

Plant functional trait change across a warming tundra biome

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228 **Summary paragraph**

229 The tundra is warming more rapidly than any other biome on Earth, and the potential
230 ramifications are far-reaching due to global-scale vegetation-climate feedbacks. A better
231 understanding of how environmental factors shape plant structure and function is critical to
232 predicting the consequences of environmental change for ecosystem functioning. Here, we
233 explore the biome-wide relationships between temperature, moisture, and seven key plant
234 functional traits both across space and over three decades of warming at 117 tundra
235 locations. Spatial temperature-trait relationships were generally strong but soil moisture had
236 a marked influence on the strength and direction of these relationships, highlighting the
237 potentially important influence of changes in water availability on future plant trait change.
238 Community height increased with warming across all sites over the past three decades, but
239 other traits lagged far behind predicted rates of change. Our findings highlight the challenge
240 of using space-for-time substitution to predict the functional consequences of future warming
241 and suggest that functions tied closely to plant height will experience the most rapid change.
242 Our results reveal the strength with which environmental factors shape biotic communities at
243 the coldest extremes of the planet and will enable improved projections of tundra functional
244 change with climate warming.

245

246 **Main text**

247 Rapid climate warming in Arctic and alpine regions is driving changes in the structure and
248 composition of tundra ecosystems^{1,2}, with potentially global consequences. Up to 50% of the
249 world's belowground carbon stocks are contained in permafrost soils³, and tundra regions
250 are expected to contribute the majority of warming-induced soil carbon loss over the next
251 century⁴. Plant traits strongly impact carbon cycling and energy balance, which can in turn
252 influence regional and global climates⁵⁻⁷. Traits related to the resource economics
253 spectrum⁸, such as specific leaf area, leaf nitrogen content, and leaf dry matter content,
254 affect primary productivity, litter decomposability, soil carbon storage, and nutrient
255 cycling^{5,6,9,10}, while size-related traits such as leaf area and plant height influence
256 aboveground carbon storage, albedo, and hydrology¹¹⁻¹³ (Extended Data Table 1).
257 Quantifying the link between the environment and plant functional traits is therefore critical to
258 understanding the consequences of climate change, but such studies rarely extend into the
259 tundra¹⁴⁻¹⁶. Thus, the full extent of the relationship between climate and plant traits in the
260 planet's coldest ecosystems has never been assessed, and the consequences of climate
261 warming for tundra functional change are largely unknown.

262

263 Here, we quantify for the first time the biome-wide relationships between temperature, soil
264 moisture, and key traits that represent the foundation of plant form and function¹⁷, using the
265 largest dataset of tundra plant traits ever assembled (56,048 measured trait observations;
266 Fig. 1a and Extended Data Fig. 1a, Table S1). We examine five continuously distributed
267 traits related to plant size (adult plant height and leaf area) and to resource economy
268 (specific leaf area (SLA), leaf nitrogen content (leaf N), and leaf dry matter content (LDMC)),
269 as well as two categorical traits related to community-level structure (woodiness) and leaf
270 phenology/lifespan (evergreenness). Intraspecific trait variability is thought to be especially
271 important where diversity is low or where species have wide geographic ranges¹⁸, as in the
272 tundra. Thus, we analyze two underlying components of biogeographic patterns in the five
273 continuous traits: intraspecific variability (phenotypic plasticity or genetic differences among
274 populations) and community-level variability (species turnover or shifts in species'
275 abundances over space). We ask: 1) How do plant traits vary with temperature and soil
276 moisture across the tundra biome? 2) What is the relative influence of intraspecific trait
277 variability (ITV) versus community-level trait variation (estimated as community-weighted
278 trait means, CWM) for spatial temperature-trait relationships? 3) Are spatial temperature-trait
279 relationships explained by among-site differences in species abundance or species turnover
280 (presence-absence)?

281

282 A major impetus for quantifying spatial temperature-trait relationships is to provide an
283 empirical basis for predicting the potential consequences of future warming¹⁹⁻²¹. Thus, we
284 also estimate realized rates of community-level trait change over time using nearly three
285 decades of vegetation survey data at 117 tundra sites (Fig. 1a, Table S2). Focusing on
286 interspecific trait variation, we ask: 4) How do changes in community traits over three
287 decades of ambient warming compare to predictions from spatial temperature-trait
288 relationships? We expect greater temporal trait change when spatial temperature-trait
289 relationships are a) strong, b) unlimited by moisture availability, and c) due primarily to
290 abundance shifts instead of species turnover, given that species turnover over time depends
291 on immigration and is likely to be slow²². Finally, because total realized trait change in
292 continuous traits is comprised of both community-level variation and intraspecific trait
293 variation (ITV), we estimated the *potential* contribution of ITV to overall trait change
294 (CWM+ITV) using the modeled intraspecific temperature-trait relationships described above
295 (see Methods and Extended Data Fig. 1b). For all analyses, we used a generalizable
296 Bayesian modeling approach, which allowed us to account for the hierarchical spatial,
297 temporal and taxonomic structure of the data as well as multiple sources of uncertainty.

298

299 *Environment-trait relationships across the tundra biome*

300 We found strong spatial associations between temperature and community height, SLA, and
301 LDMC (Fig. 2a, Extended Data Fig. 2, Table S3) across the 117 survey sites. Both height
302 and SLA increased with summer temperature, but the temperature-trait relationship for SLA
303 was much stronger at wet than at dry sites. LDMC was negatively related to temperature,
304 and more strongly so at wet than at dry sites. Community woodiness decreased with
305 temperature, but the ratio of evergreen to deciduous woody species increased with
306 temperature, particularly in dry sites (Extended Data Fig. 3). These spatial temperature-trait
307 relationships suggest that long-term climate warming should cause pronounced shifts toward
308 communities of taller plants with more resource-acquisitive leaves (high SLA and low
309 LDMC), particularly where soil moisture is high.

310

311 Our results reveal a substantial moderating influence of soil moisture on community traits
312 across spatial temperature gradients^{2,23}. Both leaf area and leaf N decreased with warmer
313 temperatures in dry sites but increased with warmer temperatures in wet sites (Fig. 2a,
314 Table S4). Soil moisture was important in explaining spatial variation in all seven traits
315 investigated here, even when temperature alone was not (e.g., leaf area; Fig. 2a and
316 Extended Data Figure 2), potentially reflecting physiological constraints related to heat
317 exchange or frost tolerance when water availability is low²⁴. Thus, future warming-driven
318 changes in traits and associated ecosystem functions (e.g. decomposability) will likely
319 depend on current soil moisture conditions at a site²³. Furthermore, future changes in water
320 availability (e.g., via changes in precipitation, snow melt timing, permafrost, and hydrology²⁵)
321 could cause substantial shifts in these traits and their associated functions irrespective of
322 warming.

323

324 We found consistent intraspecific temperature-trait relationships for all five continuous traits
325 (Fig. 2b, Table S5). Intraspecific plant height and leaf area showed strong positive
326 relationships with summer temperature (i.e., individuals were taller and had larger leaves in
327 warmer locations) while intraspecific LDMC, leaf N and SLA were related to winter but not
328 summer temperature (Extended Data Fig. 2). The differing responses of intraspecific trait
329 variation to summer versus winter temperatures may indicate that size-related traits better
330 reflect summer growth potential while resource economics traits reflect tolerance of cold-
331 stress. These results, although correlative, suggest that trait variation expressed at the
332 individual or population level is related to the growing environment and that warming will

333 likely lead to substantial intraspecific trait change in many traits. Thus, the potential for trait
334 change over time is underestimated by using species-level trait means alone. Future work is
335 needed to disentangle the role of plasticity and genetic differentiation in explaining the
336 observed intraspecific temperature-trait relationships²⁶, as this will also influence the rate of
337 future trait change²⁷. Trait measurements collected over time and under novel (experimental)
338 conditions, as yet unavailable, would enable more accurate predictions of future intraspecific
339 trait change.

340

341 Partitioning the underlying causes of community temperature-trait relationships revealed that
342 species turnover explained most of the variation in traits across space (Fig. 2c), suggesting
343 that dispersal and immigration processes will primarily govern the rate of ecosystem
344 responses to warming. Shifts in species' abundances and intraspecific trait variation
345 accounted for a relatively small part of the overall temperature-trait relationship across space
346 (Fig 2c). Furthermore, the local trait pool in the coldest tundra sites (mean summer
347 temperature < 3 °C) is constrained relative to the tundra as a whole for many traits
348 (Extended Data Fig. 4). Together, these results indicate that the magnitude of warming-
349 induced community trait shifts will be limited without the arrival of novel species from warmer
350 environments.

351

352 *Community trait change over time*

353 Plant height was the only trait for which the community weighted mean changed over the 27
354 years of monitoring; it increased rapidly at nearly every survey site (Fig. 3 a&b, Extended
355 Data Fig. 3, Table S6). Inter-annual variation in community height was sensitive to summer
356 temperature (Fig. 3c, Extended Data Fig. 2, Table S7), implying that increases in community
357 height are responding to warming. However, neither the total rate of temperature change nor
358 soil moisture predicted the total rate of CWM change in any trait (Extended Data Fig. 5,
359 Table S8). Incorporating potential intraspecific trait variation (ITV) doubled the average
360 estimate of plant height change over time (Fig. 3a and 4a, dashed lines). Because spatial
361 patterns in ITV can be due to both phenotypic plasticity and genetic differences among
362 populations, this is likely a maximum estimate of the ITV contribution, for example if
363 intraspecific temperature-trait relationships are due entirely to phenotypic plasticity. The
364 increase in community height observed here is consistent with previous findings of
365 increasing vegetation height in response to experimental warming at a subset of these
366 sites²⁸ and with studies showing increased shrub growth over time¹¹.

367

368 Increasing community height over time was due largely to species turnover (rather than
369 shifts in abundance of the resident species; Fig 3b) and was driven by the immigration of
370 taller species rather than the loss of shorter ones (Extended Data Fig. 6, Table S9). This
371 turnover could reflect the movement of tall species upward in latitude and elevation or from
372 local species pools in nearby warmer microclimates. The magnitude of temporal change was
373 comparable to that predicted from the spatial temperature-trait relationship (Fig. 4a, solid
374 lines), indicating that temporal change in plant height is not currently limited by immigration
375 rates. The importance of immigration in explaining community height change is surprising
376 given the relatively short study duration and long lifespan of tundra plants, but is nonetheless
377 consistent with a previous finding of shifts towards warm-associated species in tundra plant
378 communities^{20,29}. If the observed rate of trait change continues (e.g., if immigration were
379 unlimited), community height (excluding potential change due to ITV) could increase by 20-
380 60% by the end of the century, depending on carbon emission, warming and water
381 availability scenarios (Extended Data Fig. 7).

382

383 *Consequences & Implications*

384 Recent (observed) and future (predicted) changes in plant traits, particularly height, are likely
385 to have important implications for ecosystem functions and feedbacks involving soil
386 temperature^{30,31}, decomposition^{5,10}, and carbon cycling³², as the potential for soil carbon loss
387 is particularly great in high-latitude regions⁴. For example, increasing plant height could
388 offset warming-driven carbon loss via increased carbon storage due to woody litter
389 production⁵ or via reduced decomposition due to lower summer soil temperatures caused by
390 shading^{3,30,32} (negative feedbacks). Positive feedbacks are also possible if branches or
391 leaves above the snowpack reduce albedo^{11,12} or increase snow accumulation, leading to
392 warmer winter soil temperatures and increased decomposition rates^{3,11}. The balance of
393 these feedbacks and thus the net impact of trait change on carbon cycling may depend on
394 the interaction between warming and changes in snow distribution³³ and water availability³⁴,
395 which remain major unknowns in the tundra biome.

396

397 The lack of an observed temporal trend in SLA and LDMC despite strong temperature-trait
398 relationships over space highlights the limitations of using space-for-time substitution for
399 predicting short-term ecological change. This disconnect could reflect the influence of
400 unmeasured changes in water availability, e.g. due to local-scale variation in the timing of
401 snowmelt or hydrology, that counter or swamp the effect of static soil moisture estimates.
402 For example, we would not expect substantial changes in traits demonstrating a spatial

403 temperature x moisture interaction (LDMC, leaf area, leaf N, and SLA), even in wet sites, if
404 warming also leads to drier soils. Perhaps tellingly, plant height was the only continuous trait
405 for which a temperature x moisture interaction was not important, and was predicted to
406 increase across all areas of the tundra regardless of recent soil moisture trends (Fig. 4c&d).
407 Spatial-temporal disconnects could also reflect dispersal limitation of potential immigrants
408 (e.g., with low LDMC and high SLA), or establishment failure due to novel biotic (e.g.,
409 herbivore³⁵) or abiotic (e.g., photoperiod³⁶) conditions other than temperature to which
410 immigrants are maladapted^{22,36}. Furthermore, community responses to climate warming
411 could be constrained by soil properties (e.g., organic matter, mineralization) that themselves
412 respond slowly to warming²⁰.

413

414 The patterns in functional traits described here reveal the extent to which environmental
415 factors shape biotic communities in the tundra. Strong temperature- and moisture-related
416 spatial gradients in traits related to competitive ability (e.g., height) and resource capture and
417 retention (e.g., leaf nitrogen, SLA) reflect tradeoffs in plant ecological strategy^{9,37} from
418 benign (warm, wet) to extreme (cold, dry) conditions. Community-level trait syndromes, as
419 reflected in ordination axes, are also strongly related to both temperature and moisture,
420 suggesting that environmental drivers structure not only individual traits but also trait
421 combinations and thus lead to a limited number of successful functional strategies in some
422 environments (e.g., woody, low-SLA and low-leaf N communities in warm, dry sites;
423 Extended Data Fig. 8). Thus, warming may lead to a community-level shift toward more
424 acquisitive plant strategies³⁷ in wet tundra sites, but toward more conservative strategies in
425 drier sites as moisture becomes more limiting.

426

427 Earth system models are increasingly moving to incorporate trait-environment relationships,
428 as this can substantially improve estimates of ecosystem change³⁸⁻⁴⁰. Our results inform
429 these projections of future tundra functional change³⁸ by explicitly quantifying the link
430 between temperature, moisture, and key functional traits across the biome. In particular, our
431 study highlights the importance of accounting for future changes in water availability, as this
432 will likely influence both the magnitude and direction of change for many traits. In addition,
433 we demonstrate that spatial trait-environment relationships are driven largely by species
434 turnover, suggesting that modeling efforts must account for rates of species immigration
435 when predicting the speed of future functional shifts. The failure of many traits (e.g. specific
436 leaf area) to match expected rates of change suggests that space-for-time substitution alone
437 may inaccurately represent near-term ecosystem change. Nevertheless, the ubiquitous

438 increase in community plant height reveals that functional change is already occurring in
439 tundra ecosystems.

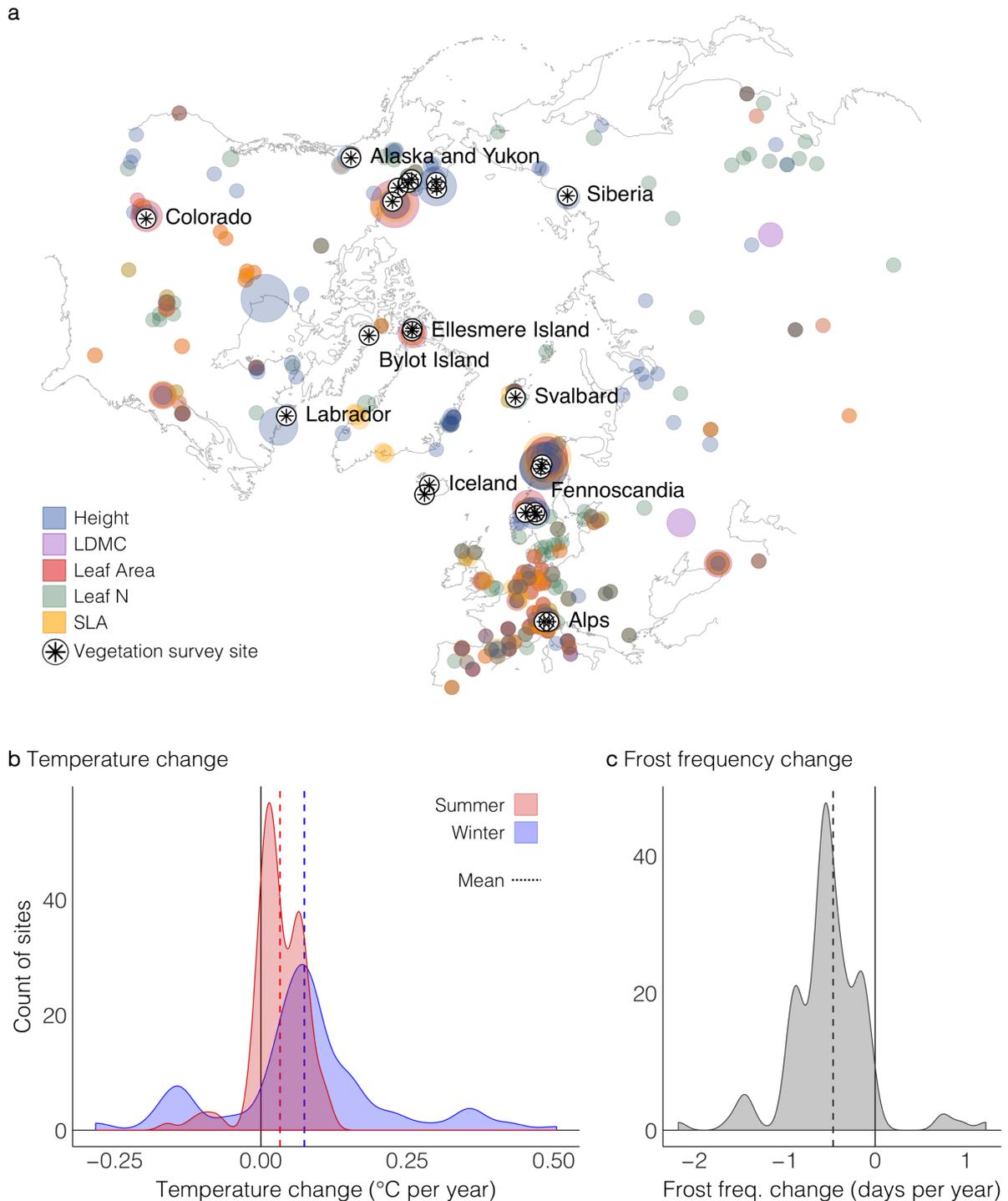
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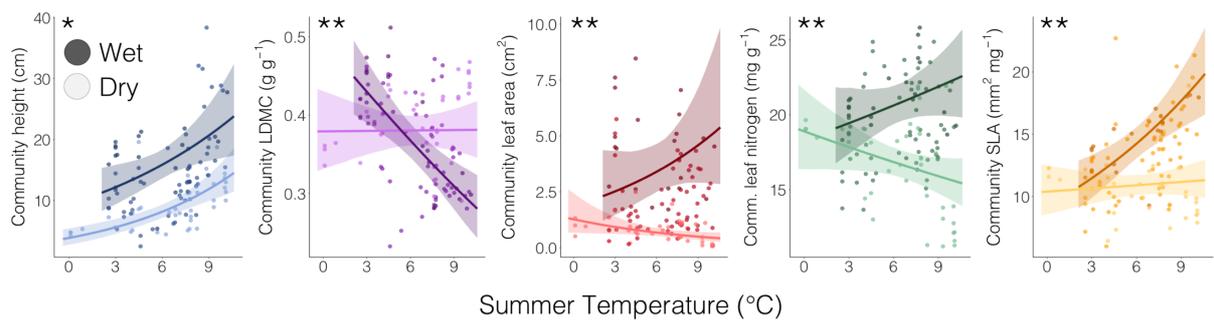
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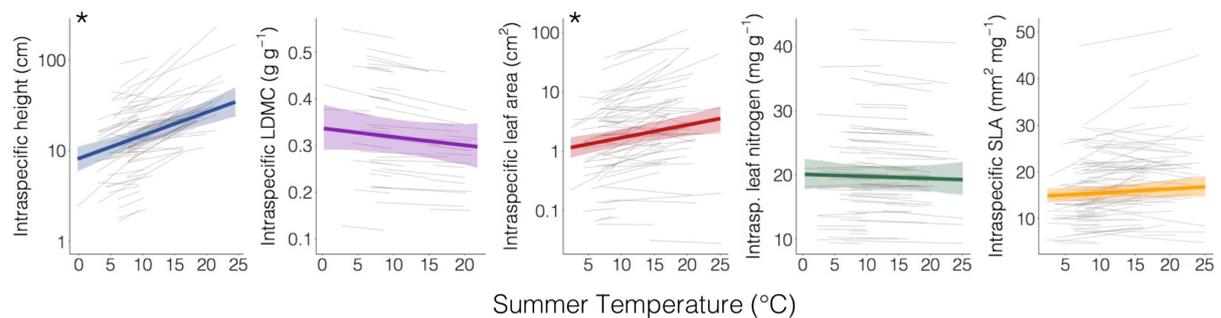
Figure 1. Geographic distribution of trait and vegetation survey data and climatic change over the study period. a. Map of all 56,048 tundra trait records and 117 vegetation survey sites. **b-c.** Climatic change across the period of monitoring at the 117 vegetation survey sites, represented as mean winter (coldest quarter) and summer (warmest quarter) temperature (**b**) and frost day frequency (**c**). The size of the colored points on the map indicates the relative quantity of trait measurements (larger circles = more measurements of that trait at a given location) and the color indicates which trait was measured. The black

545 stars indicate the vegetation survey sites used in the community trait analyses (most stars
 546 represent multiple sites). Trait data were included for all species that occur in at least one
 547 tundra vegetation survey site; thus, while not all species are unique to the tundra, all do
 548 occur in the tundra. Temperature change and frost frequency change were estimated for the
 549 interval over which sampling was conducted at each site plus the preceding four years in
 550 order to best reflect the time window over which tundra plant communities respond to
 551 temperature change^{20,29}.
 552

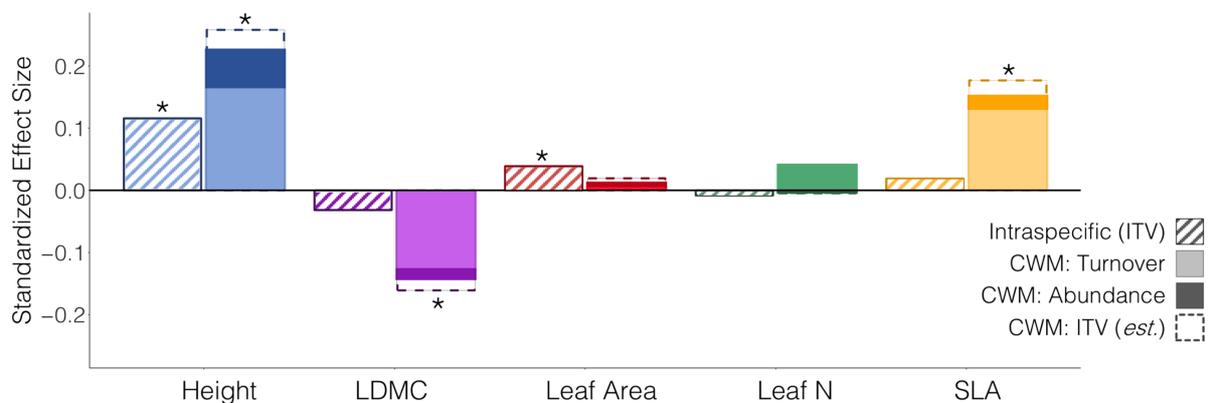
a Temperature – trait relationship: across communities (CWM)



b Temperature – trait relationship: intraspecific trait variation (ITV)

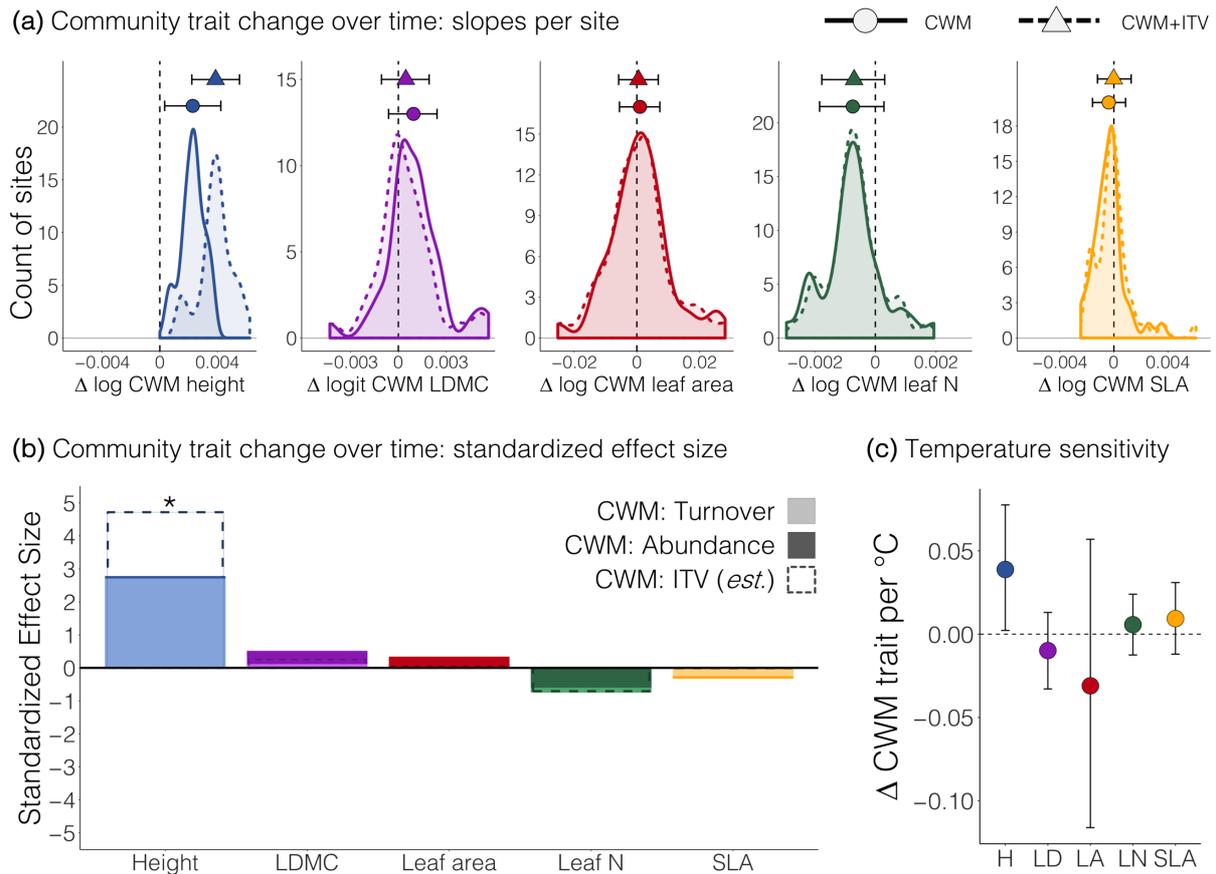


c Temperature – trait relationship: standardized effect size



553
 554 **Figure 2. Strong spatial relationships in traits across temperature and soil moisture**
 555 **gradients are primarily explained by species turnover. a, Community-level (CWM)**
 556 **variation in functional traits across space (N = 1520 plots within 117 sites within 72 regions)**

557 as related to mean summer (warmest quarter) temperature and soil moisture, and **b**,
558 intraspecific variation (ITV) across space as related to summer temperature (note the log
559 scale for height and leaf area). **c**, Standardized effect sizes were estimated for all
560 temperature-trait relationships both across communities (CWM; solid bars) and within
561 species (ITV; striped bars). Effect sizes for CWM temperature-trait relationships were further
562 partitioned into the proportion of the effect driven solely by species turnover (light bars) and
563 abundance shifts (dark bars) over space. Dashed lines indicate the estimated total
564 temperature-trait relationship over space if intraspecific trait variability is also accounted for
565 (CWM: ITV). The contribution of ITV is estimated from the spatial temperature-trait
566 relationships modeled in **(b)**. Soil moisture in **(a)** was modeled as continuous but is shown
567 predicted only at low and high values to improve visualization. Transparent ribbons in **(a)**
568 and **(b)** indicate 95% credible intervals for model mean predictions. Grey lines in **(b)**
569 represent intraspecific temperature-trait relationships for each species (height: N = 80
570 species, LDMC: N = 43, leaf area: N = 85, leaf N: N = 85, SLA: N = 108; N of observations
571 per trait shown in Table S1). In all panels, asterisks indicate that the 95% credible interval on
572 the slope of the temperature-trait relationship did not overlap zero. In panel **(a)**, two asterisks
573 indicate that the temperature x soil moisture interaction term did not overlap zero. Winter
574 temperature – trait relationships are shown in Extended Data Fig. 2. Community woodiness
575 and evergreenness are shown in Extended Data Fig. 3.
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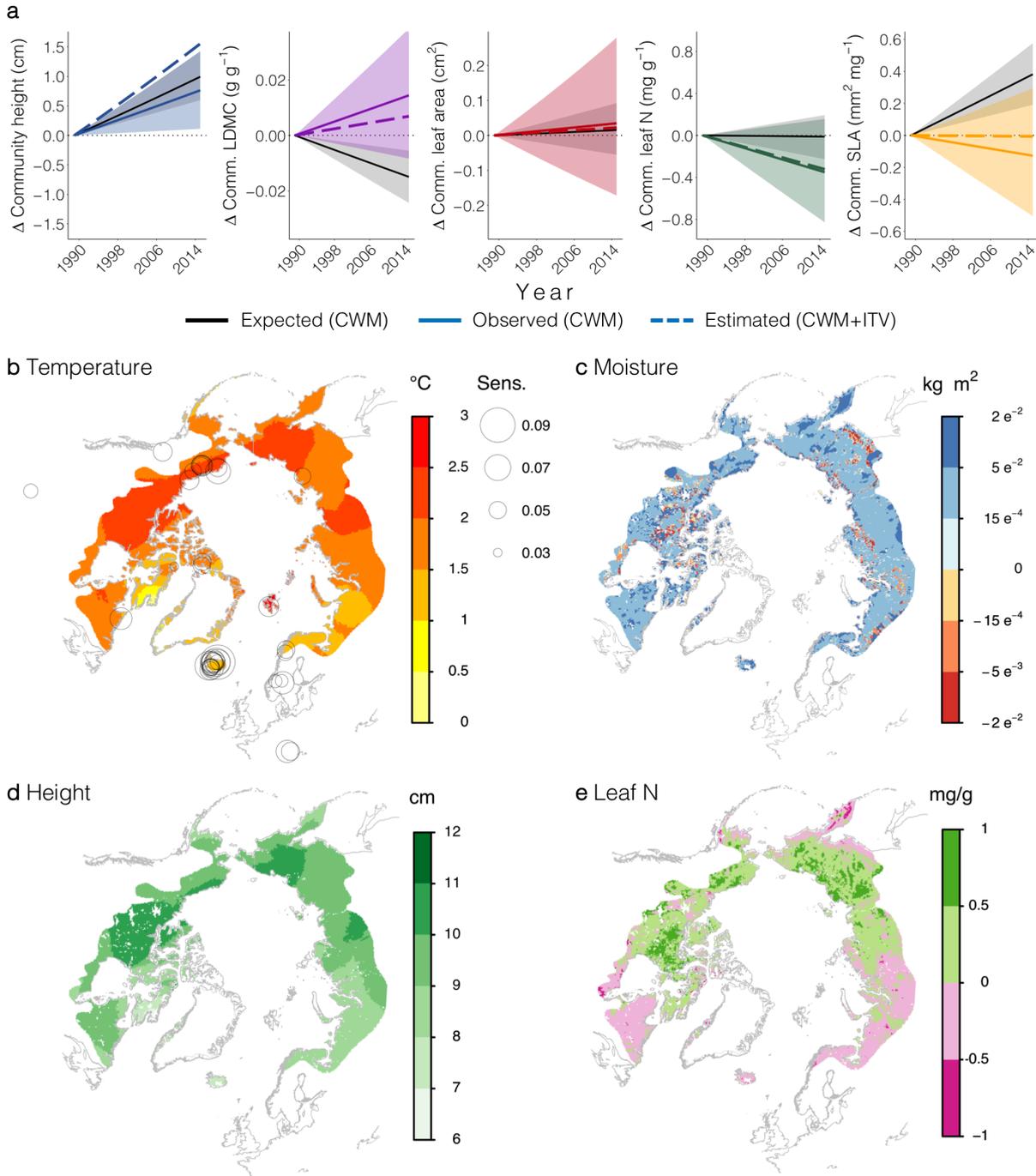
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Figure 3. A tundra-wide increase in community height over time is related to warming.

a, Observed community trait change per year (transformed units). Solid lines indicate the distribution of community-weighted mean (CWM) model slopes (trait change per site) while dashed lines indicate the community-weighted mean plus potential intraspecific trait variation modelled from spatial temperature-trait relationships (CWM+ITV). Circles (CWM), triangles (CWM+ITV) and error bars indicate the mean and 95% credible interval for the overall rate of trait change across all sites (N = 4575 plot-years within 117 sites within 38 regions). The vertical black dashed line indicates 0 (no change over time). **b**, Standardized effect sizes for CWM change over time were further partitioned into the proportion of the effect driven solely by species turnover (light bars) or shifts in abundance of resident species (dark bars) over time. Dashed lines indicate the estimated total trait change over time if predicted intraspecific trait variability is also included (CWM+ITV). Stars indicate that the 95% CI on the mean hyperparameter for CWM trait change over time did not overlap zero. **c**, Temperature sensitivity of each trait as related to summer temperature (i.e., correspondence between interannual variation in CWM trait values and interannual variation in temperature). Temperatures associated with each survey year were estimated as five-year means (temperature of the survey year and four preceding years) because this interval has been shown to be most relevant to vegetation change in tundra²⁰ and alpine²⁹ plant communities.

596 Circles represent the mean temperature sensitivity across all 117 sites, error bars are 95%
 597 credible intervals on the mean. Changes in community woodiness and evergreenness are
 598 shown in Extended Data Fig. 3.
 599



600
 601 **Figure 4. Community height increases in line with space-for-time predictions but**
 602 **other traits lag. a**, Observed community (CWM) trait change over time (colored lines)
 603 across all 117 sites vs. expected CWM change over the duration of vegetation monitoring
 604 (1989-2015) based on the spatial temperature-trait (CWM) relationship and the average rate
 605 of recent summer warming across all sites (solid black lines). Colored dashed lines indicate

606 the estimated total change over time if predicted intraspecific trait variability is also included
607 (CWM+ITV). Values on the y-axis represent the magnitude of change relative to 0 (i.e., trait
608 anomaly), with 0 representing the trait value at t_0 . **b-c**, Total recent temperature change (**b**)
609 and soil moisture change (**c**) across the Arctic tundra (1979-2016). Temperature change
610 estimates are derived from CRU gridded temperature data, soil moisture change estimates
611 are derived from downscaled ERA-Interim soil moisture data. Circles in (**b**) represent the
612 sensitivity (cm per °C) of CWM plant height to summer temperature at each site (see Fig.
613 3c). Areas of high temperature sensitivity are expected to experience the greatest increases
614 in height with warming. **d-e**, Spatial trait-temperature-moisture relationships (Fig. 2a) were
615 used to predict total changes in height (**d**) and leaf N (**e**) over the entire 1979-2016 period
616 based on concurrent changes in temperature and soil moisture. Note that (**d**) and (**e**) reflect
617 the magnitude of *expected* change between 1979 and 2016, not observed trait change. See
618 methods for details of temperature change and soil moisture change estimates. The outline
619 of Arctic areas is based on the Circumpolar Arctic Vegetation Map
620 (<http://www.geobotany.uaf.edu/cavm>).

621

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683

684 **Author contributions**

685 ADB, IHM-S and SCE conceived the study, with input from the sTundra working group (SN,
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687 GS-S, HJDT, MV, MW, and SW). ADB performed the analyses, with input from IHM-S, NR,
688 SCE, and SN. DNK made the maps of temperature, moisture, and trait change. ADB wrote
689 the manuscript, with input from IHM-S, SCE, SN, NR, and contributions from all authors.

690 ADB compiled the Tundra Trait Team database, with assistance from IHM-S, HJDT and SA-
691 B. Authorship order was determined as follows: 1) core authors, 2) sTundra participants
692 (alphabetical) and other major contributors, 3) authors contributing both trait (Tundra Trait
693 Team) and community composition (ITEX, etc.) data (alphabetical), 4) Tundra Trait Team
694 contributors (alphabetical), 5) community composition data only contributors (alphabetical),
695 and 6) TRY trait data contributors (alphabetical).

696

697 **Author Information**

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700

701 The authors declare no competing financial interests.

702

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705

706 **METHODS**

707

708 Below we describe the data, workflow (Extended Data Fig. 1b) and detailed methods used to
709 conduct all analyses.

710

711 **COMMUNITY COMPOSITION DATA**

712 Community composition data used for calculating community-weighted trait means were
713 compiled from a previous synthesis of tundra vegetation resurveys² (including many
714 International Tundra Experiment (ITEX) sites) and expanded with additional sites (e.g.,
715 Gavia Pass in the Italian Alps and three sites in Sweden) and years (e.g., 2015 survey data
716 added for Iceland sites, QHI, and Alexandra Fiord; Table S2). We included only sites for
717 which community composition data were roughly equivalent to percent cover (i.e., excluding
718 estimates approximating biomass), for a total of 117 sites (defined as plots in a single
719 contiguous vegetation type) within 38 regions (defined as a CRU⁴¹ grid cell). Plot-level
720 surveys of species composition and cover were conducted at each of these sites between
721 1989 and 2015 (see² for more details of data collection and processing). On average, there
722 were 15.2 plots per site. Repeat surveys were conducted over a minimum duration of 5 and
723 up to 21 years between 1989 and 2015 (mean duration = 13.6 years), for a total of 1,781
724 unique plots and 5,507 plot-year combinations. Plots were either permanent (i.e., staked;
725 62% of sites) or semi-permanent (38%), such that the approximate but not exact location
726 was resurveyed. The vegetation monitoring sites were located in tree-less Arctic or alpine
727 tundra and ranged in latitude from 40° (Colorado Rockies) to 80° (Ellesmere Island, Canada)
728 and were circumpolar in distribution (Fig. 1a, Table S2). Our analyses only include vascular
729 plants because there was insufficient trait data for non-vascular species. Changes in
730 bryophytes and other cryptogams are an important part of the trait and function change in
731 tundra ecosystems^{42,43}, thus the incorporation of non-vascular plants and their traits is a
732 future research priority.

733

734 *Temperature extraction for community composition observations*

735 We extracted summer (warmest quarter) and winter (coldest quarter) temperature estimates
736 for each of the vegetation survey sites from both the WorldClim⁴⁴ (for long-term averages;
737 <http://www.worldclim.org/>) and CRU⁴¹ (for temporal trends; <http://www.cru.uea.ac.uk/>)
738 gridded climate datasets. WorldClim temperatures were further corrected for elevation
739 (based on the difference between the recorded elevation of a site and the mean elevation of
740 the WorldClim grid cell) according to a correction factor of -0.005 °C per meter increase in

741 elevation. This correction factor was calculated by extracting the mean temperature and
742 elevation (WorldClim 30s resolution maps) of all cells falling in a 2.5 km radius buffer around
743 our sites and fitting a linear mixed model (with site as a random effect) to estimate the rate of
744 temperature change with elevation.

745

746 The average long-term (1960-present) temperature trend across all sites was 0.26 (range -
747 0.06 to 0.49) and 0.43 (range -0.15 to 1.32) °C/decade for summer and winter temperature,
748 respectively.

749

750 *Soil moisture for community composition observations*

751 A categorical measure of soil moisture at each site was provided by every site PI according
752 to the methods described in Elmendorf et al. 2012 and Myers-Smith et al. 2015 ^(2,45). Soil
753 moisture was considered to be 1) dry when during the warmest month of the year the top 2
754 cm of the soil was dry to the touch, 2) moist when soils were moist year round, but standing
755 water was not present, and 3) wet when standing water was present during the warmest
756 month of the year.

757

758 *Soil moisture change for maps of environmental and trait change (Fig. 4b-e)*

759 We used high-resolution soil moisture observations from ESA CCI SM v04.2. To calculate
760 the mean distribution of soil moisture, we averaged the observations from 1979-2016.
761 Because the ESA CCI SM temporal coverage is poor for our sites, temporal data were
762 instead taken from ERA-Interim (Volumetric soil water layer 1) for the same time period. We
763 downscaled the ERA-Interim data to the 0.05° resolution of ESA CCI SM v04.2 using
764 climatologically aided interpolation (delta change method)⁴⁶. The change in soil water
765 content was then calculated separately for each grid cell using linear regression with month
766 as a predictor variable. To classify the soil moisture data into three categories (wet, mesic,
767 dry) to match the community composition dataset, we used a quantile approach on the mean
768 soil moisture within the extent of the Arctic. We assigned the lowest quantile to dry and the
769 highest to wet conditions. For the trends in soil moisture between 1979-2016 we calculated
770 the percentage in change in relation to the mean first, and then calculated the change based
771 on the categorical data (e.g. 5% change from category 1 (dry) to category 2 (mesic)).

772

773 *Changes in water availability for analysis*

774 Although the strong effect of soil moisture on spatial temperature-trait relationships suggests
775 that change in water availability over time will play an important role in mediating trait

776 change, we did not use the CRU estimates of precipitation change over time because of
777 issues with precipitation records at high latitudes and the inability of gridded datasets to
778 capture localized precipitation patterns (e.g., ^{47,48}). The CRU precipitation trends at our sites
779 included many data gaps filled by long-term mean values, especially at the high-latitude
780 sites⁴⁵. As a purely exploratory analysis, we used the downscaled ERA-Interim data
781 described above to investigate whether trait change is related to summer soil moisture
782 change (June, July, and August; Extended Data Fig. 5b). However, we caution that soil
783 moisture change in our tundra sites is primarily controlled by snow melt timing, soil drainage,
784 the permafrost table and local hydrology²⁵, and as such precipitation records and coarse-
785 grain remotely sensed soil moisture change data are unlikely to accurately represent local
786 changes in soil water availability. For this same reason we did not use the ERA-Interim data
787 to explore spatial relationships between temperature, moisture and community traits, as the
788 categorical soil moisture data (described above) were collected specifically within each
789 community composition site and are therefore a more accurate representation of long-term
790 mean soil moisture conditions in that specific location.

791

792 **TRAIT DATA**

793 Continuous trait data (adult plant height, leaf area (average one-sided area of a single leaf),
794 specific leaf area (leaf area per unit of leaf dry mass; SLA), leaf nitrogen content (per unit of
795 leaf dry mass; leaf N), and leaf dry matter content (leaf dry mass per unit of leaf fresh mass;
796 LDMC); Fig. 1a & Extended Data Fig. 1a, Table S1) were extracted from the TRY⁴⁹ 3.0
797 database (available at www.try-db.org). We also ran a field & data campaign in 2014-15 to
798 collect additional in-situ tundra trait data (the “Tundra Trait Team” (TTT) dataset⁵⁰) to
799 supplement existing TRY records. All species names from the vegetation monitoring sites,
800 TRY and TTT were matched to accepted names in The Plant List using the R package
801 Taxonstand⁵¹ (v. 1.8) before merging the datasets. Community-level traits (woodiness and
802 evergreenness) were derived from functional group classifications for each species².
803 Woodiness is estimated as the proportion (abundance) of woody species in the plot, while
804 evergreenness is the proportion of evergreen woody species abundance out of all woody
805 species (evergreen plus deciduous) in a plot. Because some sites did not contain any woody
806 species (and thus the proportion of evergreen woody species could not be calculated), this
807 trait is estimated only for 98 of the 117 total sites.

808

809 *Data cleaning - TRY*

810 TRY trait data were subjected to a multi-step cleaning process. First, all values that did not
811 represent individual measurements or approximate species means were excluded. When a
812 dataset within TRY contained only coarse plant height estimates (e.g., estimated to the
813 nearest foot), we removed these values unless no other estimate of height for that species
814 was available. We then identified overlapping datasets within TRY and removed duplicate
815 observations whenever possible. The following datasets were identified as having partially
816 overlapping observations: GLOPNET – Global Plant Trait Network Database, The LEDA
817 Traitbase, Abisko & Sheffield Database, Tundra Plant Traits Database, and KEW Seed
818 Information Database (SID).

819

820 We then removed duplicates within each TRY dataset (e.g., if a value is listed once as
821 “mean” and again as “best estimate”) by first calculating the ratio of duplicated values within
822 each dataset, and then removing duplicates from datasets with more than 30% duplicated
823 values. This cutoff was determined by manual evaluation of datasets at a range of
824 thresholds. Datasets with fewer than 30% duplicated values were not cleaned in this way as
825 any internally duplicate values were assumed to be true duplicates (i.e., two different
826 individuals were measured and happened to have the same measurement value).

827

828 We also removed all species mean observations from the “Niwot Alpine Plant Traits”
829 database and replaced it with the original individual observations as provided by M.J.
830 Spasojevic.

831

832 *Data cleaning – TRY & TTT combined*

833 Both datasets were checked for improbable values, with the goal of excluding likely errors or
834 measurements with incorrect units but without excluding true extreme values. We followed a
835 series of data-cleaning steps, in each case identifying whether a given observation (x) was
836 likely to be erroneous (i.e. “error risk”) by calculating the difference between x and the mean
837 (excluding x) of the taxon and then dividing by the standard deviation of the taxon.

838

839 We employed a hierarchical data cleaning method, because the standard deviation of a trait
840 value is related to the mean and sample size. First, we checked individual records against
841 the entire distribution of observations of that trait and removed any records with an error risk
842 greater than 8 (i.e., a value more than 8 standard deviations away from the trait mean). For
843 species that occurred in four or more unique datasets with TRY or TTT (i.e., different data
844 contributors), we estimated a species mean per dataset and removed observations for which

845 the species mean error risk was greater than 3 (i.e., the species mean of that dataset was
846 more than 3 SD's away from the species mean across all datasets). For species that
847 occurred in fewer than 4 unique datasets, we estimated a genus mean per dataset and
848 removed observations in datasets for which the error risk based on the genus mean was
849 greater than 3.5. Finally, we compared individual records directly to the distribution of values
850 for that species. For species with more than 4 records, we excluded values above an error
851 risk Y , where Y was dependent on the number of records of that species and ranged from an
852 error risk of 2.25 for species with fewer than 10 records to an error risk of 4 for species with
853 more than 30 records. For species with four or fewer records, we manually checked trait
854 values and excluded only those that were obviously erroneous, based on our expert
855 knowledge of these species.

856

857 This procedure was performed on the complete tundra trait database – including species
858 and traits not presented here. In total 2,056 observations (1.6%) were removed. In all cases,
859 we visually checked the excluded values against the distribution of all observations for each
860 species to ensure that our trait cleaning protocol was reasonable.

861

862 Trait data were distributed across latitudes within the tundra biome (Extended Data Fig. 1a).
863 All trait observations with latitude/longitude information were mapped and checked for
864 implausible values (e.g., falling in the ocean). These values were corrected from the original
865 publications or by contacting the data contributor whenever possible.

866

867 *Final trait database*

868 After cleaning out duplicates and outliers as described above, we retained 56,048 unique
869 trait observations (of which 18,613 are contained in TRY and 37,435 were newly contributed
870 by the Tundra Trait Team⁵⁰ field campaign) across the five traits of interest. Of the 447
871 identified species in the ITEX dataset, 386 (86%) had trait data available from TRY or TTT
872 for at least one trait (range 52-100% per site). Those species without trait data generally
873 represent rare or uncommon species unique to each site; on average, trait data were
874 available for 97% of total plant cover across all sites (range 39-100% per site; Table S1).

875

876 *Temperature extraction for trait observations*

877 WorldClim climate variables were extracted for all trait observations with latitude/longitude
878 values recorded (53,123 records in total, of which 12,380 were from TRY and 33,621 from
879 TTT). Because most observations did not include information about elevation, temperature

880 estimates for individual trait observations were not corrected for elevation and thus represent
881 the temperature at the mean elevation of the WorldClim grid cell.

882

883 **ANALYSES**

884

885 ***Terminology***

886 Here we provide a brief description of acronyms and symbols used in the methods and
887 model equations.

888

889 **ITV** – intraspecific trait variation: variation in trait values within the same species

890 **CWM** – community weighted trait mean: the mean trait value of all species in a plot,
891 weighted by their abundance in the plot

892 **CWM + ITV** – community weighted trait mean, adjusted with the estimated contribution of
893 intraspecific trait variation based on the intraspecific temperature-trait relationship of each
894 species

895 α – alpha, used to designate lower-level model intercepts

896 β – beta, used to designate lower-level model slopes

897 γ – gamma, used to designate the model parameters of interest (e.g. the temperature-trait
898 relationship)

899

900 ***Models***

901 All analyses were conducted in JAGS and/or Stan through R (v. 3.3.3) using packages
902 *rjags*⁵² (v. 4.6) and *rstan*⁵³ (v. 2.14.1). In all cases, models were run until convergence was
903 reached, as assessed both visually in traceplots and by ensuring that all Gelman-Rubin
904 convergence diagnostic (Rhat⁵⁴) values were less than 1.1.

905

906 A major limitation of the species mean trait approach often employed in analyses of
907 environment-trait relationships has been the failure to account for intraspecific trait variation
908 (ITV) that could be as or more important than interspecific variation^{55,56}. We addressed this
909 issue by employing a hierarchical analysis that incorporates both within-species and
910 community-level trait variation across climate gradients to estimate trait change over space
911 and time at the biome scale. We used a Bayesian approach that accounts for the
912 hierarchical spatial (plots within sites within regions) and taxonomic (intra- and inter-specific
913 variation) structure of the data as well as uncertainty in estimated parameters introduced

914 through absences in trait records for some species, and taxa that were identified to genus or
915 functional group (rather than species) in vegetation surveys.

916

917 *Intraspecific trait variation*

918 We subsetted the trait dataset to just those species for which traits had been measured in at
919 least four unique locations spanning a temperature range of at least 10% of the entire
920 temperature range (2.6°C and 5.0 °C for summer and winter temperature, respectively), and
921 for which the latitude and longitude of the measured individual or group of individuals was
922 recorded. The number of species meeting these criteria varied by trait and temperature
923 variable: 108-109 for SLA, 80-86 for plant height, 74-72 for leaf nitrogen, 85-76 for leaf area,
924 and 43-52 for LDMC, for summer and winter temperature, respectively. These species
925 counts correspond to 53-73% of community abundance. The relationship between each trait
926 and temperature (Fig. 2b) was estimated from a Bayesian hierarchical model, with
927 temperature as the predictor variable and species (s) and dataset-by-location (d) modeled
928 as random effects:

929

$$\begin{aligned} 930 \quad & \text{traitobs}_i \sim \text{logNormal}(\alpha_{s,d}, \sigma_s) \\ 931 \quad & \alpha_{s,d} \sim \text{Normal}(\alpha_s + \beta_s \cdot \text{temperature}_d, \sigma_1) \\ 932 \quad & \beta_s \sim \text{Normal}(B, \sigma_2) \\ 933 \quad & \alpha_s \sim \text{Normal}(A, \sigma_3) \end{aligned}$$

934

935 where i represents each trait observation and A and B are the intercept and slope
936 hyperparameters, respectively. Because LDMC represents a ratio and is thus bound
937 between 0 and 1, we used a beta error distribution for this trait. Temperature values were
938 mean-centered within each species. We used non-informative priors for all coefficients.

939

940 We further explored whether the strength of intraspecific temperature-height relationships
941 varied by functional group. We find that all functional groups (including dwarf shrubs, which
942 are genetically limited in their ability to grow upright) show similar temperature-trait
943 relationships (Extended Data Fig. 9a). These results suggest that the intraspecific
944 temperature-trait relationships may not only be a response of individual growth changes, and
945 are not restricted to particular functional groups with greater capacity for vertical growth
946 (e.g., tall shrubs and graminoids versus dwarf shrubs and certain forb species).

947

948 *Calculation of community weighted mean (CWM) values*

949 We calculated the community-weighted trait mean (i.e., the mean trait value of all species in
950 a plot, weighted by the abundance of each species), for all plots within a site. We employed
951 a Bayesian approach to calculate trait means for every species (s) using an intercept-only
952 model (such that the intercept per species (α_s) is equivalent to the mean trait value of the
953 species) and variation per species (σ_s) with a lognormal error distribution.

954

$$955 \quad \text{traitobs}_i \sim \text{logNormal}(\alpha_s, \sigma_s)$$

956

957 Because LDMC represents a ratio and is thus bound between 0 and 1, we used a beta error
958 distribution instead of lognormal for this trait. When a species was measured multiple times
959 in several different locations, we additionally included a random effect of dataset-by-location
960 (d) to reduce the influence of a single dataset with many observations at one site when
961 calculating the mean per species:

962

$$963 \quad \text{traitobs}_i \sim \text{logNormal}(\alpha_{s,d}, \sigma_d)$$

964

$$\alpha_{s,d} \sim \text{Normal}(\alpha_s, \sigma_s)$$

965

966 We used non-informative priors for all species intercept parameters for which there were
967 four or more unique trait observations, so that the species-level intercept and variance
968 around the intercept per species were estimated from the data. In order to avoid removing
969 species with little or no trait data from the analyses, we additionally employed a “gap-filling”
970 approach that allowed us to estimate a species’ trait mean while accounting for uncertainty
971 in the estimation of this mean. For species with fewer than four but more than one trait
972 observation, we used a normal prior with the mean equal to the mean of the observation(s)
973 and variance estimated based on the mean mean-variance ratio across all species. In other
974 words, we calculated the ratio of mean trait values to the standard deviation of those trait
975 values per species for all species with greater than four observations, then took the mean of
976 these ratios across all species and multiplied this number by the mean of species X (where
977 X is a species with 1-4 observations) to get the prior for σ . For species with no observations
978 (see Table S1), we used a prior mean equal to the mean of all species in the same genus
979 and a prior variance estimated based on the mean mean-variance ratio of all species in that
980 genus or 1.5 times the mean, whichever was lower. If there were no other species in the
981 same genus, then we used a prior mean equal to the mean of all other species in the family
982 and a prior variance estimated based on the mean mean-variance ratio of all species in the
983 family or 1.5 times the mean, whichever was lower.

984

985 *Calculation of CWM values: incorporating uncertainty in species traits*

986 In order to include uncertainty about species trait means (due to intraspecific trait variation,
987 missing trait information for some species, or when taxa were identified to genus or
988 functional group rather than species) in subsequent analyses, we estimated community-level
989 trait values per plot by sampling from the posterior distribution (mean +/- SD) of each
990 species intercept estimate and multiplying this distribution by the relative abundance of each
991 species in the plot to get a community-weighted mean (CWM) distribution per plot (p):

992

$$993 \quad \text{Normal}(CWM_{mean_p}, CWM_{sd_p})$$

994

995 This approach generates a distribution of CWM values per plot that propagates the
996 uncertainty in each species' trait mean estimate into the plot-level (CWM) estimate. By using
997 a Bayesian approach, we are able to carry through uncertainty in trait mean estimates to all
998 subsequent analyses and reduce the potential for biased or deceptively precise estimates
999 due to missing trait observations.

1000

1001 *Calculation of CWM values: partitioning turnover and estimating contribution of ITV*

1002 To assess the degree to which the spatial temperature-trait relationships are caused by
1003 species turnover versus shifts in abundance among sites, we repeated each analysis using
1004 the non-weighted community mean (all species weighted equally) of each plot. Temperature-
1005 trait relationships estimated with non-weighted community means are due solely to species
1006 turnover across sites. Finally, we assessed the potential contribution of intraspecific trait
1007 variation (ITV) to the community-level temperature-trait relationship by using the modeled
1008 intraspecific temperature-trait relationship (described above) to predict trait "anomaly" values
1009 for each species at each site based on the temperature of that site in a given year relative to
1010 its long-term average.

1011

1012 An intraspecific temperature-trait relationship could not be estimated for every species due
1013 to an insufficient number of observations for some species. Therefore, we used the mean
1014 intraspecific temperature-trait slope across all species to predict trait anomalies for species
1015 without intraspecific temperature-trait relationships. These site- and year-specific species
1016 trait estimates were then used to calculate "ITV-adjusted" community-weighted means
1017 (CWM+ITV) for each plot in each year measured, and modeled as for CWM alone. As these
1018 "adjusted" values are estimated *relative to each species' mean value*, the spatial

1019 temperature-trait relationship that includes this adjustment does not remove any bias in the
1020 underlying species mean data. For example, if southern tundra species tend to be measured
1021 at the southern edge of their range while northern tundra species tend to be measured at the
1022 northern edge of their range, the overall spatial temperature-trait relationship could appear
1023 stronger than it really is for species with temperature-related intraspecific variation. This is a
1024 limitation of any species-mean approach.

1025

1026 Estimates of temporal CWM+ITV temperature-trait relationships are not prone to this same
1027 limitation as they represent relative change, but should also be interpreted with caution as
1028 intraspecific temperature-trait relationships may be due to genetic differences among
1029 populations rather than plasticity, thus suggesting that trait change would not occur
1030 immediately with warming. We therefore caution that the CWM+ITV analyses presented
1031 here represent estimates of the potential contribution of ITV to overall CWM temperature-
1032 trait relationships over space and time, but should not be interpreted as measured
1033 responses.

1034

1035 In sum, we incorporate intraspecific variation into our analyses in three ways. First, by using
1036 the posterior distribution (rather than a single mean value) of species trait mean estimates in
1037 our calculations of CWM values per plot, so that information about the amount of variation
1038 within species is incorporated into all the analyses in our study. Second, by explicitly
1039 estimating intraspecific temperature-trait relationships based on the spatial variation in
1040 individual trait observations. And finally, by using these modeled temperature-trait
1041 relationships to inform estimates of the potential contribution of ITV to overall (CWM+ITV)
1042 temperature-trait relationships over space and time.

1043

1044 *Spatial community trait models (Fig. 2 a&c)*

1045 To investigate spatial relationships in plant traits with summer and winter temperature and
1046 soil moisture we used a Bayesian hierarchical modeling approach in which soil moisture and
1047 soil moisture x temperature vary at the site level while temperature varies by WorldClim
1048 region (unique WorldClim grid x elevation groups). In total, there were 117 sites (s) nested
1049 within 73 WorldClim regions (r). We used only the first year of survey data at each site to
1050 estimate spatial relationships in community traits.

1051

1052
$$CWMmean_p \sim Normal(\alpha_s + \alpha_r, CWMsd_p)$$

1053
$$\alpha_s \sim Normal(\gamma_1 \cdot moisture_s + \gamma_2 \cdot moisture_s \cdot temperature_s, \sigma_1)$$

$$\alpha_r \sim \text{Normal}(\gamma_0 + \gamma_3 \cdot \text{temperature}_r, \sigma_2)$$

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Where CWM_{mean_p} is the mean of the posterior distribution of the community-weighted mean (CWM) estimate per plot (p) and CWM_{sd_p} is the standard deviation of the posterior distribution of the CWM estimate per plot, as described in the “*Calculation of CWM values: incorporating uncertainty in species traits*” section. See supplementary information for complete STAN code.

As woodiness and evergreenness represent proportional data (bounded between 0 and 1, inclusive), we used a beta-Bernoulli mixture model of the same structure as above to estimate trait-temperature-moisture relationships for these traits (Extended Data Fig. 3 a&b). The discrete and continuous components of the data were modeled separately, with mixing occurring at the site- and region-level estimates (α_s and α_r).

Because Arctic and alpine tundra sites might differ in their trait-environment relationships due to environmental differences in e.g. soil drainage, we also performed a version of the spatial community trait analyses in which the elevation of each site is visually indicated (not modeled; Extended Data Fig. 9b). We did not attempt to separately analyze trait-environment relationships for Arctic and alpine sites due to the ambiguity in defining this cut-off (i.e., many sites can be categorized as both Arctic and alpine, particularly in Scandinavia and Iceland) and because of the small number of southern, high-alpine sites (European Alps and Colorado Rockies).

For estimation of the overall temperature-trait relationship, we used a model structure similar to that above but with only temperature as a predictor (i.e., without soil moisture). This model was used for both community-weighted mean (CWM) and non-weighted mean estimates in order to determine the degree to which temperature-trait relationships over space are due to species turnover alone (non-weighted mean) and for CWM+ITV plot-level estimates to determine the likely additional contribution of intraspecific trait variation to the overall temperature-trait relationship, as described above.

Standardized effect sizes for CWM temperature-trait relationships (Fig. 2c) were obtained by dividing the slope of the temperature-trait relationship by the standard deviation of the CWM model residuals. Effect sizes for ITV, turnover only, and CWM: ITV were estimated relative

1088 to the CWM value for that same trait based on the slope values of each temperature-trait
1089 relationship.

1090

1091 *Trait change over time (Fig. 3 a&b)*

1092 Change over time was modeled at the CRU grid cell (region) level (r), with site (s) as a
1093 random effect when there was more than one site per region (to account for non-
1094 independence of sites within a region) and plot (p) as a random effect for those sites with
1095 permanent (repeating) plots (to account for repeated measures on the same plot over time).
1096 We did not account for temporal autocorrelation as most plots were not measured annually
1097 (average survey interval = 7.2 years) and did not have more than 3 observations over the
1098 study period (average number of survey years per plot = 3.1). Year (y) was centered within
1099 each region.

1100

$$1101 \quad CWM_{mean_{p,y}} \sim Normal(\alpha_p + \alpha_s + \alpha_{r,y}, CWM_{sd_{p,y}})$$

1102

1103 Where CWM_{mean_p} is the mean of the posterior distribution of the community-weighted
1104 mean (CWM) estimate per plot (p) and CWM_{sd_p} is the standard deviation of the posterior
1105 distribution of the CWM estimate per plot, as described in the “*Calculation of CWM values:
1106 incorporating uncertainty in species traits*” section. For non-permanent plots and for sites
1107 that were the only site within a region, α_p or α_s , respectively, were set to 0. Region-level
1108 slopes were then used to fit an average trend of community trait values over time:

1109

$$1110 \quad \alpha_{r,y} \sim Normal(\alpha_r + \beta_r \cdot year_{y,r}, \sigma_0)$$

1111

$$\beta_r \sim Normal(B, \sigma_1)$$

1112

$$\alpha_r \sim Normal(A, \sigma_2)$$

1113

1114 where A and B are the intercept and slope hyperparameters, respectively. See
1115 supplementary information for complete STAN code. This model was used for both
1116 community-weighted mean (CWM) and non-weighted mean plot-level estimates in order to
1117 determine the degree to which temporal trait change is due to species turnover alone (non-
1118 weighted mean) and for CWM+ITV plot-level estimates to determine the potential additional
1119 contribution of intraspecific trait variation to overall trait change.

1120

1121 Standardized effect sizes for CWM change over time (Fig. 3b) were obtained by dividing the
1122 slope of overall trait change over time (mean hyperparameter across 117 sites) by the

1123 standard deviation of the slope estimates per site. Effect sizes for turnover-only and
1124 CWM+ITV change are estimated relative to the CWM change value for that trait based on
1125 the slope values of each.

1126

1127 To estimate change in the proportion of woody and evergreen species over time (CWM
1128 change only; Extended Data Fig. 3 c&d) we used a beta-Bernoulli mixture model of the
1129 same form described above. The discrete and continuous components of the data were
1130 modeled separately, with mixing occurring at the region x year effect ($\alpha_{r,y}$). We additionally
1131 assessed whether the rate of observed trait change over time was related to the duration of
1132 vegetation monitoring at each site. There was no influence of monitoring duration for any
1133 trait (not shown).

1134

1135 *Temperature sensitivity (Fig. 3c)*

1136 Temperature sensitivity was modeled as the variation in CWM trait values with variation in
1137 the five-year mean temperature (i.e., the mean temperature of the survey year and the four
1138 preceding years). A four-year lag was chosen because this interval has been shown to best
1139 explain vegetation change in tundra²⁰ and alpine²⁹ plant communities. The model specifics
1140 are exactly as shown above for “Trait change over time”, but with temperature in the place of
1141 year. Temperatures were centered within each region.

1142

1143 *Observed vs. expected trait change (Fig. 4a)*

1144 We first calculated the mean rate of temperature change across the 38 regions in our study,
1145 and then estimated the *expected* degree of change in each trait over the same period based
1146 on this temperature change and the spatial relationship between temperature and CWM trait
1147 values (described in the “*Spatial community trait models*” section). We then compared this
1148 *expected* trait change to actual trait change over time (described in the “*Trait change over*
1149 *time*” section). To create Fig. 4a we used the overall predicted mean value of each trait in
1150 the first year of survey (1989) as an intercept, and then used the expected and observed
1151 rates of trait change (+/- uncertainty) to predict community trait values in each year
1152 thereafter. We subtracted the intercept from all predicted values in order to show trait
1153 change as an anomaly (difference from 0). The difference between the expected (black) and
1154 observed (colored) lines in Fig. 4a represents a deviation from expected. To calculate total
1155 trait change including the estimated contribution of intraspecific change (colored dashed
1156 lines), we followed the same procedure as described for “observed” trait change but where
1157 this observed change was based on plot-level CWM+ITV estimates that varied by year

1158 based on the temperature in that year and the temperature-trait relationship per species
1159 (described in the “*Calculation of CWM values: partitioning turnover and estimating*
1160 *contribution of ITV*” section).

1161

1162 *Trait change vs. temperature change and soil moisture (Extended Data Fig. 5)*

1163 To determine whether the rate of trait change can be explained by the rate of temperature
1164 change at a site, the (static) level of soil moisture of a site, or their interaction, we modeled
1165 the rate of trait change as described above (“Trait change over time”) and compared it to the
1166 rate of temperature change over the same time interval (with a lag of four years) and soil
1167 moisture:

1168

$$1169 \quad \beta_r \sim \text{Normal}(\gamma_0 + \gamma_1 \cdot \text{temp}_r + \gamma_2 \cdot \text{moisture}_r + \gamma_3 \cdot \text{temp}_r \cdot \text{moisture}_r, \sigma)$$

1170

1171 where β_r is the rate of trait change per region (Extended Data Fig. 5a). When sites within a
1172 region were measured over different intervals or contained different soil moisture estimates
1173 they were modeled separately in order to match with temperature change estimates over the
1174 same interval and soil moisture estimates, which vary at the site level.

1175

1176 We also conducted this analysis using estimates of soil moisture change (with a lag of four
1177 years) from downscaled ERA-Interim (volumetric soil water layer 1). This model took the
1178 same form as above, but with moisture change in place of static soil moisture estimates
1179 (Extended Data Fig. 5b). Trait change was modeled at the site (rather than region) level
1180 because estimates of soil moisture change vary at the site level. Because ERA-Interim data
1181 were not available for every site, this analysis was conducted with a total of 101 rather than
1182 117 sites. We note that the results of this analysis should be interpreted cautiously, as local
1183 changes in soil moisture may not be well represented by coarse-scale remotely sensed data,
1184 as described previously.

1185

1186 *Species gains and losses as a function of traits (Extended Data Fig. 6)*

1187 We estimated species gains and losses at the site (rather than plot) level to reduce the effect
1188 of random fluctuations in species presences/absences due to observer error. Thus, sites
1189 with repeating and non-repeating plots were treated the same. A “gain” was defined as a
1190 species that did not occur in a site in the first survey year but did in the last survey year,
1191 while a “loss” was the reverse. We then modeled the probability of gain or loss separately as
1192 a function of the mean trait value of each species. For example, for “gains,” all newly

1193 observed species received a response type of 1 while all other species in the site received a
1194 response type of 0:

1195

$$1196 \quad \text{response}_i \sim \text{Bernoulli}(\alpha_s + \alpha_r + \beta_r \cdot \text{trait}_i)$$

$$1197 \quad \alpha_r \sim \text{Normal}(A, \sigma_1)$$

$$1198 \quad \beta_r \sim \text{Normal}(B, \sigma_2)$$

$$1199 \quad \alpha_s \sim \text{Normal}(0, \sigma_r)$$

1200

1201 We included a random effect for site (s) only when there were multiple sites within the same
1202 region (r), otherwise α_s was set to 0. We considered species' responses to be related to a
1203 given trait when the 95% credible interval on the slope hyperparameter (B) did not overlap
1204 zero.

1205

1206 *Trait projections with warming (Extended Data Fig. 7)*

1207 We projected trait change for the minimum (RCP2.6) and maximum (RCP8.5) IPCC carbon
1208 emission scenarios from the NIMR HadGEM2-AO Global Circulation Model. We used the
1209 midpoint years of the WorldClim (1975) and HadGem2 (2090) estimates to calculate the
1210 expected rate of temperature change over this time period. We then predicted trait values for
1211 each year into the future based on the projected rate of temperature change and the spatial
1212 relationship between temperature and community trait values (described in the "*Spatial
1213 community trait models*" section).

1214

1215 These projections are not intended to predict actual expected trait change over the next
1216 century, as many other factors not accounted for here will also influence this change. In
1217 particular, future changes in functional traits will likely depend on concurrent changes in
1218 moisture availability, which are less well understood than temperature change. Recent
1219 modeling efforts predict increases in precipitation across much of the Arctic⁵⁷, but it is
1220 unknown whether increasing precipitation will also lead to an increase in soil moisture/water
1221 availability for plants, as the drying effect of warmer temperatures (e.g. due to increased
1222 evaporation and/or decreased duration of snow cover⁵⁸) may outweigh the impact of
1223 increased precipitation. Instead, these projections are an attempt to explore theoretical trait
1224 change over the long-term when using a space-for-time substitution approach.

1225

1226 *Principal component analysis (PCA; Extended Data Fig. 8)*

1227 We performed an ordination of community-weighted trait mean values per plot on all seven
1228 traits. Because community evergreenness could only be estimated for plots with at least one
1229 woody species, the total number of plots included in this analysis is reduced compared to
1230 the entire dataset (1098 plots out of 1520 in total). We used the R package *vegan*⁵⁹ (v. 2.4.6)
1231 to conduct a principal component analysis of these data. This analysis uses only trait means
1232 per plot, and therefore information about CWM uncertainty due to intraspecific trait variation
1233 and/or missing species is lost. The analysis was performed on log-transformed trait values⁴⁹.
1234 We extracted the axis coordinates of each plot from the PCA and used the spatial trait-
1235 temperature-moisture model described above (section “*Spatial community trait models*”) to
1236 determine whether plot positions along both PCA axes varied with temperature, moisture,
1237 and their interaction.

1238

1239 *Trends in species abundance (Supplementary Information, Table S10)*

1240 In order to provide more insight into the species-specific changes occurring over time in
1241 tundra ecosystems, we calculated trends in abundance for the most common (widespread
1242 and abundant) species in the community composition dataset. We estimated trends for all
1243 species that occurred in at least 5 sites at a minimum abundance of 5% cover (mean of all
1244 plots within a site) across all years. We additionally included species that occurred at low
1245 abundance (1% or more) but were widespread (at least 10 sites). This technique yielded a
1246 total of 79 species. Abundance changes were modeled as described for trait change over
1247 time, but because abundance (proportion of plot cover) is bounded between 0 and 1,
1248 inclusive, we used a beta-Bernoulli mixture model. Abundance change was then estimated
1249 per species (*sp*) across all regions (*r*):

1250

$$1251 \quad \alpha_{sp,r,y} \sim Normal(\alpha_{sp,r} + \beta_{sp,r} \cdot year_{sp,r,y}, \sigma_{sp})$$

$$1252 \quad \beta_{sp,r} \sim Normal(B_{sp}, \sigma_1)$$

$$1253 \quad \alpha_{sp,r} \sim Normal(A_{sp}, \sigma_2)$$

1254

1255 We additionally extracted region-specific slopes per species ($\beta_{sp,r}$) in order to calculate a
1256 proportion of regions in which a given species was increasing or decreasing (“Prop.
1257 Increase” and “Prop. Decrease” in Table S10). Because regional slopes are modeled as
1258 random effects, these estimates are not entirely independent (i.e., they will be pulled toward
1259 the overall species mean slope), but provide an approximate estimate of whether directional
1260 trends in abundance are consistent across a species’ range.

1261

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- 1380

1381 **DATA AVAILABILITY**

1382

1383 *Trait data*

1384 Data compiled through the Tundra Trait Team are publicly accessible⁵⁰ (data paper
1385 published in Global Ecology & Biogeography). The public TTT database includes traits not
1386 considered in this study as well as tundra species that do not occur in our vegetation survey
1387 plots, for a total of nearly 92,000 trait observations on 978 species. Additional trait data from
1388 the TRY trait database can be requested at try-db.org.

1389

1390 *Composition data*

1391 Most sites and years of the vegetation survey data included in this study are available in the
1392 Polar Data Catalogue (ID # 10786_iso). Much of the individual site-level data has
1393 additionally been made available in the BioTIME database⁹⁰ ([https://synergy.st-
1394 andrews.ac.uk/biotime/biotime-database/](https://synergy.st-andrews.ac.uk/biotime/biotime-database/)).

1395

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1403

1404 **CODE AVAILABILITY**

1405

1406 STAN code for the two main models (spatial temperature-moisture-trait relationships and
1407 community trait change over time) is provided in the Supplementary Information associated
1408 with this study (available online).

1409 **Extended Data Fig. 1. Overview of trait data and analyses.** **a**, Count of traits per latitude
1410 (rounded to the nearest degree) for all georeferenced observations in TRY and TTT that
1411 correspond to species in the vegetation survey dataset. **b**, Work flow and analyses of
1412 temperature-trait relationships. Intraspecific temperature-trait relationships over space were used to
1413 estimate the potential contribution of ITV to overall temperature-trait relationships over space and time
1414 (CWM + ITV) as trait measurements on individuals over time are not available.

1415

1416 **Extended Data Fig. 2. All temperature-trait relationships.** Slope of temperature-trait
1417 relationship over space (within-species (ITV) and across communities (CWM)) and with
1418 interannual variation in temperature (community temperature sensitivity). Spatial – ITV is the
1419 average intraspecific trait variation as related to temperature over space, Spatial – CWM is
1420 the relationship between community-weighted trait means and summer temperature, and
1421 Temporal sensitivity – CWM is the temperature sensitivity of community-weighted trait
1422 means (i.e., correspondence between interannual variation in CWM values with interannual
1423 variation in temperature). Error bars represent 95% credible intervals on the slope estimate.
1424 We used five-year mean temperatures (temperature of the survey year and four previous
1425 years) to estimate temperature sensitivity because this interval has been shown to explain
1426 vegetation change in tundra²⁰ and alpine²⁹ plant communities. All slope estimates are in
1427 transformed units (height = log cm, LDMC = logit g/g, leaf area = log cm², leaf nitrogen = log
1428 mg/g, SLA = log mm²/mg). Community (CWM) temperature-trait relationships are estimated
1429 across all 117 sites; intraspecific temperature-trait relationships are estimated as the mean
1430 of 108-109 species for SLA, 80-86 species for plant height, 74-72 species for leaf nitrogen,
1431 85-76 species for leaf area, and 43-52 species for LDMC, for summer and winter
1432 temperature, respectively (see *Methods: Analyses: Intraspecific Trait Variation* for details).

1433

1434 **Extended Data Fig. 3. Community woodiness and evergreenness over space and time.**
1435 **a-b**, Variation in community woodiness (**a**) and evergreenness (**b**) across space with
1436 summer temperature and soil moisture. Community woodiness is the abundance-weighted
1437 proportion of woody species versus all other plant species in the community. Community
1438 evergreenness is the abundance-weighted proportion of evergreen shrubs versus all shrub
1439 species (deciduous and evergreen). The evergreen model was conducted on a reduced
1440 number of sites (98 instead of 117) because some sites did not have any woody species
1441 (and it was thus not possible to calculate a proportion evergreen). Both temperature and
1442 moisture were important predictors of community woodiness and evergreenness. The 95%
1443 credible interval for a temperature * moisture interaction term overlapped zero in both

1444 models (-0.100 to 0.114 and -0.201 to 0.069 for woodiness and evergreenness,
1445 respectively). **c-d**, There was no change over time in woodiness (**c**) or evergreenness (**d**).
1446 Thin lines represent slopes per site (woodiness: n = 117 sites, evergreenness, n = 98 sites).
1447 In all panels, bold lines indicate overall model predictions and shaded ribbons designate
1448 95% credible intervals on these model predictions.

1449

1450 **Extended Data Fig. 4. Range in species mean values of each trait by summer**
1451 **temperature.** Black dashed lines represent quantile regression estimates for 1% and 99%
1452 quantiles. Species mean values are estimated from intercept-only Bayesian models using
1453 the estimation technique described in *Methods: Analyses: Calculation of community*
1454 *weighted mean (CWM) values*. Species locations are based on species in the 117
1455 vegetation survey sites. All values are back-transformed into their original units (height = cm,
1456 LDMC = g/g, leaf area = cm², leaf nitrogen = mg/g, SLA = mm²/mg).

1457

1458 **Extended Data Fig. 5. The rate of community trait change is not related to the rate of**
1459 **temperature change or soil moisture for any trait. a-b**, Rate of community-weighted
1460 mean change over time per site (N = 117 sites) as related to temperature change and long-
1461 term mean soil moisture (**a**) or soil moisture change (**b**) at a site. Points represent mean trait
1462 change values for each site, lines represent the predicted relationship between trait change,
1463 temperature change and soil moisture/soil moisture change, and transparent ribbons are the
1464 95% CI's on these predictions. Both mean soil moisture and soil moisture change were
1465 modeled as a continuous variables, but are shown as predictions for minimum and
1466 maximum values/rates of change. Trait change estimates are in transformed units (log for
1467 height, leaf area, leaf nitrogen, and SLA, and logit for LDMC). Soil moisture change was
1468 estimated from downscaled ERA Interim data and may not accurately represent local
1469 changes in moisture availability at each site.

1470

1471 **Extended Data Fig. 6. Increasing community height is driven by the immigration of**
1472 **taller species, not the loss of shorter ones.** Probability that a species newly arrived in a
1473 site ("gained") or disappeared from a site ("lost") as a function of its traits (N = 117 sites).
1474 Lines and ribbons represent overall model predictions and the 95% credible intervals on
1475 these predictions, respectively. Dark ribbons and solid lines represent species gains while
1476 pale ribbons and dashed lines represent species losses. Only for plant height was the trait-
1477 probability relationship different for gains and losses.

1478

1479 **Extended Data Fig. 7. Comparison of actual (colored lines), expected (solid black**
1480 **lines), and projected (dotted/dashed black lines) CWM trait change over time.**
1481 Expected trait change is calculated using the observed spatial temperature-trait relationship
1482 and the average rate of recent summer warming across all sites. Note that these projections
1483 assume no change in soil moisture conditions. The dotted/dashed black lines after 2015
1484 show the projected trait change for the maximum (8.5) and minimum (2.6) IPCC carbon
1485 emission scenarios, respectively, from the HadGEM2 AO Global Circulation Model given the
1486 expected temperature change associated with those scenarios. Points along the left axis of
1487 each panel show the distribution of present-day community-weighted trait means per site (N
1488 = 117 sites) to better demonstrate the magnitude of projected change. Values are in original
1489 units (height = cm, LDMC = g/g, leaf area = cm², leaf nitrogen = mg/g, SLA = mm²/mg).

1490

1491 **Extended Data Fig. 8. Community trait co-variation is structured by temperature and**
1492 **moisture. a**, Principal component analysis of plot-level community-weighted traits for seven
1493 key functional traits demonstrating how communities vary in multidimensional trait space.
1494 Trait correlations are highest between SLA and leaf nitrogen, and evergreenness and
1495 woodiness. Variation in SLA, leaf nitrogen, evergreenness and woodiness (PC1) are
1496 orthogonal to variation in height (PC2). Variation in leaf area and LDMC are explained by
1497 both PC 1 and 2. The color of the points indicates the soil moisture status of each plot at the
1498 site-level. **b-c**, Plot scores along PC axis 1, related to plant resource economy, vary with
1499 summer temperature, soil moisture, and their interaction (**b**) while plot scores along PC axis
1500 2 vary only with soil moisture (**c**). The color of the points indicates the soil moisture of each
1501 site. Because not all plots and sites had woody species (and thus proportion evergreen
1502 could not be calculated) this analysis was conducted on a subset of 1098 (out of 1520) plots
1503 in 98 (out of 117) different sites.

1504

1505 **Extended Data Figure 9. Temperature–trait relationships by growth form and site**
1506 **elevation. a**, Mean (+/- SD) intraspecific temperature-height relationships (N = 80 species)
1507 per functional group. Dwarf shrubs are defined as those that do not grow above 30 cm in
1508 height (as estimated by regional floras: Flora of North America, USDA, Royal Horticultural
1509 Society, etc.) and are generally genetically limited in their ability to grow upright. There are
1510 no differences among functional groups in the magnitude of mean intraspecific temperature-
1511 height relationships. **b**, Relationship between community-weighted trait values, summer
1512 temperature, and soil moisture across biogeographic gradients, as in Fig. 2a. Points
1513 represent mean estimates per site (N = 117 sites) and are sized by the elevation of the site

1514 (larger circles = higher elevation). Ribbons represent the overall trait-temperature-moisture
1515 relationship (95% credible intervals on predictions at minimum and maximum soil moisture)
1516 across all sites.

1517

1518 **Extended Data Table 1. Ecosystem functions influenced by each of the seven plant**
1519 **traits investigated.**