, Asia, and Africa). Levels of grazer offtake at the 46
510 sites with exclosures range from none to ~85% of total annual plot-level
511 biomass^{53,54}. We classify “grasslands” as low-statured non-forested plant communities,
512 including treed savanna, prairie, planted permanent-cover pasture, montane meadows,
513 and arctic-alpine tundra. Our sites cover a wide range of “Whittaker biomes” defined by
514 the ratio of MAP to MAT (Fig S1). They also have some degree of geographic
515 clustering, with an average minimum distance globally of 379.3 km (range: 1 to 3,087
516 km). This means that several sites have identical estimates of N-deposition given the
517 spatial resolution of those data (2° × 2.5°). Our ratio of arid-to-mesic grasslands
518 (71%:29% - Table S1) matches the global ratio³⁰ but the continental distribution of our

519 sites is not proportional to the global range of grasslands. Almost half of our sites are
520 from North America even though its continental coverage of grassland is only 13%
521 globally. Australia and South America have similar ratios between number of our sites
522 versus their global coverage (14:13%; 10:9% respectively), while Asia and Africa are
523 under-represented (Fig. S1). For our invaded sites, there could be a concern that our
524 data misrepresent invasion impacts on NDVI change because of the gap between the
525 start of the remote sensing data (mid-1980s) and the field sampling (2007). Although we
526 cannot definitively eliminate this possibility (e.g., an uninvaded site becoming heavily
527 invaded after 1986), the odds are low as all sites occur in regions of the world with long
528 legacies of invasion dating back a century or more⁶⁸. Our study began with 127 sites but
529 was ultimately reduced to 84 based on screening for extreme outliers, poor image
530 resolution especially due to cloud cover, and confounding site factors such as tree cover
531 (see below).

532 Our analyses combined NDVI calculated from Landsat images starting no earlier
533 than 1986, climate data including PET³⁵, modelled N deposition data³⁶, and field data
534 collected from 84 grassland sites from the Nutrient Network (NutNet), a globally
535 distributed experiment²⁹. All NDVI satellite data were extracted from unmodified areas
536 adjacent to plots associated with NutNet (Fig. S12). All NutNet plot data were collected
537 by local site scientists, starting in 2007 or later depending on when the site joined the
538 network. Field sampling occurred within thirty permanently marked 5 x 5 m plots laid out
539 in a grid (Fig S12). We used data from the year prior to the application of any
540 experimental treatment (i.e., “Year 0” pre-treatment data, when all plots were
541 unmodified) and from subsequent years (Years 1, 2, etc.) in the subset of plots that
542 were untreated (i.e., all data in this study only come from unmodified control plots). Plot
543 data were collected annually at peak biomass and included total aboveground biomass,

544 clipped to ground level from two 10 cm x 100 cm strips within a larger 5 m x 5 m plot,
545 with the clipping locations differing each year²⁹. Clipped biomass was sorted to live,
546 non-vascular, and litter, and then dried to a constant mass at 60° C and weighed.
547 Differentiating biomass into live vascular, live non-vascular, and litter is one of several
548 important novelties of our study, given the NDVI estimations of standing plant biomass
549 can sometimes be insensitive to, or biased by, the latter two factors. Indeed, 53% of all
550 Nutnet grasslands globally have been found to support non-vascular plant growth, with
551 standing biomass as high as 635 g m⁻² (Virtanen et al. submitted).

552 Our 84 sites captured a wide variation in the relative abundance of major
553 functional groups, including graminoids (e.g., grasses and sedges), forbs, and, to a
554 lesser degree and mostly in the Arctic, low-statured woody plants, lichens, and
555 bryophytes. There was a wide range in the percentage of non-native flora per site. Many
556 sites in Europe, Africa, and Asia had few or no non-natives, while some grasslands in
557 North America, South America, and Australia were >90% exotic taxa⁶⁸. Species
558 composition data were used to calculate two measures of community-level trait
559 variation, functional diversity (FD) and community weighted mean (CWM)³⁷. FD, an
560 estimate of trait variability, relates to degrees of trait converge or divergence within plots
561 based on Rao's index of quadratic entropy. CWM (also referred to as FI³⁷), an estimate
562 of trait averages, is based on the community weighted mean for each trait in each plot.
563 Trait data were compiled from TRY (public version), AusTraits (version 1.1.0), BIEN
564 (version 1.2.5), and NutNet (leaf traits), for six continuous traits (height, leaf surface
565 area (LAI), specific leaf area (SLA – the ratio of leaf area to leaf mass), leaf N, leaf P,
566 leaf C), that have relatively high coverage for species recorded in NutNet (93, 95, 87,
567 91, 86, 75, 81% for each trait, respectively). For species that do not have trait values,
568 we used the mean values from their genus (see Table S3)

569 The only Nutnet treatment data were for grazer offtake, derived from fenced but
570 unfertilized plots^{53,54}. Grazing effects were expressed as the log response ratio of
571 differences in clipped biomass between control plots in fenced and unfenced areas at a
572 subset of 46 sites (the remaining 38 sites did not have exclosures). Typically, there
573 were three fenced plots per site, and the fences were ~2.3 m tall with the lower 90 cm
574 being 1 cm steel mesh and the upper portion surrounded by strands of barbless wire²⁹.
575 These grazing offtake data were calculated only in the first year after the exclosures
576 were constructed (Year 1), given that longer-term exclosure effects can be confounded
577 by shifts in plant species richness and relative abundance⁵¹. Levels of grazer offtake
578 ranged from very low or nil with some sites lacking detectable grazing, to very high
579 especially in parts of Australia, Africa, and western Europe (e.g., sheep grazing in
580 Lancaster UK, domesticated reindeer grazing in Kilpisjarvi, Finland)^{53,54}.

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

585 *NDVI measurements and phenological dates*

586 We used images from Landsat missions 4, 5, 7, and 8, to calculate the normalized
587 difference vegetation index (NDVI) at each site starting as far back as 1986 (depending
588 on image quality) and extending annually to 2020 at a resolution of 30 m in an
589 unmodified circular area selected near the Nutnet plots (Fig. S12). In these plots, we
590 extracted a series of phenological NDVI measures within each growing season,
591 modified from Buitenwerf et al.⁸ given that we only targeted a single vegetation type
592 (i.e., grasslands): off-season ‘trough’ when plants are inactive, start-of-season
593 “emergence”, peak NDVI, end-of-season “senescence”, and “growing season length”

594 derived from the number of days from emergence to senescence each year (Fig. S13).
595 Elsewhere, NDVI has been used to detect trends in phenology and related biomass
596 responses^{9,16}, including in grasslands where it has been shown to strongly align with
597 live biomass⁶². Our work supports this significant relationship, albeit with increasing
598 variation beyond NDVI values of 0.6 (Fig. 4). We conducted a series of analyses to
599 identify sources of error for NDVI including tests for influences by outliers, the influences
600 of regional-scale factors relating to latitude and elevation, and local-scale factors
601 including non-vascular flora (described below – Table S4). We removed two sites that
602 failed uniformity tests when conducting linear fits between annual peak NDVI and time,
603 based on comparisons with a Theil-Sen median regressor and trend-filtering using a
604 Mann-Kendall Trend Test – both were sparsely vegetated sites of the Icelandic tundra
605 and arid grassland of central North America.

606 Location of the circular “NDVI plots” was done visually using Google Earth
607 images. We located a central point in an area adjacent to the NutNet experiment, given
608 that the Nutnet plots are readily detectable from the images (Fig. S12). This adjacent
609 area was selected to contain vegetation identical to the vegetation within the
610 experiment, in consultation with each Nutnet site PI. It was positioned at least 50 m from
611 the closet NutNet plot to avoid the influence of any experimental treatments associated
612 with the NutNet manipulations, while leveraging the site-specific vegetation and soil
613 information derived from the experiment. There is always potential risk of positioning
614 error using Google Earth – a global analysis of high-resolution Google Earth imagery
615 has estimated an overall horizontal geo-registration accuracy of 39.7 m RMSE with an
616 accuracy of 24 m RMSE in some countries⁶⁹ and subsequent studies demonstrate
617 improved horizontal accuracy of 10.5 m RMSE⁷⁰. We explicitly tested RSME error for
618 eight of our sites, contrasting plot-level coordinate data generated using a hand-held

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

622 In each circular plot per site, we extracted reflectance data from within a circular
623 buffer within 30 m around this point (Fig. S12). This was done using images from top-of-
624 atmosphere (TOA) reflectance collections in Google Earth Engine. The images were
625 taken between 1982 and 2020, although the specific date ranges and sampling
626 frequency varies at each site. All of our analyses using remote sensed data that start no
627 earlier than 1986 as site data prior to this was found to be too sporadic (Fig. S13). In all
628 cases, the spatial resolution of each image is 30 m. We used all available images from
629 both Tier 1 and Tier 2 quality, which were aggregated and processed using Google
630 Earth Engine. Tier 2 data were essential for obtaining images taken during the snow-
631 covered “trough” portion of the year. The horizontal geo-registration accuracy of Tier 1
632 scenes is \leq 12-meter root mean square error (RMSE) whereas the Tier 2 accuracy is >
633 12 m RMSE⁷¹. Landsat Collection 1 was used, although Collection 2 is the only
634 collection currently available for download but both collections have the same published
635 geo-registration accuracies⁷¹. For each image, we calculated NDVI using the
636 corresponding near-infra red and red bands 4 and 3 for Landsat 4, 5, and 6, and bands
637 5 and 4 for Landsat 8. We also extracted information about image quality (BQA band)
638 containing statistics from the image data and post-processing information⁶⁹. BQA values
639 were used to filter images to exclude any pixels that had a high likelihood of including
640 clouds or cloud shadows. Using manual inspection, we included only pixels associated
641 with clear, cloud-free imagery (Landsat 4, 5, and 7 BQA = 672, 680, 676, 680, 684;
642 Landsat 8 BQA = 2720) or imagery over snow (Landsat 4, 5, and 7 BQA = 1696, 1700,

643 1704, 1708; Landsat 8 BQA = 3744). We discarded images where resolution was
644 uncertain (e.g., clouds versus snow - <0.5% of all images).

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

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

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

$$\begin{aligned} \text{675} \quad \text{Threshold} = & \left(0.5 \times \left(\overline{\text{MaximumNDVI}} \right. \right. \\ \text{676} \quad & \left. \left. - \overline{\text{MinimumNDVI}} \right) \right) + \overline{\text{MinimumNDVI}} \end{aligned}$$

678
679 where the average maximum and minimum NDVI values were calculated across all
680 years at each site. This green threshold allowed for flexibility to include sites with
681 different minimum NDVI values (e.g., sites which become snow-covered and sites which
682 do not) as well as different maximum NDVI values. In using a threshold, we were also
683 able to ensure that a green-up or senescence date was biologically comparable across
684 all years (indicating the same NDVI).

685 In all cases of fitting cubic splines, we forced a minimum NDVI value of 0 (if
686 measured NDVI was < 0, we re-assigned the value to 0), as our smoothing and post-
687 processing was dependent on consistency during the growing season troughs when
688 data were typically sparse. During the growing season troughs, band quality information
689 often indicated that pixels were cloud covered when visual analysis of images revealed
690 snow cover (both cloud and snow cover containing water). We excluded pixels
691 indicating cloud cover in this analysis. To overcome sparse data points during these

692 periods in Tier 1 datasets we additionally used Tier 2 data. Given that data from both
693 tiers were required and the radiometric calibration was top-of-atmosphere reflectance,
694 alternative variations of NDVI that adjust for noise due to soil brightness and
695 atmospheric light scattering, such as the enhanced vegetation index (EVI)^{72,73}, were not
696 employed - indices with numerical constants can be inconsistent due to atmospheric
697 noise⁶⁹. Furthermore, snow cover decreases NDVI values but increases EVI values⁷⁰
698 and such sensitivity would confound the phenological analysis.

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

704 *Climate and N-deposition trends*

705 Monthly long-term temperature (MAT) and precipitation (MAP) averages per site
706 were obtained from the WorldClim database, from 1970-2020. MAT and MAP served to
707 describe baseline levels of temperature and precipitation among sites. To determine
708 annual deviations in temperature and precipitation from baseline MAP and MAT, we
709 calculated a monthly time series for temperature and precipitation during the study
710 period (1986-2020), with data obtained at the site level using the Climatic Research Unit
711 (CRU) time-series (TS) version 4.03 data³⁵. These annual deviations were calculated as
712 slopes of change over time. Estimates of potential evapotranspiration (PET) were also
713 obtained from the CRU time series³⁵, which calculates PET using mean, maximum, and
714 minimum monthly temperatures, vapor pressure, and cloud cover (1970-2020).

715 Given predictions of increased interannual seasonal variability in climate, with the
716 potential to affect phenology and peak biomass, we calculated slopes of 36-year trends

717 in temperature and precipitation seasonality at each site. We targeted these calculations
718 for two phenophases: (i) green-up based on a two-month window around the date of
719 typical site-specific green-up date (the typical month of green-up, plus one month
720 before), and (ii) maximum NDVI as a five-month window around the date of typical site-
721 specific maximum NDVI (the typical month of NDVI max, plus two months before and
722 after). These seasonal calculations allowed us to test more detailed climatic drivers of
723 phenological change, which may not be detected by overall annual trends including the
724 possibility of warmer springs, warmer and drier summers, and even seasonal cooling as
725 is sometimes observed (e.g., Fig. S8)⁴⁸.

726 Atmospheric nitrogen (N) deposition was estimated for each of the sites using the
727 GEOS-Chem Chemical Transport Model³⁶. The model estimates wet and dry deposition
728 of inorganic N using models of atmospheric chemistry together with meteorological data
729 and emissions data. Outputs are at a 2° × 2.5° resolution averaged across the years
730 2014, 2015, and 2016. Although the N deposition model uses meteorological data, there
731 were weak and non-significant correlations between precipitation and estimates of N
732 deposition ($r^2 = 0.009$).

733 *Analysis*

734 Our primary analysis tested drivers of change in maximum NDVI over the period
735 starting from 1986 to 2020, based on site-specific slopes of biomass change over time
736 (Fig. 1). We used a multi-model selection approach to evaluate the relative importance
737 of variables associated with our four interacting hypotheses: (i) changes in climate
738 including temperature, precipitation, and PET, (ii) changes in phenology including the
739 timing of emergence, the timing of senescence, and growing season length, (iii) levels
740 of atmospheric N deposition, and (iv) biotic factors of species richness, grazing
741 intensity, traits, and exotic (non-native) species. We simplified our analytical models by

742 removing factors that were tightly correlated, using principal coordinate analysis (e.g.,
743 Figs. S2, S3). For example, we found that overall changes in temperature and
744 precipitation (the 36-year temporal trends based on slope) were tightly correlated with
745 seasonal changes in spring and summer temperature and precipitation – we thus used
746 the former in our models. Similarly, sites differed widely in changes to emergence and
747 senescence over time, but we excluded both for our main models as their effects were
748 significantly captured by trends in growing season length – sites that started earlier
749 often had longer growing seasons, as did sites that senesced later (although only 39%
750 of sites had both earlier emergence and later senescence – see Main Text).

751 Accordingly, we built a maximal linear model in R^{74} that assessed the response of
752 site-level biomass slopes (change in NDVI from as early as 1986 to 2020, depending on
753 the site – Fig. 1) to all independent effects and pairwise interactions of a subset of
754 factors: latitude, elevation, N deposition, species richness, growing season length,
755 aridity, percent exotic species, overall annual temperature slope (warming since 1986),
756 and overall annual precipitation slope (changes in precipitation since 1986). We
757 included grazing in a separate model for these factors, for the 46 sites that had
758 exclosures (Table. S2). All of these variables included in the final maximal model had
759 low collinearity, as indicated by assessment of variance inflation factors⁷⁵. These factors
760 also met assumptions of normality (or were log transformed to aid this – e.g., N
761 deposition), and were standardized to a mean of zero and standard deviation of 0.5
762 using the ‘arm’ package⁷⁶, as required for model comparison⁷⁷. Further we adjusted our
763 regression models using the inverse of the standard error of the slope from each site, so
764 as to down-weight parameters estimated with larger error (e.g., Seabloom et al.⁷⁸). We
765 evaluated the fit of subsets of this model using the MuMIn package⁷⁴ and conducted a
766 model averaging procedure for all candidate models within two AIC of the best model.

767 We present the full averages of parameter estimates from our final model (e.g., Tables
768 1, S2)⁷⁵⁻⁷⁷.

769

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

772

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791 **Author contributions:**

792 Conceptualization: ASM, EE with MS, CB, KL, JO

793 Methodology: EE with ASM, OC, CB, QC, EWS, TO, ETB

794 Investigation: EE, ASM

795 Visualization: ASM, EE

796 Analyses: ASM, with OC, CB, EE, TO, ES, and QC

797 Funding acquisition: ASM, with ETB and EWS

798 Project administration: ASM

799 Supervision: ASM

800 Writing – original draft: ASM with EE

801 Writing – review & editing: ASM, EE and all co-authors

802 Data collection and contribution: all co-authors

803

804 **Competing interests:** Authors declare that they have no competing interests.

805

806 **Tables**

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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

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816

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Figure Captions

818

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).*

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827

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

828

829

830

831 are also significant relationships between (B) increasing NDVI and the slope of
832 temperature increase by site ($F_{1,83} = 6.6$; $p=0.012$; note: all sites warmed) and (C)
833 increasing NDVI and the slope of changes in annual precipitation ($F_{1,83} = 5.3$; $p=0.023$).
834 For species richness (D), there was no univariate impact on changing NDVI ($F_{1,83} = 0.34$;
835 $p = 0.56$), although it interacted significantly with growing season length and warming
836 (Table 1, Fig. S9). The inserted dashed lines in Figs. 2A-C indicate areas of no net
837 change. All tests are linear regressions among the 84 sites of this study.

838

839 **Fig. 3. Global maps showing variation among sites in (A) shifting average annual**
840 **temperature, (B) average annual precipitation, (C) growing season length for**
841 **1986-2020, and (D) levels of atmospheric N deposition modelled for 2014-2016.**

842 *Data for temperature and precipitation came from CRU³⁵. The largest temperature*
843 *increases are mostly in the northern hemisphere – southern hemisphere sites have*
844 *higher mean annual temperatures, but lower levels of warming since the 1980s.*
845 *Growing season length were derived by site and over time based on differences*
846 *between remotely sensed spectral greening and spectral browning each year.*
847 *Atmospheric nitrogen (N) deposition was estimated using the GEOS-Chem Chemical*
848 *Transport Model³⁶, which estimates wet and dry deposition of inorganic N using models*
849 *of atmospheric chemistry together with meteorological data and emissions data – these*
850 *N data have a $2^\circ \times 2.5^\circ$ resolution.*

851

852 **Fig. 4. Relationship between annual remotely sensed maximum NDVI and annual**
853 **live aboveground biomass. The best-fit curvilinear regression line ($F_{2,410} = 72.7$; p**
854 **<0.0001) derives from sites with three or more years of live biomass, with the red shaded**
855 **area (confidence curves for the fitted line) showing how estimation bias begins to widen**

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

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