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REVIEW

The need to understand the stability of arctic vegetation during rapid climate change: An assessment of imbalance in the literature

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Abstract In early studies, northern vegetation response to global warming recognised both increases in biomass/cover and shrinking of species' distributional ranges. Subsequent field measurements focussed on vegetation cover and biomass increases ("greening"), and more recently decreases ("browning"). However, satellite observations show that more than 50% of arctic vegetation has not changed significantly despite rapid warming. While absence of change in remote sensing data does not necessarily mean no ecological change on the ground, the significant proportion of the Arctic that appears to be stable in the face of considerable climate change points to a greater need to understand Arctic ecosystem stability. In this paper, we performed an extensive review of the available literature to seek balances or imbalances between research focussing on "greening", "browning" and "stability/no change". We find that greening studies dominate the literature though two relatively small areas of the Arctic are disproportionately represented for this main change process. Critically, there are too few studies anywhere investigating stability. We highlight the need to understand the mechanisms driving Arctic ecosystem stability, and the potential longer-term consequences of remaining stable in a rapidly changing climate.

Keywords Arctic · Browning · Climate change · Greening · Heterogeneity · Stability · Vegetation

INTRODUCTION

Arctic ecological research has experienced few paradigm shifts in the past 50 years. One profound shift in research focus was from seeking to understand how Arctic (and polar) organisms survive in cold, harsh environments (e.g. Bliss et al., 1981; Chernov, 1985) to how these organisms survive in a more benign and warmer environment, concurrent with an increasing interest in global warming (Chapin et al., 1992; Callaghan et al., 1992). The way such paradigm shifts develop are difficult to predict, as is the extent to which they are taken up to become the new dominant understanding. One reason is some researchers will understandably focus on applying what has been found elsewhere to their geographical area. Arctic research can also suffer (as all areas of science) from a focus on "stories" rather than "non-stories". Indeed, although the "greening of the Arctic" (an increase in plant growth and productivity: Jia et al., 2003) is clearly the dominant vegetation "change" response to climate warming (Xu et al, 2013; Epstein et al., 2015; Phoenix and Bjerke 2016), a greater area of Arctic tundra is showing no apparent change. So, while it is right that such a substantial and important response to climate change as arctic greening receives considerable research effort, here we explore the degree to which the stability of arctic vegetation is under-represented in the literature.

Even before the start of modern research (1980s onwards) into climate change, studies using repeat photography (Sandberg 1963) at the treeline in Swedish Lapland showed an increase in shrub growth (now called "shrubification"; Myers-Smith et al. 2011). Later, Sturm et al. (2001) used a similar approach but with a much more extensive set of photographs, to demonstrate increases in shrub and tree growth in Alaska: the assumption was that

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this was caused by climate warming. Numerous papers around this period, from ground observations, satellite data and experiments provided evidence of greening, including causal links to warming (e.g. Walker et al., 2006; Bhatt et al., 2010; Myers-Smith et al., 2011; Park et al., 2016). Within these studies was also an understanding that the greening response to warming was heterogeneous (van Wijk et al., 2004; Elmendorf et al., 2012a, b) and a few studies predominantly reported no or trivial changes in plant growth, flora and vegetation structure, even over very long time scales: e.g. up to 70 years in some areas of Svalbard (Prach et al., 2010), 49 years in West Greenland (Callaghan et al, 2011) and up to 40 years on Taymyr (at Ust Tareya and Dickson) (Matveyeva and Zanokha, 2013). More recently, a "browning" of vegetation has been described that adds complexity to the greening trend (Myers-Smith et al., 2020) and arises from physical damage/mortality to vegetation e.g. by extreme events (Bokhorst et al., 2009; Bjerke et al., 2014) and reductions in productivity (Epstein et al., 2015; Myers-Smith et al., 2020). These modern concepts of browning come decades after models (Davis, 1988), and reviews (Melillo et al., 1990 in the first IPCC Assessment) reported that climate envelopes would relocate during warming faster than species ranges could shift. This, it was argued, would result in some species' southern ranges experiencing climates to which they were not adapted and subsequent reduced performance.

When considering the Arctic trends of greening, browning and stability, the most recent analysis of satellite data (1985 to 2016) shows that of 37.3% the Arctic has greened, 4.7% has browned, with 58% showing no change (Berner et al., 2020). These greening, browning and no change proportions are similar to other recent analyses, e.g. between the years 1982 and 2012, 39.4% of the Arctic's vegetation greened significantly, 4.5% browned and 51% showed no significant change (3.4% of the area had no valid NDVI data) (Xu et al, 2013). While there is good understanding of cases of greening and browning in some locations, the vastness of the Arctic and challenges in remote sensing and ground observations create uncertainty about what is causing change in any one specific region (Myers-Smith et al., 2020), though finer scale analyses are starting to improve greening attribution (e.g. Berner et al., 2020). Indeed, it is recognised that there are numerous challenges in detecting genuine ecological change using remotely sensed data, arising from issues based in sensor and vegetation index differences, physical factors (e.g. snow cover, water bodies) and scaling issues among many (Myers-Smith et al., 2020). Those challenges also apply when seeking to quantify ecosystem stability: no change in satellite-derived vegetation indices does not necessarily mean no change on the ground. None-the-less, methodological and technological improvements are addressing these issues. However, there appears to be much less research on the ecological mechanisms behind stability in Arctic ecosystems and the extent to which genuine ecosystem stability may be occurring, despite no change being prevalent in the remotely sensed data. Such stability is perhaps, surprising given the Arctic's rapid warming, even in a Holocene perspective, up to 2.4 °C mean annual temperature between 2002 and 2018 in parts of Siberia (Anisimov and Zimov, 2020) while near surface temperature anomalies for January to June 2020 reached over 7.5 °C compared to the same period in 1981–2010 (https://www.worldweatherattribution.org/siberian-heatwave-of-2020-almost-impossible-without-climate-change).

Ecological research has provided greater understanding of what controls the sensitivity of Arctic ecosystem responses (e.g. shrub climate sensitivity is greatest at northern latitudinal or elevation range limits, and spatial trait analyses suggesting that warming will lead to taller and more diverse plant communities (Cazzolla Gatti, 2016; Cazzolla Gatti et al., 2017, 2018, 2019), especially so in areas of high soil moisture (Myers-Smith et al., 2015; Bjorkman et al., 2018)). However, while understanding the factors that might control ecosystem sensitivity to change provides insight into why some areas are more responsive than others, are we missing asking the more direct question of what mechanisms drive Arctic ecosystem stability in the face of some of the greatest warming on the planet?

We note here that it has been recently highlighted that there is considerable disagreement on the concept of stability among ecologists; a problem arising from multiple definitions and synonyms, and two schools of thought based on equilibrium and non-equilibrium properties of stability (Meerbeek et al., 2021). Because our literature search covers disciplines across ecology and remote sensing, and the definition of stability in those are often not stated, we deliberately do not seek to adhere to any one definition of stability (see also Methods). Ecologically, we agree with the definition of Meerbeek et al. (2021) that characteristics of ecological stability arise from resistance (ability to withstand change), resilience (return after change), recovery (capacity to fully return), latitude (the extent of change possible before recover cannot occur) and tolerance (the ability of a system to tolerate disturbance). We also recognise that ecosystems could have compositional change that allow maintenance (stability) of structure and function. Actually, we suggest that there is much need to investigate these attributes in apparently stable Arctic ecosystems, but we do not use them to delineate our literature search here (see Methods) to avoid excluding studies that may demonstrate ecosystem stability.

In this paper, we explore the balance of research on greening, browning and stability of arctic vegetation during the past 34 years, and we compare how well these perspectives are represented compared to the areas they represent using analysis of the literature. We learn from the literature what are the main drivers for stability but due to limited focus on the causes and consequences of stability in the literature, we suggest additional basic arctic plant characteristics that might explain the dominant response of stability. We also suggest possible consequences of neglecting a fuller understanding of Arctic ecosystem stability, a topic that we could not find in our literature search.

METHODS

We use the term “Greening” to denote increases in NDVI (Normalised Difference Vegetation Index—a proxy for plant biomass and productivity) or other vegetation indices, directly measured increases in growth, biomass and productivity, increases in plant cover and successional replacement of slow growing species by more productive species. The term “Browning” is used for decreases in biomass, productivity and cover, including satellite proxies for these, as well as plant tissue damage. We do not use the term for minor, annual deviations in NDVI from long-term trends. “Stability” is used to denote no change across all scales of time and space and not necessary to infer ecological stability (i.e. no detectable change may simply be a detection issue). The wide definitions are used here to allow the separation of ecosystem change from no change, independent of scale and method. More precise definitions for greening and browning have recently been recommended (Myers-Smith et al., 2020), but since our study is based on literature prior to this, we use broader definitions to reflect that past work. For our study, we follow the methodology used by Cooper (2014) who explored the bias in papers on winter and summer ecology studies in the Arctic. We searched the literature using the ISI Web of Science (Thomson Reuters) index on September 19, 2016, to quantify the papers dealing with greening of arctic vegetation, browning, no change and heterogeneous responses by applying a series of filters in the searches. The timespan was 1982–2016 to coincide with major publications resulting from remote sensing. The search strings and subsequent refinements for the filters are presented in Supplementary Material S1.

After the searches and refined filters, a total of 473 manuscripts was examined to ensure that the main focus of the publications was on vegetation change or stability over a multiyear time period and we added some relevant papers, for example on stability, that were missed by the web search. As we included papers with primary data and review and synthesis papers, some duplication of information might exist leading to slight overestimates of numbers of papers reflecting a particular dynamic, but the relative amounts of greening, browning and stability papers should remain little effected. The methodology of each paper is contained in the Supplementary Materials (S3, S4 to S9, S10).

We emphasise that our intention is to report on the focus of the research within the literature. So, while a paper that finds a dominance of greening in its data, for instance, will naturally have greening as the focus of the paper, it is certainly not our intention to use the balance of research as some sort of estimate of the amount of the Arctic that is greening, browning, or undergoing no change. Similarly, we point out that where a paper that focusses on a change process (greening or browning) this does not mean it makes no contribution relevant to stability (e.g. change processes papers may discuss different sensitivities to change among vegetation types), but none-the-less will still not have stability as the focus of the work or findings.

RESULTS

After the removal of duplications from the 473 papers initially filtered, we arrived at a total of 121 usable papers and 296 papers that we could not use for our analysis. Of the usable papers, there were 22 showing heterogeneous responses (supplementary material S3, S4), 9 reporting stability (supplementary material S5, S6), 14 studies focussed on browning (supplementary material S7, S8) and 77 studies focussed on greening (supplementary material S9, S10).

Studies that could not be used

Many studies could not be used for various reasons (Supplementary Material S2). Often, more than one reason applied to a particular publication but here we comment on what we assessed as the major reason.

Two of the reasons for not being able to use studies related to either the weakness of the search parameters or the search engines. These categories were “Not relevantly related to terrestrial vegetation” that included fresh water ecology, etc. and “Not related to arctic, northern alpine or northern treeline vegetation” that included studies from Australia, Tibet, etc. Together, these two categories accounted for 33.5% of the 296 studies that were not used. Some 21% of papers identified focussed on soil science and other topics rather than vegetation change, 1.4% were methodological development and 2.7% were palaeoecology studies with no appropriate data for the recent past. Publications more relevant to our study were limited by the short duration of data (7.4%) and the absence of explicit time series data on vegetation change and/or changes in species composition (16.2%). Two categories focussed on either manipulation experiments or modelling. Sadly, many of these studies (16.9% for the two categories) failed to give appropriate data (time series) for the experiment controls. In one case, the interpretation was unclear as the approach confounded natural changes with a manipulation experiment and in another there was insufficient data to make an assessment (Supplementary Material S2).

Heterogeneity

Twenty-two studies focussed on heterogeneous responses (Supplementary Material S3, S4 and S11). Variables measured included biomass (field measurements and NDVI), growth including dendrochronology, phenology, morphology, species composition and cover, range changes such as treeline shifts and persistence of alien species. The locations were Alaska and Nunavut/Canada (10 papers: 9 Alaska and 1 Canada/Nunavut), Svalbard and Northern Europe (5 papers: 1 for Svalbard, 4 for Scandinavia), Russia (2 papers) and Greenland (1 study). Three remote sensing papers covered all of the circumpolar area, four covered Alaska and two covered Eurasia. The vegetation types ranged from fellfield through tundra to treeline areas while one study focussed on alien species. Nine of these studies were remote sensing studies covering most or all of the vegetation types. Together, the studies covered the period 1885 to 2015, the older studies using past records of alien plant species or dendrochronology and the recent studies using various field-based methods such as productivity measurements, plant biometrics and phenology, species distribution and composition and remote sensing.

Stability

We identified 8 papers focussing mainly on the stability/no change of vegetation (Supplementary Material S5, S6 and S11). Variables measured included biomass, morphology, growth, onset of the growing season and species cover. The locations were Svalbard and Northern Europe (2 and 3 studies, respectively), Canada/Nunavut (2). One study covered Greenland, Svalbard and the Barents Region. None were related to Arctic Russia. The vegetation types ranged from the High Arctic to treeline with no dominant type emerging. The studies together covered the period 1920 to 2013. Information came from controls of experiments (2 studies), remote sensing/aerial photography (3 studies) and non-experimental field measurements (3 studies). Some papers (e.g. G22, supplementary material S9, S10) were included in the greening analysis even though greening was observed to a far lesser extent than no change (e.g. 6.1% of the area greening) because there was no focus on stability in the paper.

Browning

Fourteen studies focussed on browning (Supplementary Material S7, S8 and S11). More papers reported on the browning of the boreal forest but we focus here only on treeline forests and tundra. The causes of browning included multiple stressors (3 studies), extreme winter warming events (3 studies), herbivory (2 studies), spring/summer temperatures (2 studies), changes in minimum temperatures (1 study), moisture limitation (1 study) and fire (1 study). Four studies covered the whole circumpolar north (3 were remote sensing studies and one was a review), five covered northern Europe, three were located in Alaska, one was based on Svalbard and one in Canada/Nunavut. There were no studies specific to Greenland or Arctic Russia. Eight of the studies included ground-based measurements and six included remote sensing while one was a review. (The total exceeds 14 because one study combined both in situ and remote sensing methods.) The studies covered the period starting in 1046 (dendrochronology) to 2014. The 8 in situ studies ranged from High arctic vegetation (1 study), through tundra (2 studies), sub-arctic dwarf shrub heath and birch forest (4 studies) to coniferous forest treeline (1 study). The variables measured in these studies included phenology, species cover, growth and shoot mortality, diversity and carbon balance.

Greening

Seventy-seven papers focussed on greening (Supplementary Material S9, S10 and S11). The regions covered included Canada (19 studies), Alaska (17 studies), Russia (13 studies), Northern Europe (including Iceland) (12 studies), the whole Polar Region (11 studies), Greenland (4 studies) and Svalbard (4 studies). As some studies addressed more than one country, the sum of the number of studies per region exceeds the total number of screened papers.

The clear majority of studies (41) focussed on tundra (including tall shrub vegetation). Fifteen studies focussed on the sub-Arctic treeline, eleven remote sensing projects focussed on all northern vegetation, ten focussed on the conifer treeline and only 5 reported on greening in High Arctic and fellfield vegetation. Again, the total exceeds 78 because some studies observed different vegetation types.

The methodologies were almost equally divided between ground-based field measurements (36 studies) and remote sensing studies including aerial photography (35 studies). Vegetation variables included estimates and measurements of cover, biomass/net primary production/NDVI, phenology, species composition and plant traits. Ten studies used dendrochronological methods to study the growth of shrubs and treeline trees and three studies reported on carbon cycling.

Putative causes of greening were numerous and several causes (and sometimes their interactions) were presented in some studies. Putative causes of greening included overall warming (23 studies), spring temperature increase (including increased length of the growing season) (7 studies), early summer and summer temperature increase (9 studies) and milder winters (2 studies). In addition to increasing temperature effects, 8 studies cited precipitation/moisture changes, mainly in winter, as causes of greening. Five studies recognised the influence on greening of biotic factors including herbivory including the effect of herbivory on reducing vegetation responses to increasing temperature. Six studies referred to general climate change (4 studies) and general weather systems (2 studies) as causes of greening. Three studies showed there was no warming effect on greening and seven studies explicitly related greening to disturbances that included permafrost thaw, human disturbance and fire. No information on causes of change could be found in 22 studies.

DISCUSSION

Of the 121 identified and analysed papers, 64% focussed on greening, 11.5% browning, 18% heterogeneity and 6.6% stability, (Supplementary Material S11). This can be compared with Xu et al. (2013) who showed that 39.4% of the Arctic's vegetation had greened significantly, 4.5% had browned and 51% had not changed significantly. Similar proportions of greening, browning and no change are seen in other datasets, for instance the MaxNDVI from 1985 to 2016 in the analysis of Berner et al. (2020) shows 37.3% greened, 4.7% browned and 58% did not change. For northern vegetated land ($> 45^{o}$N), Park et al. (2016) reported 44% with significant greening, 2.4% with significant browning (1982–2014) and more than 50% with no significant trend.

Greening dominates over browning in the literature, which is appropriate given the greater amount of greening compared to browning detected across the Arctic. However, our most important point in relation to past published research in our analysis is that a *focus* on lack of vegetation change is greatly under-represented compared with the *area* of no change quantified by satellite observations. While this predominance of no change does not necessarily indicate ecosystem stability on the ground (as discussed earlier), the dominance of no change suggests stability may well be widespread despite rapid climate warming. In contrast, studies identified using a sampling regime on the ground show a predominance of greening and studies capturing the dominant "no change" may not have been captured for various reasons. Firstly, researchers are limited by the geographical area they can cover. These areas vary from 100 s of metres in the analyses of relevés by vegetation scientists (e.g. Walker et al., 2005; Matveyeva and Zanokha, 2013) to 1.5 by 1.5 m plots used by ecologists in ITEX (International Tundra Experiment) monitoring plots (Henry and Molau, 1997). Furthermore, the location of monitoring plots is often pre-defined by proximity to logistical infrastructure such as base camps and research stations rather than a statistically designed sampling framework for the whole Arctic or its sub-regions. The use of data sources (photos, maps, relevés, plot records) pre-dating the climate change issue (see papers in Callaghan and Tweedie, 2011) suffers from some of the bias of more recent monitoring but have the benefit of a) being selected without an awareness of the possibility of vegetation change and b) in the case of photographs, covering landscape level phenomena such as treeline (e.g. Van Bogaert et al., 2011).

The data show a bias in geographical coverage of studies (Fig. 1 and Supplementary Material S11). Russia is only well represented in greening research despite large areas of Arctic Russia showing stability and browning, although this might be to some extent an artefact of the online search being restricted to papers in the English language. Still, the number of studies is not proportional to the vast land mass of the Russian Arctic (Callaghan et al. 2021). Similarly, for the North American Arctic, Alaska has nearly as much greening research as Canada, despite the huge area difference. The same can be said when comparing the Eurasian Arctic, where there are similar amounts of greening research in Scandinavia compared to Russia. So in short, we do not do enough research anywhere to look at stability, and when looking at the main change process (greening), two relatively small areas of the Arctic are disproportionately represented (Alaska and Scandinavia). This analysis of sampling bias agrees with that of Metcalf et al. (2018) who showed that 31% of all Arctic climate change impact studies arise from sites within 50 km of just two research stations, Toolik Lake, Alaska and Abisko, Sweden. One consequence of this geographical bias is that there are far fewer studies focussing on High Arctic and fellfield vegetation (13.4%) than on tundra and tall shrub vegetation (46.1%) (Fig. 2). As stability is more represented in High Arctic and fellfield vegetation than other ecosystem types (Fig. 2), our understanding of the importance of stability is further restricted.

So, without greater research on stability we clearly lack understanding of why many Arctic ecosystems may be showing such little change in the face of rapid climate change. This lack of mechanistic insight contrasts strongly with greening and browning research. In many cases of greening both correlation studies and field simulations of

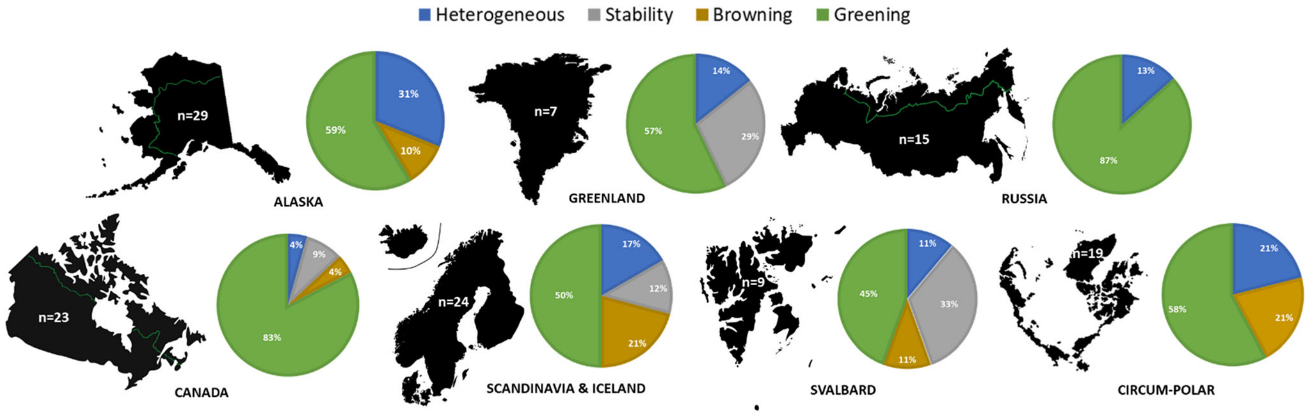

Fig. 1 Overall representation of geographical areas and vegetation types from the analysis of publications on vegetation change in the Arctic summarised from appendices III to VII. The number of studies are contained within the maps; the green line on the maps of Alaska, Canada and Russia represent their treeline limit. **a** data came from only the Arctic and northern treeline areas of the regions illustrated and **b** the total numbers of classifications of regions and vegetation types do not equal the respective number of studies because some focussed on more than one region and/or vegetation type

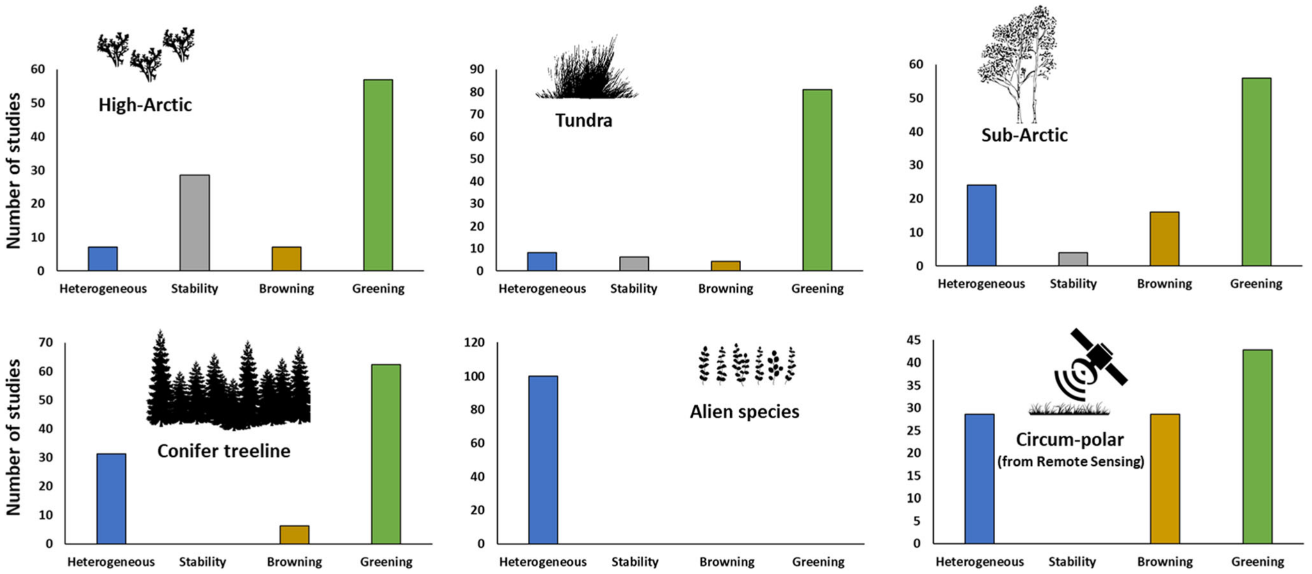

Fig. 2 Overall representation of vegetation change related to vegetation types from analysis of publications on vegetation change in the Arctic summarised from appendices III to VI. Studies using satellite images for the circum-arctic region were not included in this analysis

warming provide compelling evidence of a greening Arctic caused by warming and they give a mechanistic insight into the causes (Walker et al., 2006; Elmendorf et al., 2012a; Bjorkman et al., 2018). However, other mechanisms for greening exist and arguably should receive the attention they deserve. Olofsson et al., (2009) and others, for instance, showed experimentally that herbivores (reindeer and lemmings/voles) reduced greening with the implication that recent pan-Arctic reductions in both types of herbivore could have led to a greening signal or at least enhanced this signal: lemming population peaks have declined (Kausrud et al., 2008) and reindeer populations have decreased (e.g. Sokolov et al. 2016). The importance of herbivores is also seen in modelling work that indicates the current reduction in biomass by existing *Rangifer* populations is similar in magnitude to the increase in biomass predicted from warming over the twenty-first century (Yu et al., 2017). Changes in managed reindeer populations in northern Sweden more than 70 years ago are likely to have contributed to recent greening of vegetation (Callaghan et al., 2013) yet identifying such historic causes is extremely challenging. This emphasises the need to cooperate with local residents and Indigenous Peoples who are excellent observers of their environment throughout all the seasons and hold invaluable Traditional Ecological Knowledge (e.g. Riseth et al., 2010; Eira et al., 2013; Lavrillier and Gabychev 2021).

Browning is an area of increasing research interest (e.g. Bjerke et al., 2014; Phoenix & Bjerke, 2016). MaxNDVI values have declined for 3 consecutive years for the North American Arctic and the Arctic as a whole, while whole Time-Integrated NDVI values of the past three years include some of the lowest since records began in 1982 (Frost et al., 2019). The year 2012 showed particularly low values and productivity in Northern Scandinavia was the lowest on record (Bjerke et al., 2014). Bjerke et al. (2014) list 14 different categories of weather events leading to browning in the Nordic Region, including severe winter cold with no snow protection, rain-on-snow events and storms. Further, browning was caused by biotic events such as outbreaks of insects and fungal pests. Moreover, a combination of Sami traditional ecological knowledge (Riseth et al.2010), ground-based experiments and satellite monitoring showed that in 2007, a few warm days in winter of the previous December could decrease plant productivity by 30% over an area of 1400 km^2 of northern Scandinavia (Bokhorst et al., 2009). Now, there is an increasing awareness of the importance of short-term extreme events that are difficult to observe and even more difficult to predict and mitigate (Phoenix and Bjerke 2016). Some of these events are responsible for the deaths of tens of thousands of animals through, for example, starvation: lemming cycles have been dampened in many areas (Kausrud et al., 2008); and 55,500 reindeer were killed during a rain-on-snow event in the Yamal Nenets area during 2013 (Sokolov et al., 2016). Such large decreases in herbivore populations largely through winter weather events are highly likely to increase greening in subsequent summers independent of warming during summertime. So while some extreme events directly cause browning, where herbivores are killed, an extreme event may lead to greening. We still have too little understanding of how different greening and browning drivers, whether trend or event, interact to produce the observed changes in Arctic biomass.

Our main point, however, is that understanding Arctic ecosystem stability in a changing climate has not been thoroughly researched. Of the eight “stability” papers identified, three presented no explanation for stability, two suggested that herbivore activity masked the response of vegetation to climate change, two reported a lack of warming and one cited the slow invasion of more productive species (On-line Supplementary Material S5). So, what could be other mechanisms of stability of Arctic ecosystems, and which mechanisms seen elsewhere operate in the Arctic? For instance, could spatial heterogeneity and movement of species at the micro-scale drive resilience in composition and function? This has been shown to operate at fine scales in grasslands of long-lived perennials (Fridley et al, 2011) but many Arctic ecosystems are not species rich at such fine scales which might limit the capacity for this mechanism. Spatial heterogeneity at the micro-topographic scale, as seen for some alpine plant communities (Suding et al., 2015) may be a more attractive proposition for explaining stability in Arctic tundra (Matveyeva and Zanokha 2013; Graae et al. 2018). Functional redundancy (Laliberté et al., 2010) within arctic plant communities could also allow stability in ecosystem function even if composition is not stable, though in the many arctic plant communities constructed of super-dominants, the capacity for other species to continue to provide the same level of function would seem limited. Despite the considerable change in climate, physiological plasticity of component species may support stability in Arctic ecosystems. This could be facilitated by pre-adaptation of some arctic plant species to warmer climates, for instance by geographically wide ranging species: *Eriophorum vaginatum* is a “super-dominant” species in many tundra locations throughout the Arctic (Fetcher and Shaver, 1983) yet thrives in the uplands between Manchester and Sheffield UK. Some clonal plant species of the sub-Arctic such as *Lycopodium annotinum* are clonal and clones can survive for over 1000 years (Oinonen, 1968). In Siberia, clones of *Carex* can survive for about 3000 years (Jónsdóttir et al., 2000). During these periods, it can be assumed that the genotypes have experienced many climate and weather extremes that are within the current range, i.e. over the past 30 years. Although their growth forms can hinder displacement by competitors responding more to warming, it is expected that eventually, competition rather than direct responses to warming will shift their ranges.

Another cause of stability is likely to result from the inability of some plant species to respond to higher temperatures by increasing their growth through mechanical limitations. Thus the vertical growth of the moss *Hylocomium splendens* is limited by the mechanical properties of the stem (Ross et al., 1998) and the grass *Phleum alpinum* is at its morphological height growth limit at its northernmost geographical limit in West Greenland (Callaghan, 1974): it simply cannot grow taller to respond to warming. Consequently, a “greening” process is limited both by the lack of growth potential of existing populations with associated increased biomass and leaf area, and by the dispersal abilities of a potential immigrant species. Shrubs and trees, in contrast, have sufficient meristems (Bret-Harte et al., 2001) and growth potential to respond to warming (Elmendorf et al., 2012b; Myers-Smith et al., 2015).

Stability of vegetation can also result from trophic interactions. Herbivore pressure can mask effects of climate change (On-line Supplementary Material S5). Removing a top predator such as the wolf in northern Sweden can increase herbivore populations such as the moose which selectively browse aspen, thereby retarding the rate of aspen invasion during climate warming (Van Bogaert et al., 2009). In the same area, the effect of increased winter temperatures on increased forest pest survival results in birch forest death (browning) that dominates over any greening due to increased summer temperatures (e.g. Bjerke et al. 2014) and the balance between sub-Arctic forest trees appears to result from responses of their vertebrate and invertebrate herbivores to climate and management.

One particular problem with the lack of focus on stability is that long-lived species and stable vegetation may be vulnerable to thresholds that remain unknown, whereas vegetation that has browned or greened has passed a threshold that can be identified. Pre-emption of space of long-lived perennial plants has been shown to be key to stability in the face of climate change in some systems (Grime et al., 2000, 2008). Further, it can be difficult for many species to establish in undisturbed tundra vegetation, especially from seed (Milbau et al., 2013). This raises the possibility of Arctic ecosystems forming "tensioned landscapes" where plant communities exist at the limits of their climatic tolerance, but change does not occur because new species cannot establish and the existing biomass is long-lived (Brooker et al., 2007). The "tension" provides an opportunity for events which remove or open up the existing vegetation (e.g. fire, extreme winter warming, herbivore outbreaks) to cause substantial state changes as in the boreal forest (Chapin et al., 2004). This has some analogy with the concept of extinction debt where disturbances cause extinctions in ecosystems many years after the disturbance has occurred (Tilman et al., 1994). Here though, the extinction debt is being built up within an unchanging, but increasingly tensioned, landscape, with the debt to be paid when a major disturbance event occurs. As stable systems may cover most of the Arctic, and much of the Arctic is covered by "super-dominant" species, sudden steep changes might be possible for much of the Arctic.

CONCLUSIONS

Our literature search shows for the first time that relatively few studies report on vegetation stability, even though satellite observations show that more than 50% of the Arctic's vegetation has shown no detectable change despite rapid warming. Furthermore, while there is a good abundance of studies on the main change process—that of greening—two relatively small areas of the Arctic are disproportionately represented. Few studies offered explanations of causes of stability and none considered the consequences of stability. A particular concern over the lack of understanding of vegetation stability during rapid climate change is that if widespread landscapes are tensioned, then when they exceed their stability thresholds, rapid and substantial changes to vegetation, biodiversity and ecosystem services could occur.

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