### Yamal LCLUC Synthesis

A synthesis of remote-sensing studies, ground observations and modeling to understand the socialecological consequences of climate change and resource development on the Yamal Peninsula, Russia and relevance to the circumpolar Arctic

### Grant NNX14AD90G

Annual Report, 31 March 2018

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# Table of contents

Table of contents Introduction	. 2 . 3
Component 1: Eurasia Arctic Transect (EAT)	
Yamal LCLUC workshop at Arctic Science Summit Week (ASSW), 6 April 2017, Prague, CZ ASSW Science Session (no. 13.2) "Properties of bio-geophysical and socio-economic systems along Arctic transects"	. 3
Arctic Vegetation Archive (AVA) and Classification (AVC) Workshop at ASSW, 30-31 March 2017 Synthesis manuscript regarding EAT vegetation	
Component 2: Progress on synthesis social ecological impacts of infrastructure and climate	
(RATIC)	. 4
"Sustainable Arctic Infrastructure Forum (SAIF)" at ASSW 2017 Cumulative effects of infrastructure manuscript submitted to Frontiers in Ecology and the Environment	
Component 3: Modeling and circumpolar extrapolation	
Circumpolar arctic tundra biomass and productivity dynamics in response to projected climate change and herbivory	
Greening of the Arctic report for the 2017 State of the Climate Report and Arctic Report Card Contributions to the AMAP Snow Water Ice and Permafrost in the Arctic (SWIPA) 2017 report	. 6 . 7
Request for a No Cost Extension Reviewed 2017-2018 publications* and other presentations	

### INTRODUCTION

The Yamal LCLUC project began in 2007 as a project of the International Polar Year 2007-8 called "Greening of the Arctic", which focused on the trends in sea ice, summer land temperature, greening trends, and human interactions with greening along two Arctic transects in North America and Eurasia. The two primary goals of the current (2013-2018) Yamal synthesis activities are to: 1) develop a better understanding of variations in Arctic ecological systems along the Yamal and Circumpolar Arctic climate gradients to aid in interpretation of Arctic remotely sensed imagery, and 2) develop tools including modeling and remote-sensing approaches that can be used to help Arctic people, government agencies and policy makers predict and adapt to impending rapid climate change and resource development.

The overall Yamal LCLUC project has had three NASA-funded projects. The latest one (NASA Grant No. NNX14AD90G) began in Jun 2013, and we are currently in a no-cost extension (NCE) through December 31, 2017. Last year's annual report included a thorough summary of progress through 2016. This report presents the major highlights of the current NCE (April 1, 2017 to March 31, 2018). We are requesting another NCE this year to complete several synthesis aspects of the project. Here, we organize the main accomplishments of the last year according to the three principal components of the project: The Eurasia Arctic Transect (EAT), the social-ecological-system (SES), and modeling. This is followed by the request for the NCE, and finally the list of refereed publications and presentations at conferences and workshops.

### COMPONENT 1: EURASIA ARCTIC TRANSECT (EAT)

### Yamal LCLUC workshop at Arctic Science Summit Week (ASSW), 6 April 2017, Prague, CZ.

This workshop took advantage of the ASSW location to gather the Russian and European participants for a final workshop to go over progress and outline propose products for the Yamal LCLUC synthesis effort. Several papers are completed or in preparation regarding the vegetation (Walker *et al.* 2018 in press), soils (Matyshak *et al.* 2017), active layer and permafrost dynamics (Babkina *et al.* 2018 in press; Romanovsky *et al.* 2017b), biomass-LAI-NDVI relationships (Epstein *et al.* 2017a), status of new vegetation sampling and research across the Yamal-Gydan region (Ermokhina *et al.* 2017), and cryogenic geosystems of Belyy Ostrov (Orekhov *et al.* 2017). The participants agreed that once the disciplinary synthesis papers are written, a summary Yamal LCLUC Synthesis e-book will be completed.

ASSW Science Session (no. 13.2) "Properties of bio-geophysical and socio-economic systems along Arctic transects". Arctic terrestrial environments extend along thousands of kilometers of latitude from forest-tundra transitions to the extreme High Arctic. While ground-based observational studies of the complete Arctic bioclimate gradient are rare because of the challenging logistic involved, a few latitudinal and elevation transects exist in different parts of the Arctic. The two best examples are the North America Arctic Transect and the Eurasia Arctic Transect. Remote sensing and simulation modeling also provide mechanisms for examining arctic systems along climatic gradients. The session was sponsored in part by the International Permafrost Association. Abstracts of the 10 oral presentations and 11 posters are included in the Conference proceedings, S13.2, p. 138-144, http://www.assw2017.eu/files/assw2017-abstractbook.pdf.

### Arctic Vegetation Archive (AVA) and Classification (AVC) Workshop at ASSW, 30-31 March

*2017.* This workshop also took advantage of the ASSW venue to bring together Russian, Canadian, Greenland, Svalbard and U.S. contributors to the Arctic Vegetation Archive and Circumpolar Arctic

Vegetation Mapping efforts. Fourteen papers presented a summary of Arctic plot data and data management approaches from around the Arctic. The authors summarized approximately 31,000 plot distributions onto a map that was published in a paper summarizing the status of circumpolar Arctic vegetation classification (Walker *et al.* 2017b). The proceedings of the workshop are available on line at http://www.geobotany.uaf.edu/library/pubs/2017\_ava-workshop-prague\_iasc-report.pdf.

*Synthesis manuscript regarding EAT vegetation.* The paper synthesizes four years of groundbased vegetation observations along the 1700-km Eurasia Arctic Transect, including the first vegetation data from Hayes Island, Franz Josef Land (Walker *et al.* 2018 in press). Vegetation data were collected at six locations, one in each of the five Arctic bioclimate subzones and the foresttundra transition. The Braun-Blanquet approach was used to sample mesic loamy and sandy sites at each location (14 total study sites). Trends in cover-abundance of plant growth forms (PGFs), species diversity, and environmental factors were examined along the summer-warmth-index (SWI) gradient on loamy and sandy soils. Cover of plant growth forms and species richness within the shrub, herb, and cryptogam layers have mostly nonlinear trends along the bioclimate gradient, with distinct trends on loamy and sandy soils. Each layer of the plant canopy has a distinct region of peak abundance along the bioclimate gradient. Seven numerically defined clusters of plots align with six described classes of the European Vegetation Classification with clear relationships to subzone and soil texture. Summer temperature and soil texture have clear effects on tundra canopy structure and species composition, with consequences to numerous ecosystem properties.

# COMPONENT 2: PROGRESS ON SYNTHESIS SOCIAL ECOLOGICAL IMPACTS OF INFRASTRUCTURE AND CLIMATE (RATIC)

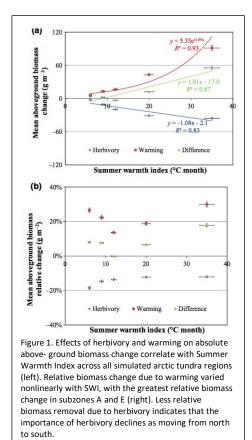
*"Sustainable Arctic Infrastructure Forum (SAIF)" at ASSW 2017.* This was an activity of the LCLUC/IASC Rapid Arctic Transitions due to Infrastructure and Climate (RATIC) initiative. The major task of SAIF was to address the cumulative effects of four major types of infrastructure systems: indigenous infrastructure (e.g., camps, trails, corrals, migration corridors, etc.); onshore oil & gas fields (networks of roads, drilling and facility pads, pipelines, etc.); remote communities (village infrastructure); and urban infrastructure (cities). "Corridors" and "nodes" emerged as an organizing framework for developing research themes related to the various types of infrastructure. The workshop consisted of: (1) a series of introductory talks, (2) a keynote student presentation by Will Tyson (Canada), (3) breakout sessions to address a journal publication and a RATIC strategy document. The workshop report is at <a href="http://www.geobotany.uaf.edu/library/pubs/2017">http://www.geobotany.uaf.edu/library/pubs/2017</a> ratic-saif-workshop-prague iasc-report.pdf.

*Cumulative effects of infrastructure manuscript submitted to* Frontiers in Ecology and the Environment. Cumulative effects (CE) of arctic industrial development and climate change are circumpolar concerns that triggered a new initiative of the International Arctic Science Committee (IASC) called Rapid Arctic Transitions due to Infrastructure and Climate (RATIC). This paper reports the history of landscape change in the Prudhoe Bay oilfield, Alaska. Little change occurred between 1949 and the start of development in 1968. Between 1969–1983, roadside flooding, dust, and other disturbance factors caused the development of local thermokarst mainly near infrastructure. Starting in approximately 1990, a thermal threshold was crossed that resulted in the melting of the tops of ice-wedges, extensive ponding of water, widespread regional thermokarst, and a catastrophic flood in 2015. If warming continues, a second threshold will likely follow involving the formation of taliks (layers of year-round unfrozen ground) that will further destabilize infrastructure and ecosystems. Conclusions from a recent RATIC workshop point to the need for a

clear strategy to develop an integrated scientific research program focused on infrastructure– climate-change interactions (Walker *et al.* 2018 submitted).

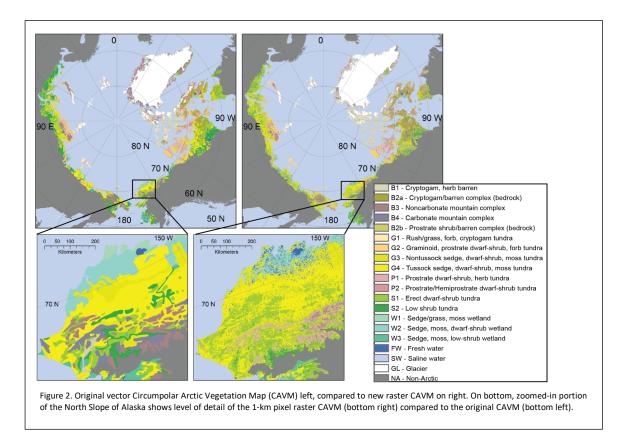
### COMPONENT 3: MODELING AND CIRCUMPOLAR EXTRAPOLATION

Circumpolar arctic tundra biomass and productivity dynamics in response to projected climate change and herbivory (Fig. 1). Satellite remote sensing data have indicated a general 'greening' trend in the arctic tundra biome. These trends are strongly affected by warming temperatures, but the trends are modified by other factors such as herbivory by reindeer. A new paper examines how productivity of circumpolar tundra productivity would be affected by a combination of a warming climate and reindeer grazing along the Eurasia Arctic Transect and projects these trends to the circumpolar region (Yu et al. 2017). The ArcVeg model is an arctic tundra vegetation dynamics model that estimates potential changes in vegetation biomass and net primary production (NPP) at the plant community and functional type levels. Here ArcVeg is driven by soil nitrogen output from the Terrestrial Ecosystem Model with herbivory of existing densities of Rangifer populations, and projected summer temperature changes by the NCAR CCSM4.0 general circulation model across the Arctic. The model quantified the changes in aboveground biomass and NPP resulting from (i) observed herbivory only, (ii) projected climate change only, and (iii) coupled effects of projected climate change



and herbivory. The model outputs included the absolute and relative differences in biomass and NPP by country, bioclimate subzone, and floristic province. Estimated potential biomass increases resulting from temperature increase only are approximately 5% greater than the biomass modeled due to coupled warming and herbivory. Such potential increases are greater in areas currently occupied by large or dense *Rangifer* herds such as the Nenets-occupied regions in Russia (27% greater vegetation increase without herbivores). In addition, herbivory modulates shifts in plant community structure caused by warming. Plant functional types such as shrubs and mosses were affected to a greater degree than other functional types by either warming or herbivory or coupled effects of the two.

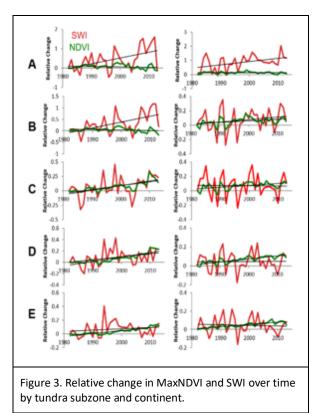
*New raster-version of the Circumpolar Arctic Vegetation Map* (**101** 2). The 1-km pixel raster Circumpolar Arctic Vegetation Map (CAVM) provides much finer resolution than was possible with the original hand-drawn vector map, in a format that is convenient for use in models with raster satellite data. The map will be published at 1:7.5 million-scale (Raynolds *et al.* 2018). The map uses the same circumpolar legend developed for the CAVM. The map units show a similar distribution as the original, with similar class characteristics of summer temperature, elevation and NDVI, but shows larger total area of finely dispersed cover types such as lakes and erect shrubs in lowland areas and prostrate dwarf shrubs in mountainous areas. This was expected, since land cover patches of 5 to 150 km<sup>2</sup> were too small to be mapped in the vector version. The early results from the map were presented at the 2016 Circumpolar Remote Sensing Conference (Raynolds & Walker 2016). The final map was presented at the 2018 Alaska Botany Forum in Fairbanks, Alaska (Raynolds & Walker 2018). It will also be presented at the International Arctic Workshop in Boulder, Colorado in April 2018; at the International Association for Vegetation Science (IAVS) Annual Symposium in Bozeman, Montana in July 2018; at the 15<sup>th</sup> International Circumpolar Remote Sensing Symposium in Potsdam, Germany in September 2018; and at the Arctic Biodiversity Congress in Rovaniemi, Finland in October 2018. An analysis of the Raster CAVM will also be submitted to a peer-reviewed journal in 2018, likely to *Remote Sensing of Environment*.

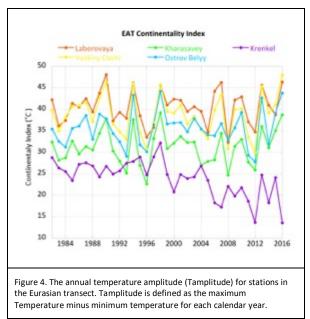


## Greening of the Arctic report for the 2017 State of the Climate Report and Arctic Report Card.

We contribute annually to the State of the Climate report of the Bulletin of the American Meterological Society (BAMS) and NOAA's Arctic Report Card (Epstein *et al.* 2017a, b; Romanovsky *et al.* 2017b). Key findings this year were: 1) Tundra greenness increased substantially throughout the Arctic over the past two years (2015-2016), following 3-4 years of continuous declines.

Additionally, we have been examining the NDVI and SWI trends and relationships by tundra subzone (A-E) and continent (North America and Eurasia) (Reichle *et al.* submitted). We found that SWI increased relatively faster than NDVI in the northern tundra subzones, and the difference between the trends decreased with decreasing latitude (Fig. 3). However, the inter-annual response of NDVI to SWI was strongest in the mid subzones of the tundra (B and C). Finally, we continue to analyze the spatial patterns of phytomass and vegetation indices (NDVI and LAI) along the Eurasian Arctic Transect (Epstein *et al.* 2017a)





We are also exploring a larger diversity of climate parameters in the context of drivers of tundra changes. Figure 4 shows a measure of continentality index (CI) for stations in each subzone along the Eurasian transect. CI is

defined as the annual maximum mean monthly air temperature minus the annual minimum mean monthly air temperature. The spatial patterns of the CI trends for the tundra regions provides insights on potential drivers of vegetation change. The northernmost point in the transect, Krenkel in bioclimate subzone A, had over a 50% reduction in CI since 1998. This is also in proximity of the area of largest sea ice decline in the Arctic. More southern points in the transect have larger mean values and weak trends of CI.

### Contributions to the AMAP Snow Water Ice and Permafrost in the Arctic (SWIPA) 2017

*report.* SWIPA 2017 is an update of the 2011 assessment coordinated by Arctic Monitoring and Assessment Programme (AMAP 2017). The report presents key findings and implications of the second SWIPA assessment, conducted from 2010 to 2016 and published in 2017. Access to reliable and up-to-date information is essential for the development of science-based decision-making regarding ongoing changes in the Arctic and their global implications. Contributions by the Yamal LCLUC project included circumpolar assessment of permafrost changes (Chapter 4) (Romanovsky *et al.* 2017a, p. 65–102) and a hierarchical evaluation at circumpolar, regional, landscape and plot scales of the linkages between vegetation greenness, and snow, water, ice, and permafrost in Chapter 10, Section 10.3 of the report (Mård *et al.* 2017, p. 235–241).

### REQUEST FOR A NO COST EXTENSION

We are requesting a no-cost extension to finish synthesizing the large quantity of material that resulted from the three workshops and sessions at Arctic Science Summit Week 2017. We are still in the process of assembling the disciplinary papers for the EAT synthesis, and we still intend to

write a final e-book that will synthesize the results of our full Greening of the Arctic Eurasian activities that began with the International Polar Year in 2007-2008.

#### **REVIEWED 2017-2018 PUBLICATIONS\* AND OTHER PRESENTATIONS**

A full list of publications from earlier years of the LCLUC Yamal project along with other projectrelated information including annual reports, proposals, photos, participants, and workshops is on the Yamal-Synthesis web page (<u>http://www.geobotany.uaf.edu/yamal/</u>).

- \*AMAP. (2017). *Snow, water, ice and permafrost in the Arctic (SWIPA) 2017* (pp. 1–269). Oslo: Arctic Monitoring and Assessment Programme, Oslo. (Contributions to Chapters 4 and 10).
- \*Bhatt, U. S., D. A. Walker, M. K. Raynolds, P. A. Bieniek, H. E. Epstein, J. C. Comiso, J. E. Pinzon, C. J. Tucker, M. A. Steele, W. Ermold, and J. Zhang. (2017). *Changing seasonality of Panarctic tundra vegetation in relationship to climatic variables*. (special biomass issue) *Environmental Research Letters*. 12 (2017) 055003 <u>https://doi.org/10.1088/1748-9326/aa6b0b</u>
- Bhatt, U. S., D. A. Walker, M. K. Raynolds, P. A. Bieniek, H. E. Epstein, J. C. Comiso, J. E. Pinzon, C. J. Tucker.
  (2017). *Climate Drivers of Tundra Vegetation Greening/Browning in the Arctic,* IARC Salon, Fairbanks Alaska, Thursday April 13, 2017
- Bhatt, U. S. (2017). *Arctic observations from the point of view of a data user*, Finnish Meteorological Institute Arctic Science Networking Workshop, FMI, Helsinki Finland, 30 August 2017
- \*Bratsch, S. N., H. E. Epstein, M. Buchhorn, D. A. Walker, and H. A. Landes. (2017). Relationships between hyperspectral data and components of vegetation biomass in Low Arctic tundra communities at Ivotuk, Alaska. *Environmental Research Letters* 12:025003.
- Bhatt, U. S., D.A. Walker, M.K. Raynolds, P.A. Bieniek, H.E. Epstein, J.C. Comiso, J.E. Pinzon, C.J. Tucker, On Understanding the Climate Drivers of Tundra Vegetation Greening/Browning in the Arctic, Chapman Chair Symposium, Fairbanks Alaska, Tuesday Sept 3, 2017.
- Bhatt, U. S., D. A. Walker, M. K. Raynolds, H. E. Epstein, P. A. Bieniek, C. Comiso, J. E. Pinzon, and C. J. Tucker.
  (2017) *Humidification of the Arctic: Effects of changing sea-ice on summer land temperatures, continentality and NDVI along transects in Eurasia and North America*, Svalbard Biomass Workshop Oct 9-12 2017 Longyearbyen, Norway, October 11, 2017.
- Bhatt, U. S., D. A. Walker, M. K. Raynolds, P. Bieniek, H. E. Epstein, J. C. Comiso, J. E. Pinzon & C.J Tucker.
  (2017), *Possible causes of Arctic Tundra Vegetation Productivity Declines*, (Invited oral presentation)
  Session Proposal: B43J Drivers of Vegetation Change and Impacts on Biogeochemical and Biogeophysical
  Processes in Arctic Tundra Ecosystems II AGU 2017 New Orleans, Thursday Dec 14, 2017
- Bhatt, U. S., D. A. Walker, M. Raynolds, and H. Epstein. (2017) Humidification of the Arctic. Effects of more open ocean water on land temperatures and tundra productivity along continental and maritime bioclimate transects AGU Fall Meeting, New Orleans LA, Thursday AM December 14, 2017, (Invited poster), Session: B41A Drivers of Vegetation Change and Impacts on Biogeochemical and Biogeophysical Processes in Arctic Tundra Ecosystems I Posters
- \*Babkina, E. A., Leibman, M. O., & Khomutov, A. V. (2018 in press). Active layer dynamics on Central Yamal, Russia due to climatic fluctuations, (pp. 1–3). Presented at the EUCOP 5, Chamonix.
- Breen, A., Sibik, J., Druckenmiller, L., Daniels, F., Hennekens, S., Walker, M., et al. (2017). Status of the Circumpolar Alaska Vegetation Archive and the regional arctic Alaska prototype (Oral presentation abstract O 038, p. 129). Presented at the Arctic Science Summit Week, Prague, 31 Mar-07 Apr.
- Epstein, H., Walker, D., Sibik, J., Chasnikova, S., Frost, G., Leibman, M., et al. (2017a). Vegetation community and ecosystem properties along the Eurasian Arctic Transect (EAT) (Oral presentation abstract O 065, p. 139). Presented at the Arctic Science Summit Week, Prague, 31 Mar-07 Apr.
- \*Epstein, H., U. Bhatt, M. Raynolds, D. Walker, B. C. Forbes, T. Horstkotte, M. Macias-Fauria, A. Martin, G. Phoenix, J. Bjerke, H. Tømmervik, P. Fauchald, H. Vickers, R. Myneni, and C. Dickerson. (2017b) *Tundra Greenness [in Arctic Report Card 2017]*, http://www.arctic.noaa.gov/Report-Card.
- Ermokhina, K. (2017). Russian arctic datasets of releves meeting requirements for classification of vegetation using Braun-Blanquet approach (Poster abstract P 142, p. 134). Presented at the Arctic Science Summit Week, Prague, 31 Mar-07 Apr.

- \*Frost, G. V., Epstein, H. E., Walker, D. A., Matyshak, G., & Ermokhina, K. (2017). Seasonal and long-term changes to active-layer temperatures after Tall shrubland expansion and succession in arctic tundra. *Ecosystems*, *16*, 1296. http://doi.org/10.1007/s10021-017-0165-5
- \*Mård, J., Box, J. E., Brown, R., Mack, M., Mernild, S. H., Walker, D., & Walsh, J. (2017). Cross-cutting scientific issues. In AMAP (Ed.), *Snow, Water, Ice and Permafrost in the Arctic (SWIPA) 2017* (pp. 231– 256). Oslo, Norway: Arctic Monitoring and Assessment Programme (AMAP).
- Matyshak, G., Walker, D. A., Epstein, H. E., Leibman, M. O., Moskalenko, N. G., Orekhov, P. T., et al. (2017). Characteristics of cryogenic soils along the latitudinal transect in the northwestern Siberia, Russia (Oral presentation abstract O 066, p. 141). Presented at the Arctic Science Summit Week, Prague, 31 Mar-07 Apr.
- Orekhov, P., Slagoda, E., & Popov, K. (2017). Factors of spatial differentiation of cryogenic geosystems of the Bely Island arctic tundras (Oral presentation abstract O 069, p. 141). Presented at the Arctic Science Summit Week, Prague, 31 Mar-07 Apr.
- Raynolds, M. K. & Walker, D. A. (2016). A raster version of the Circumpolar Arctic Vegetation Map (CAVM). Presented at the 14th Circumpolar Remote Sensing Symposium, Homer, AK, - September.
- Raynolds, M. K. and Walker, D. A. (2018). A raster-based circumpolar arctic vegetation map. Presented at the 48th Annual International Arctic Workshop, Boulder, CO, USA.
- \*Romanovsky, V., Isaksen, K., Drozdov, D., Anisimov, O., Instanes, A., Leibman, M., et al. (2017a). Changing permafrost and its impacts. In AMAP (Ed.), *Snow, Water, Ice and Permafrost in the Arctic (SWIPA) 2017* (pp. 65–102). Oslo, Norway: Arctic Monitoring and Assessment Programme (AMAP).
- Romanovsky, V., Nicolsky, D., Cable, W., Kholodov, A., Farquharson, L., Panda, S., et al. (2017b). Measured and modeled changes in permafrost along North American Arctic Transect (Oral presentation abstract O 100, p. 141). Presented at the Arctic Science Summit Week, Prague, 31 Mar-07 Apr.
- \*Romanovsky, V. E., S. L. Smith, N. I. Shiklomanov, D. A. Streletskiy, K. Isaksen, A. L. Kholodov, H. H. Christiansen, D. S. Drozdov, G. V. Malkova, and S. S. Marchenko, (2017c) [The Arctic] Terrestrial Permafrost [in "State of the Climate in 2016"]. Bull. Amer. Meteor. Soc., Vol. 98, No. 8, S147-S151, 2017.
- \*Walker, D. A., Epstein, H. E., Šibík, J., Bhatt, U., Romanovsky, V. E., Breen, A. L., et al. (2018, in press). Vegetation of the Eurasia Arctic Transect, Yamal Peninsula and Franz Josef Land, Russia. *Applied Vegetation Science*.
- \*Walker, D. A., Daniëls, F. J. A., Matveyeva, N. V., Šibík, J., Walker, M. D., Breen, A. L., et al. (2017b). Circumpolar Arctic Vegetation Classification. *Phytocoenologia*, 1, <u>http://doi.org/10.1127/phyto/2017/0192</u>
- \*Walker, D. A., Shur, Y., Kanevskiy, M., Raynolds, M., Kofinas, G., Romanovsky, V., et al. (2018 submitted). Cumulative effects of oilfield infrastructure and climate change in the Prudhoe Bay Oilfield, Alaska, illustrate the need for an international strategy to address rapid arctic transitions due to infrastructure and climate. *Frontiers in Ecology and the Environment*.
- Walker, D. A. (2017a). Arctic transects as a concept: examples from Russia & North America: what do transects offer that normal one-site studies do not? Presented at the SVAL-GREEN Workshop, 22-24 May, Longyearbyn, Svalbard.
- Walker, D. A. (2017b). Cumulative effects of arctic oil development: planning for a sustainable future. Presented at the Kuukpik UAF Workshop, UAF, 5 Jun.
- Walker, D. A. (2017c). Vegetation of the European Arctic Transect (EAT) Yamal Peninsula and Franz Jozef Land, Russia. Presented at the Slovak Academy of Sciences, Institute of Botany, Bratislava, Slovak Republic, 12 April, Bratislava, Slovak Republic.
- Walker, D. A. (2017d). Vegetation of the European Arctic Transect (EAT) Yamal Peninsula and Franz Jozef Land, Russia. Presented at the Arctic Biomass Workshop, Longyearbyn, Svalbard, 9-12 Oct, 2017.
- Walker, D. A., Breen, A. L., Druckenmiller, L. A., Šibík, J., Hennekens, S., Daniëls, F. J. A., et al. (2017e). An Arctic Vegetation Archive for circumpolar arctic vegetation classification (Poster abstract P 150, p. 137). Presented at the Arctic Science Summit Week, Prague, 31 Mar-07 Apr.
- Walker, D. A., Kanevskiy, M., Shur, Y., Raynolds, M., Buchhorn, M., & Matyshak, G. (2017c). Rapid transitions caused by infrastructure and climate, Prudhoe Bay Oilfield, Alaska, USA (Oral presentation abstract O 115, p. 171). Presented at the Arctic Science Summit Week, Prague, 31 Mar-07 Apr.

- Walker, D. A., Šibík, J., Chasnikova, S., Epstein, H. E., Ermokhina, K., Frost, G. V., et al. (2017d). Vegetation of the European Arctic Transect (EAT), Yamal Peninsula and Franz Jozef Land, Russia (Oral presentation abstract O 064, p. 142). Presented at the Arctic Science Summit Week, Prague, 31 Mar-07 Apr.
- \*Yu, Q., Epstein, H., Engstrom, R., & Walker, D. (2017). Circumpolar arctic tundra biomass and productivity dynamics in response to projected climate change and herbivory. *Global Change Biology*, *94*, 713. http://doi.org/10.1111/gcb.13632