TERRESTRIAL BIODIVERSITY IN A RAPIDLY CHANGING ARCTIC

Non-native vascular flora of the Arctic: Taxonomic richness, distribution and pathways

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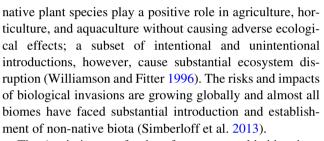
Received: 7 September 2019/Revised: 6 November 2019/Accepted: 14 November 2019

Abstract We present a comprehensive list of non-native vascular plants known from the Arctic, explore their geographic distribution, analyze the extent of naturalization and invasion among 23 subregions of the Arctic, and examine pathways of introductions. The presence of 341 non-native taxa in the Arctic was confirmed, of which 188 are naturalized in at least one of the 23 regions. A small number of taxa (11) are considered invasive; these plants are known from just three regions. In several Arctic regions there are no naturalized non-native taxa recorded and the majority of Arctic regions have a low number of naturalized taxa. Analyses of the non-native vascular plant flora identified two main biogeographic clusters within the Arctic: American and Asiatic. Among all pathways, seed contamination and transport by vehicles have contributed the most to non-native plant introduction in the Arctic.

Keywords Alien species · Arctic · Invasive species · Non-native species · Pathways · Vascular plants

INTRODUCTION

Non-native species are among the most significant contributors to global loss of biodiversity, ecological disruption, and economic loss (Dukes and Mooney 2004; Pimentel et al. 2005; Simberloff et al. 2013). Although non-native animals generally receive more attention from the public than plants, non-native plants have a higher likelihood of causing irreversible ecosystem impacts (Vilà et al. 2011). Many non-



The Arctic is one of only a few areas worldwide where ecosystems remain minimally affected by non-native species (Lassuy and Lewis 2013). Limited large-scale human disturbance, low human population size, light traffic volumes, harsh climatic conditions, and short growing seasons likely act as constraints on non-native plant invasion in the Arctic and adjacent regions (Carlson and Shephard 2007; Alsos et al. 2015). However, climate change (IPCC 2018) and increasing industrial activities (Reeves et al. 2012) are particularly acute in the Arctic (Descamps et al. 2016; IPCC 2018), possibly diminishing many of the constraints to the importation and establishment of non-native plant species. Milder climatic conditions and longer growing seasons coupled with anthropogenic disturbance may facilitate a shift in the composition of the non-native flora in the Arctic.

Inventories of non-native plant taxa (e.g., Pyšek et al. 2017) constitute an indispensable element of research focused on understanding the nature and pace of biological invasions and they are necessary for informed natural resource management. Comprehensive non-native plant inventories have been compiled and published for many regions, especially in lower latitudes (Pyšek et al. 2017). The situation in the Arctic, however, is different. Apart from a few notable exceptions (Wasowicz et al. 2013; AKEPIC 2018; Sandvik et al. 2019), the non-native flora of the Arctic is still not well known and catalogs of the non-

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s13280-019-01296-6) contains supplementary material, which is available to authorized users.

native flora in many regions have never been published. Improving our knowledge of the composition of the nonnative flora in the Arctic will contribute to our understanding of the current state of the flora and will serve as a baseline for assessing the pace and pattern of future changes.

Most catalogs and analyses of non-native plants are based on political borders rather than natural ecoregions as boundary-delimiting factors (e.g., Seebens et al. 2017). While this approach has obvious practical value, it is problematic for characterizing the non-native flora of the Arctic. Political boundaries of most Arctic nations, states, and territories extend into boreal or even temperate biomes, such as in Alaska (Carlson and Shephard 2007) and the two provinces and three territories in Canada that comprise both Arctic and boreal ecozones. As such, catalogs of nonnative taxa in these politically defined areas may include species found only in their southern, non-Arctic portions, with no indication of the ecozone in which each non-native taxon has been recorded. Species lists compiled for administrative regions that include the Arctic ecozone but also extend beyond it can thus significantly distort understanding of plant invasions in the Arctic. We overcame the bias of many previous local studies by accepting the natural boundary of the Arctic as defined by vegetation (i.e., Circumpolar Arctic Vegetation Map; Raynolds et al. 2019) rather than by political boundaries.

Ecological disruption caused by invasive non-native plant species requires three basic steps: transportation of propagules, population establishment, and a subsequent increase in population size. Increasing attention is being directed at the first step of an invasion in the Arctic and beyond: managing pathways of non-native propagules (Conn et al. 2008, 2010; Conn 2012; Ware et al. 2012). In general, the pathways of invasive species mirror the movements of people, and the movements of people and their goods are closely tied to commerce and trade; the volume and rate of globally traded goods has increased dramatically in recent decades, facilitating the transport of non-native species (Hulme 2009). The Arctic is no exception; increased shipping within the region has been recorded over the past 40 years (MOSJ 2018).

Non-native plant species may arrive to a new region by one of six primary pathways: intentional release, escape from confinement, transport contaminant, transport-stowaway, corridor, or unaided (Hulme 2009; CBD 2014). Globally, the majority of non-native plant species have been introduced intentionally (Dodet and Collet 2012), and most plants follow either an escape from confinement or intentional release pathway (Hulme 2009). Some groups of species, such as shrubs and trees, have been almost entirely intentionally released (Reichard and Hamilton 1997). Container-grown ornamentals, hay and straw, and agricultural seed harbor substantial amounts of non-native plant seeds (e.g., 585 weed seeds/kg of hay and straw bales in Alaska) (Conn et al. 2008, 2010; Conn 2012). Footwear of travelers is also a significant pathway of viable nonnative seed to high latitudes. For example, the average visitor to the Arctic archipelago of Svalbard transports approximately four seeds on their hiking boots, with 40% of visitors transporting at least one species (Ware et al. 2012).

The Arctic is a partially inter-connected area with geologically recent ice-free exposure of terrains into which many plant species have naturally migrated and colonized post glacially (Abbott and Brochmann 2003; Alsos et al. 2007). The geology and partially connected geography leads to high similarity of the native arctic floras, even on different continents (Hultén 1958). Regional relationships among the non-native components of the arctic flora, however, have not been explored.

In the present paper we: (1) provide an account of nonnative plant introductions to the Arctic, (2) explore the basic taxonomic and biogeographic characteristics of the non-native flora, (3) compare the extent of non-native plant naturalization and invasion among analyzed regions, and (4) analyze the pathways of non-native plant introductions.

MATERIALS AND METHODS

Study area

Our definition of the Arctic followed the borders of the Circumpolar Arctic Vegetation Map (Raynolds et al. 2019). The total investigated land area was ca. 5 438 000 km². We subdivided the Arctic into 23 regions that largely correspond to the floristic regions used by the PanArctic Flora Checklist (PAF; Elven et al. 2011) (Table S1). Iceland, Jan Mayen, Svalbard, and Franz Joseph Land were treated as separate regions in our study due to their geographic isolation and differences in the composition of their non-native floras.

Lists of non-native plant taxa

To characterize the composition of the non-native vascular flora of the Arctic, we consulted diverse data sources including comprehensive national/regional databases of non-native species (e.g., AKEPIC, Artsdatabanken), nonnative plant compendia, national and regional lists of nonnative plants published in scientific journals and books, books and online compendia of national and subnational floras with information on non-native plants, the Global Biodiversity Information Facility (GBIF), and major herbaria holding collections from the Arctic (ALA, AMNH, BABY, C, CAN, ICEL, UAAH). We also considered the list of non-native taxa in the Arctic included in the PanArctic Flora Checklist (Elven et al. 2011) and reviewed the evidence supporting non-native records recorded there. As certain regions of the Arctic are more intensively researched than others, it is unavoidable that some of the regional inventories of non-native species are more comprehensive than others, but we aimed to include the most comprehensive and most recent data in our regional lists. No time limits were introduced during the process of data collection. A complete list of sources consulted is available in Table S2. Each record of a taxon in a given region is supported by a reference to herbarium collection or relevant literature record (or both) and is available in Table S3.

We classified each non-native taxon according to their invasion status as "casual" or "naturalized" (Richardson et al. 2000; Pyšek et al. 2004, for definitions see Table S4). Naturalized taxa were further subdivided into "invasive" or "transformers" (sensu Richardson et al. 2000, Table S4). Taxa were classified as native or non-native in each region separately because taxa native in some Arctic regions are non-native or invasive in other regions (e.g., *Lupinus nootkatensis* is native to the W Alaska Arctic region but is an established and aggressively expanding adventive in Iceland).

When available, systematic invasiveness ranking values were used to set thresholds for determining invasive and transforming e.g., invasiveness ranks of ≥ 60 in Alaska and Yukon (Carlson et al. 2008), or categories of non-native species according to their degree of establishment in Svalbard (Blackburn et al. 2011; Sandvik et al. 2019).

Pathway of introduction analysis

Within each region, putative pathways of introduction of each taxon were identified based on the available evidence, including personal observations, notes from herbarium specimens, and data available from local databases. We used the pathway categorization accepted by the Convention of Biological Diversity (CBD 2014), consisting of six major categories: (1) Release in nature, (2) Escape from confinement, (3) Transport contaminant, (4) Transport-stowaway, (5) Corridor, (6) Unaided. Within each category a number of subcategories were used (see Fig. S1 for a complete list). An additional "unknown" category was used when there was no information available to assign a taxon to a pathway. Each taxon in each region was assigned to at least one pathway; multiple pathways for the same taxa were possible, when our data clearly suggested introduction through multiple pathways. The number of introductions by each pathway was calculated for each region and the entire Arctic for three groups: (1) all non-native plant taxa, (2) naturalized taxa, and (3) invasive taxa.

Multivariate analysis

Clustering analysis (Ward method) and Multidimensional scaling (MDS) were used to investigate overall similarity/ dissimilarity of the non-native flora among Arctic regions. All calculations were conducted using R 3.5.1. (R Development Core Team 2018). Regions with less than 10 non-native taxa were excluded from these analyses to avoid distortion of the analysis caused by regions with few records of non-native taxa.

RESULTS

We documented 341 non-native vascular plant taxa in the Arctic (see Table S1 for the complete list of taxa, details on their invasion status and distribution in investigated regions). There are 188 taxa naturalized in at least one floristic region, and 153 are casual in one or more region. The total share of non-native taxa in the Arctic flora is 8.6%.¹

We excluded 38 taxa from the non-native flora of the Arctic that have been referenced previously, either due to erroneous reports or because these taxa records fell outside the geographical limits accepted in this study (i.e., they should be classified as sub-Arctic).

The 341 non-native taxa recorded for the Arctic belong to 39 families and 180 genera (see Table S5). The greatest number of non-native plant taxa in the Arctic belong to Poaceae (51 taxa), Asteraceae (48) and Brassicaceae (45). The genera richest in Arctic non-native taxa are *Rumex* (12 taxa), *Poa* (8), *Ranunculus* (7), *Trifolium* (7) and *Vicia* (7).

Chenopodium album is the most widespread non-native taxon in the Arctic (recorded in 13 of the 23 regions), followed by *Stellaria media* (11 regions), and *Fallopia convolvulus* (11 regions). Most non-native taxa have limited distributions in the Arctic (Fig. 1). The number of taxa that are naturalized follows a similar pattern, with the majority of naturalized taxa occurring in one or only a few regions. *Stellaria media* is the most widely naturalized taxon (10 regions) followed by *Chenopodium album* and *Trifolium repens* (9 regions). *Draba nemorosa* and *Puccinellia hauptiana* were naturalized in eight of the 23 regions investigated.

The total richness of non-native plant taxa varies greatly among regions, ranging from zero (in Ellesmere Land – Northern Greenland, Franz Joseph Land and Anabar–Olenyok) to 206 (in Kanin–Pechora) (Fig. 2a). The average number of non-native plant taxa per region is

¹ There are 1981 plant taxa native (excluding borderline taxa) according to Daniëls et al. (2013). See Table S1 for detailed regional data.

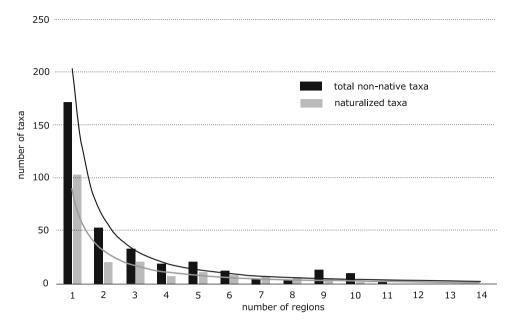


Fig. 1 Frequency distribution and corresponding trend line of non-native plant taxa (total number and naturalized taxa) recorded in Arctic regions (n = 23)

 40.39 ± 48.57 (median = 19). We observed a similar pattern for naturalized taxa (Fig. 2b); no naturalized nonnative taxa are recorded from Wrangel Island, Ellesmere Land–Northern Greenland, Anabar–Olenyok and Franz Joseph Land, while 120 taxa are naturalized in Kanin– Pechora. The average number of naturalized non-native taxa per region is 21.30 ± 26.75 (median = 13).

Plant invasion in the Arctic is limited both geographically (Fig. 2c) and in terms of the number of invasive taxa present overall (Table 1). Only three regions have taxa recorded as invasive or transformers: North Alaska–Yukon Territory, Western Alaska, and Northern Iceland. Although not determined to be invasive, the same taxa were present and regarded as casual or naturalized non-natives in other regions (with the exception of *Prunus padus* restricted to North Alaska–Yukon Territory).

Eleven taxa are considered invasive or transformers in at least one region (Table 1); most are located in North Alaska–Yukon Territory (8 taxa) and Western Alaska (5), with two taxa present in both of these regions. Two invasive taxa are present in Northern Iceland. Most Arctic invaders belong to Fabaceae (4 taxa), Asteraceae (2) and Poaceae (2). The three remaining taxa belong to Apiaceae, Plantaginaceae and Rosaceae. Three taxa are classified as transformers and they all belong to Fabaceae. The predominant life form in this group is dwarf-shrub (chamaephyte, 73%).

The results of multidimensional scaling (MDS) of the composition of non-native flora of the Arctic regions identified two geographically clustered major units: American and Asian (Fig. 3). The non-native floras of the

North American Arctic regions are clustered together, while the Asiatic parts of the Arctic (consisting of nine Siberian-Arctic regions) formed another cluster. Northern Iceland and Svalbard group within the American cluster.

We also examined the pattern of diversity of non-native taxa per km² in investigated regions (Fig. 4). The value of this index ranges from 0 (Franz Joseph Land and Ellesmere Land–Northern Greenland, Anabar–Olenyok) to 0.014 (Northern Iceland). The median value of this index is 0.000153. When the number of non-native taxa recorded for a region is scaled proportionally to the size of the region, regions such as Northern Iceland, Jan Mayen, Northern Fennoscandia, Kharaulakh, Svalbard and Kanin–Pechora display high (upper quartile) densities of non-natives (Fig. 4).

All six major pathway categories have contributed to the introduction of non-native plants into the Arctic. However, the proportion of this contribution varies greatly among pathway categories (Fig. 5). *Escape from confinement* is responsible for introduction of 48% of invasive vascular plant taxa. *Transport-stowaway* was the second most active pathway for invasive taxa (37% of all introductions) and most active pathway for naturalized taxa (contributing to the importation of 19% of naturalized taxa). *Unaided spread* and spread through *corridor* do not play a significant role in the Arctic.

Further analyses of the pathway subcategories (Fig. S1) revealed that *Seed contaminant* is the most active introduction pathway (when the total set of non-native taxa was analyzed) and contributes to 14% of all introductions. *Vehicles (car, train, etc.)* are the second most active

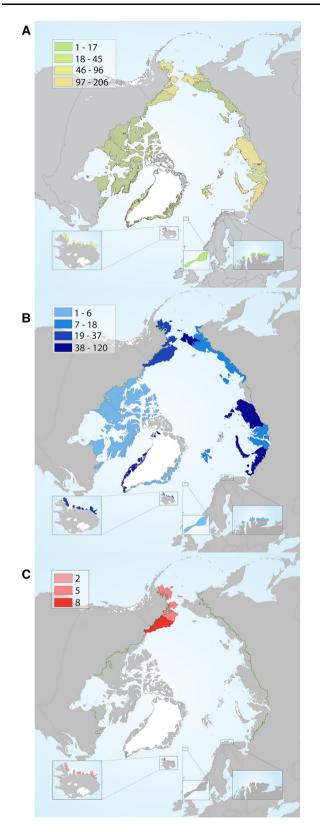


Fig. 2 Taxonomic richness of non-native plants in Arctic regions: a total non-native taxa (casual and naturalized), b naturalized taxa, c invasive taxa

pathway and contributes to 14% of all introductions. Fortythree percent of introductions are assigned to an "unknown" category, due to lack of sufficient data. The remaining pathways contribute to ca. 32% of all introductions, but the contribution of each pathway is usually equal or lower than 5% (Fig. S1).

The analyses indicate that the most active pathway for naturalized taxa is *Vehicles* which contributes to 11% of all introductions. *Seed contaminant* is the second most active pathway (8%), followed by *People and their luggage/equipment (in particular tourism)* (5%) and *Transport of habitat material* (5%). Pathway of introduction is unknown in 49% of all naturalized non-native vascular plants in the Arctic (Fig. S1).

A different picture emerges when only invasive taxa are analyzed. Here, *horticulture* is the most active pathway contributing to 26% of all introductions of invasive taxa. *Agriculture* and *Machinery/equipment* are less important, contributing to 15% of introductions each. The pathway *People and their luggage/equipment* is responsible for 11% of all introductions, while *Vehicles* and *Research and* ex situ *breeding* contribute to 7.4% of introductions each (Fig. S1). Only 4% of all invasive taxa introductions was classified as unknown.

DISCUSSION

We present a comprehensive treatment of Arctic non-native vascular plant presence, richness, naturalization and invasion status using a defined natural geographic delimitation and standardized terminology. Our study reflects the most up-to-date knowledge on non-native and invasive plants in the Arctic and represents a new baseline that will allow better understanding of future changes in the composition and distribution of the non-native flora of the Arctic. Currently, most non-native plants in the Arctic are confined to human settlements, roads and infrastructure, but with increasing propagule pressure and higher temperatures these plants might be able to invade areas beyond their current distribution limits. Data presented here differ from previous assessments in terms of the number of nonnative taxa recorded in the Arctic. For example, the Arctic Biodiversity Assessment (Daniëls et al. 2013) listed only 190 non-native taxa (both casual and naturalized) present in the Arctic. In some regions (e.g., Kanin-Pechora) the number of naturalized aliens was substantially underestimated: 52 naturalized aliens in Daniëls et al. (2013) versus 120 taxa in the present study. Furthermore, the number of casual taxa recorded by the Arctic Biodiversity Assessment for many regions with a long history of human settlement was surprisingly low: e.g., only two casual introductions

Table 1 Invasive non-native plant taxa recorded in the Arctic

Species	Family	Regions	Origin	Life form	Transformer (cf. Table S4)
Anthriscus sylvestris (L.) Hoffm. subsp. sylvestris	Apiaceae	NI	Europe, Asia	hc	
Bromus inermis Leyss.	Poaceae	AN,AW	Europe, Asia	hc	
Caragana arborescens Lam.	Fabaceae	AW	Asia	Ph	
Cirsium arvense (L.) Scop.	Asteraceae	AN	Europe, Asia	Gn	
Hordeum jubatum L.	Poaceae	AN,AW	Asia, N America	hc	
Leucanthemum vulgare Lam.	Asteraceae	AN,AW	Europe, Asia	hc	
Linaria vulgaris Mill.	Plantaginaceae	AN	Europe, Asia	hc	
Lupinus nootkatensis Donn ex Sims	Fabaceae	NI	N America	hc	+
Melilotus albus Medik.	Fabaceae	AN	Europe, Asia	hc	+
Prunus padus L.	Rosaceae	AN	Europe, Asia	Ph	
Vicia cracca L.	Fabaceae	AN,AW	Europe, Asia	hc	+

NI North Iceland, AN North Alaska-Yukon, AW Western Alaska, hc chamaephyte, Gn non-bulbous geophyte, Ph phanerophyte

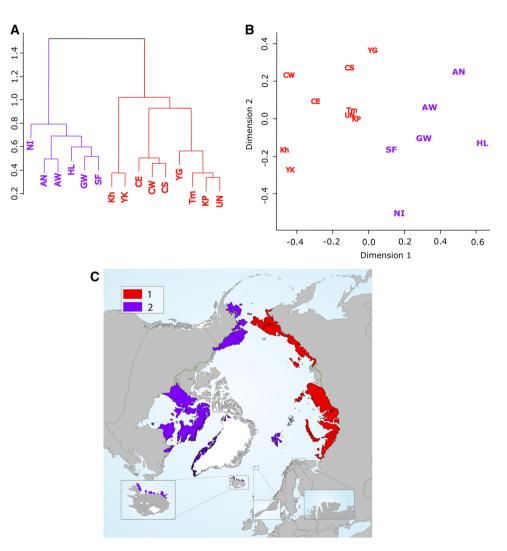


Fig. 3 Hierarchical clustering (Ward method) (a) and multidimensional scaling (Kulczynski index) (b) showing similarities/dissimilarities of analyzed regions based on non-native flora composition (total non-native flora). c Geographical distribution of identified clusters. Note that regions with a low number of non-native taxa (< 10) were omitted from the analysis

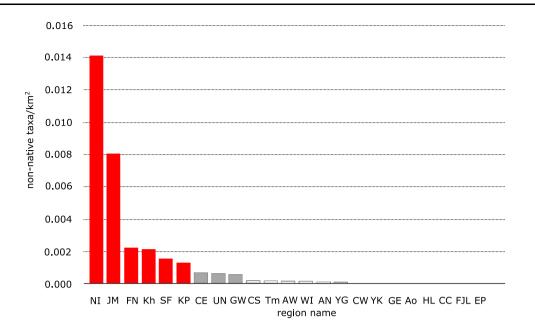


Fig. 4 Number of non-native taxa per km² in the Arctic: *NI* North Iceland, *JM* Jan Mayen, *FN* North Fennoscandia, *Kh* Kharaulakh, *SF* Svalbard, *KP* Kanin–Pechora, *CE* East Chukotka, *UN* Polar Ural–Novaya Zemlya, *GW* Western Greenland, *CS* South Chukotka, *Tm* Taimyr-Severnaya Zemlya, *AW* Western Alaska, *WI* Wrangel Island, *AN* North Alaska–Yukon Territory, *YG* Yamal-Gydan, *CW* West Chukotka, *YK* Yana–Kolyma, *GE* Eastern Greenland, *AO* Anabar–Olenyok, *HL* Hudson Bay–Labrador, *CC* Central Canada, *FJL* Franz Joseph Land, *EP* Ellesmere Land–Northern Greenland. Regions with the number of non-natives per km² within the upper quartile were marked with red

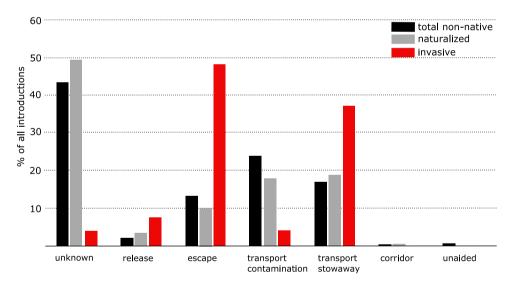


Fig. 5 Significance of introduction pathways of non-native plant taxa to the Arctic, measured by the percent of introductions through each pathway category: unknown, release in nature, escape from confinement, transport contamination, transport-stowaway, corridor and unaided

were listed from Northern Iceland and Jan Mayen by Daniëls et al. (2013) versus 62 taxa listed here.

Non-native plants can be divided into two groups: "old" non-natives or archaeophytes and "new" non-natives or neophytes (see Table S4 for definitions), which have been introduced more recently. We excluded "old" non-natives from our study in cases where sufficient evidence for their status as archaeophytes exists. For some taxa, status had to be decided by expert judgement, because few written sources are available for the history of the arctic flora before the middle of the 18th century. In some regions, however, where the distinction between "new" and "old" non-natives is unclear, some "old" non-natives may be included in our lists.

By combining pan-Arctic data, we were able to provide a robust picture of the most successful non-native vascular plants in the Arctic. We identified a set of taxa widely naturalized in the ecozone: *Stellaria media*, *Chenopodium album*, *Trifolium repens*, *Draba nemorosa*, *Puccinellia hauptiana*. However, in many cases geographically clustered regions share unique assemblages of non-native taxa. Our data indicate that the non-native flora of the Arctic is not uniform and that clear clusters of regions with similar alien flora can be recognized. Factors that could potentially contribute to this differentiation include different species' source pools and isolation in terms of historical patterns of trade.

By organizing our data in a geographic context we were able to identify regions where the processes of non-native plant naturalization and invasion are advanced, such as Alaska, Northern Iceland, and the European part of the Russian Arctic. We determined that hotspots of plant naturalization and invasion only partially match geography: invasive taxa were recorded only in two regions with confirmed occurrence of over 20 non-native taxa. We did not record invasive taxa from regions with the highest number of naturalized taxa (Kanin-Pechora, Western Greenland, Polar Ural-Novaya Zemlya). These results suggest that in many of these regions new invasive plant taxa are likely to emerge in the near future. Another possibility is that in some regions invasive taxa are present but not yet recorded, given logistical challenges of field exploration across the Arctic.

Our results indicate that the number of non-native plant taxa in the Arctic is low and that few taxa are currently perceived to be causing significant ecological alterations. This confirms the general observation that the proportion of non-natives in the polar regions is generally lower than elsewhere (Frenot et al. 2005; Alsos et al. 2015). This pattern in the distribution of non-natives in general (and non-native plants in particular) may reflect low propagule pressure in the Arctic (caused by low human activity) and the cold climate, which may prevent survival and reproduction of many non-native taxa. In fact, a large number of non-native taxa in the Arctic are restricted to hot springs in the Alaskan Arctic (Pilgrim Hot Springs on the Seward Peninsula) and to the extreme southern boundary of our area of interest with longer growing seasons; no non-native taxa have been recorded in the colder regions of northern Alaska despite large settlements and significant commerce (Carlson et al. 2015). The rate of temperature increase in the Arctic has so far been the highest in a global context, and it seems that this trend will continue in the predictable future (IPCC 2018). This has major consequences for all Arctic ecosystems leading to changes in species phenology (Alsos et al. 2013, 2015) and influencing natural distribution patterns (Elmhagen et al. 2015). Although the effect of climate change on non-native species will be complex and multi-directional (Bellard et al. 2013), we expect that the distribution of non-native plant species in the Arctic will be impacted by these major environmental changes. It seems reasonable to assume that climate niche availability for both naturalized and casual non-native plants will increase. This may in turn lead to increased persistence of casual species and promotion of naturalization and invasion. Indeed, recent studies carried out in Iceland indicate that the number of non-native plant taxa is increasing sharply (Wasowicz et al. 2013; Wasowicz 2016) and that some highly invasive species have been recorded either from the Arctic or from the bordering sub-Arctic regions (Carlson and Shephard 2007; Lassuy and Lewis 2013; Wasowicz et al. 2013; AKEPIC 2018; Sandvik et al. 2019). These observations suggest that climate change is already impacting wide areas of the sub-Arctic, where the potential pool of future Arctic invaders is constantly increasing. On the other hand, there is an opposite trend for many non-native species to disappear when inhabited places are abandoned and human activities ceased (Alsos et al. 2015). However, such changes are local and do not necessarily lead to the complete loss of a species from the territory.

We determined that plant invasion in the Arctic is currently limited to a local scale and that there are no universally successful invaders in many Arctic regions. Examining the exact factors driving the patterns of nonnative plant richness in the Arctic was beyond the focus of the present study. However, some general conclusions can be drawn from our data. It seems to be quite clear that regions with a long history of human settlement and relatively high population density are among the most impacted by non-native plant species.

A comprehensive picture of important pathways by which non-native plant species are introduced to the Arctic emerged from our study, highlighting unintentional dispersal by *escape from confinement* and *transport-stowaway* pathways. The identification of these pathways is important in developing biosecurity measures at local and regional scales. It may also help in developing strict international biosecurity measures that do not yet exist in the Arctic.

The Arctic wilderness is becoming a major tourist attraction, rapidly increasing the significance of anthropogenic disturbance as a pathway for non-native species. In some areas of the Arctic, the increase in the number of visitors is high and unprecedented. For example, in Svalbard, the number of tourists has increased sharply over the last decades, and the number of places visited by cruise passengers going ashore has more than tripled from 1996 to 2016 (MOSJ 2018). In Iceland the number of international visitors has grown from 72 600 per year in 1982 to over 2 000 000 per year in 2017 (Freðamálastofa 2018). The recent increase in the number of visitors and human population will likely contribute to increases in the number of introductions through a range of pathways.

Non-native species are only one of the many factors that are currently putting pressure on Arctic terrestrial ecosystems. It has been difficult to predict how they may affect terrestrial ecosystems in the Arctic due to the complex nature of the region, its size, and context-specific outcomes of species introductions. The Circumpolar Biodiversity Monitoring Program (CBMP) aims to overcome these limitations by developing Arctic Biodiversity Monitoring Plans and non-native plants have been identified as a focal ecological component (FEC: Christensen et al. 2013). To effectively monitor the impact of non-native species the introduction-naturalization-invasion continuum should be used as a conceptual framework (Richardson and Pyšek 2012). Close monitoring of populated places, harbors, roadsides, and other tracks for plant propagule transportation is recommended in order to detect new non-native species arriving into the Arctic. Monitoring of heavily disturbed and semi-natural plant communities will be crucial in detecting taxa that are becoming naturalized as well as early stages of invasion, which may allow for timely reaction. Main points of entry of non-native plant propagules should be identified, networks of such points established and be monitored on a regular basis. According to the Arctic Invasive Alien Species strategy and action plan (ARIAS; CAFF and PAME 2017), we have a unique opportunity for urgent and effective action necessary to protect the Arctic from invasive alien species, and common protocols for early detection and reporting of non-native species should be incorporated into CAFF's Circumpolar Biodiversity Monitoring Plan.

Acknowledgements We thank Hólmgrímur Helgason from CAFF secretariat for his help in the preparation of Figs. 2 and 3.

REFERENCES

- Abbott, R.J., and C. Brochmann. 2003. History and evolution of the Arctic flora: In the footsteps of Eric Hultén. *Molecular Ecology* 12: 299–313. https://doi.org/10.1046/j.1365-294x.2003.01731.x.
- Alsos, I.G., P.B. Eidesen, D. Ehrich, I. Skrede, K. Westergaard, G.H. Jacobsen, J.Y. Landvik, P. Taberlet, et al. 2007. Frequent longdistance plant colonization in the changing Arctic. *Science* 316: 1606–1609. https://doi.org/10.1126/science.1139178.
- Alsos, I.G., E. Müller, and P.B. Eidesen. 2013. Germinating seeds or bulbils in 87 of 113 tested Arctic species indicate potential for ex situ seed bank storage. *Polar Biology* 36: 819–830. https://doi. org/10.1007/s00300-013-1307-7.
- Alsos, I.G., C. Ware, and R. Elven. 2015. Past Arctic aliens have passed away, current ones may stay. *Biological Invasions* 17: 3113–3123. https://doi.org/10.1007/s10530-015-0937-9.
- AKEPIC. 2018. Alaska exotic plants information clearinghouse (AKEPIC). Retrieved 22 Aug, 2018, from http://accs.uaa. alaska.edu/invasive-species/non-native-plants/.
- Blackburn, T.M., P. Pyšek, S. Bacher, J.T. Carlton, R.P. Duncan, V. Jarošík, J.R.U. Wilson, and D.M. Richardson. 2011. A proposed unified framework for biological invasions. *Trends in Ecology & Evolution* 26: 333–339. https://doi.org/10.1016/j.tree.2011.03. 023.

- Bellard, C., W. Thuiller, B. Leroy, P. Genovesi, M. Bakkenes, and F. Courchamp. 2013. Will climate change promote future invasions? *Global Change Biology* 19: 3740–3748. https://doi.org/ 10.1111/gcb.12344.
- CAFF and PAME. 2017. Arctic invasive alien species: Strategy and action plan. Akureyri: CAFF. https://www.caff.is/strategies-series/415-arctic-invasive-alien-species-strategy-and-action-plan.
- Carlson, M.L., and M. Shephard. 2007. The spread of invasive exotic plants in Alaska: is establishment of exotics accelerating?. In *Meeting the challenge: Invasive plants in pacific northwestern ecosystems.* ed. Harrington, T.B. and S.H. Reichard. USDA Forest Service, Pacific Northwest Research Station, Gen. Tech. Rep. PNW-GTR-694.
- Carlson, M.L., I.V. Lapina, M. Shephard, J.S. Conn, R. Densmore, P. Spencer, J. Heys, J. Riley, and J. Nielsen. 2008. Invasiveness ranking system for non-native plants of Alaska. USDA, Forest Service, General Technical Report R10-TP-143.
- Carlson, M.L., M. Aisu, E.J. Trammell, and T. Nawrocki. 2015. Biotic Change Agents: Invasive Species. In North slope rapid ecoregional assessment. Prepared for the bureau of land management, U.S. Department of the Interior, ed. E.J. Trammell, M.L. Carlson, N. Fresco, T. Gotthardt, M.L. McTeague, and D. Vadapalli, D1–D20. Anchorage: University of Alaska Anchorage.
- CBD. 2014. Pathways of introduction of invasive species, their prioritization and management. Retrieved 22 Aug, 2018, from https://www.cbd.int/doc/meetings/sbstta/sbstta-18/official/sbstta-18-09-add1-en.pdf.
- Christensen, T., J. Payne, M. Doyle, G. Ibarguchi, J. Taylor, N.M. Schmidt, M. Gill, M. Svoboda, M. Aronsson, et al. 2013. *The Arctic terrestrial biodiversity monitoring plan.* Akureyri: CAFF.
- Conn, J.S., C.A. Stockdale, and J.C. Morgan. 2008. Characterizing pathways of invasive plant spread to Alaska: I. Propagules from container-grown ornamentals. *Invasive Plant Science and Man*agement 1: 331–336. https://doi.org/10.1614/ipsm-08-063.1.
- Conn, J.S., C.A. Stockdale, N.R. Werdin-Pfisterer, and J.C. Morgan. 2010. Characterizing pathways of invasive plant spread to Alaska: II. Propagules from imported hay and straw. *Invasive Plant Science and Management* 3: 276–285. https://doi.org/10. 1614/ipsm-d-09-00041.1.
- Conn, J.S. 2012. Pathways of invasive plant spread to Alaska: III. Contaminants in crop and grass seed. *Invasive Plant Science and Management* 5: 270–281. https://doi.org/10.1614/ipsm-d-11-00073.1.
- Daniëls, F.J.A, L.J. Gillespie, and M. Poulin. 2013. Plants. In Arctic biodiversity assessment. status and trends in Arctic biodiversity, ed. H. Meltofte, A.B. Josefson, and D. Payer. pp. 310–353. Akureyri: CAFF. http://arcticlcc.org/assets/resources/ ABA2013Science.pdf.
- Descamps, S., J. Aars, E. Fuglei, K.M. Kovacs, C. Lydersen, O. Pavlova, Å.Ø. Pedersen, V. Ravolainen, et al. 2016. Climate change impacts on wildlife in a High Arctic archipelago– Svalbard, Norway. *Global Change Biology* 23: 490–502. https:// doi.org/10.1111/gcb.13381.
- Dodet, M., and C. Collet. 2012. When should exotic forest plantation tree species be considered as an invasive threat and how should we treat them? *Biological Invasions* 14: 1765–1778. https://doi.org/10.1007/s10530-012-0202-4.
- Dukes, J.S., and H.A. Mooney. 2004. Disruption of ecosystem processes in western North America by invasive species. *Revista Chilena de Historia Natural* 77: 411–437. https://doi.org/10. 4067/s0716-078x2004000300003.
- Elmhagen, B., J. Kindberg, P. Hellström, and A. Angerbjörn. 2015. A boreal invasion in response to climate change? Range shifts and

community effects in the borderland between forest and tundra. *Ambio* 44: 39–50. https://doi.org/10.1007/s13280-014-0606-8.

- Elven, R., D.F. Murray, V.Y. Razzhivin, and B.A. Yurtsev. 2011. Annotated checklist of the Panarctic Flora (PAF): Vascular plants. Retrieved 22 Aug 2018, from http://panarcticflora.org/.
- Freðamálastofa. 2018. Fjöldi ferðamanna. Retrieved 22 Aug, 2018, from https://www.ferdamalastofa.is/is/tolur-og-utgafur/fjoldiferdamanna.
- Frenot, Y., S.L. Chown, J. Whinam, P.M. Selkirk, P. Convey, M. Skotnicki, and D.M. Bergstrom. 2005. Biological invasions in the Antarctic: Extent, impacts and implications. *Biological Reviews* 80: 45–72. https://doi.org/10.1017/s1464793104006542.
- Hulme, P.E. 2009. Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of Applied Ecology* 46: 10–18. https://doi.org/10.1111/j.1365-2664.2008. 01600.x.
- Hultén, E. 1958. The Amphi-Atlantic plants and their phytogeographical connections. *Kungliga Svenska Vetenskapsakademiens Handlingar, ser. 4b,* 7: 1–340.

IPCC 2018. Global Warming of 1.5°C. IPCC, Geneva.

- Lassuy, D.R., and P.N. Lewis 2013. Invasive species: Humaninduced. In Arctic biodiversity assessment. Status and trends in Arctic biodiversity, ed. H. Meltofte, A.B. Josefson, and D. Payer. pp. 558–565. Akureyri: CAFF. http://arcticlcc.org/assets/ resources/ABA2013Science.pdf.
- MOSJ. 2018. Miljøovervåking Svalbard og Jan Mayen. Retrieved 22 Aug, 2018, from http://www.mosj.no/no/om/.
- Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* 52: 273–288. https://doi.org/10.1016/j.ecolecon.2004.10.002.
- Pyšek, P., D.M. Richardson, M. Rejmánek, G.L. Webster, M. Williamson, J. Kirschner, P. Pyšek, and M. Rejmanek. 2004. Alien plants in checklists and floras: Towards better communication between taxonomists and ecologists. *Taxon* 53: 131. https://doi.org/10.2307/4135498.
- Pyšek, P., J. Pergl, F. Essl, B. Lenzner, W. Dawson, H. Kreft, P. Weigelt, M. Winter, et al. 2017. Naturalized alien flora of the world. *Preslia* 89: 203–274.
- Raynolds, M.K., Donald A. Walker, A. Balser, C. Bay, M. Campbell, M.M. Cherosov, F.J.A. Daniëls, et al. 2019. A raster version of the Circumpolar Arctic Vegetation Map (CAVM). *Remote Sensing of Environment* 232: 111297. https://doi.org/10.1016/j. rse.2019.111297.
- R Development Core Team. 2018. R 3.5.1. for Windows. Retrieved 22 Aug, 2018, from https://cran.r-project.org/bin/windows/base/.
- Reeves, R., C. Rosa, J.C. George, G. Sheffield, and M. Moore. 2012. Implications of Arctic industrial growth and strategies to mitigate future vessel and fishing gear impacts on bowhead whales. *Marine Policy* 36: 454–462. https://doi.org/10.1016/j. marpol.2011.08.005.
- Reichard, S.H., and C.W. Hamilton. 1997. Predicting invasions of woody plants introduced into North America. *Conservation Biology* 11: 193–203. https://doi.org/10.1046/j.1523-1739.1997. 95473.x.
- Richardson, D.M., P. Pyšek, M. Rejmanek, M.G. Barbour, F.D. Panetta, and C.J. West. 2000. Naturalization and invasion of alien plants: Concepts and definitions. *Diversity and Distributions* 6: 93–107. https://doi.org/10.1046/j.1472-4642.2000. 00083.x.
- Richardson, D.M., and P. Pyšek. 2012. Naturalization of introduced plants: Ecological drivers of biogeographical patterns. *New Phytologist* 196: 383–396. https://doi.org/10.1111/j.1469-8137. 2012.04292.x.

- Sandvik, H., D. Dolmen, R. Elven, T. Falkenhaug, E. Forsgren, H. Hansen, K. Hassel, V. Husa, G. Kjærstad, et al. 2019. Alien plants, animals, fungi and algae in Norway: An inventory of neobiota. *Biological Invasions* 21: 2997–3012. https://doi.org/ 10.1007/s10530-019-02058-x.
- Seebens, H., T.M. Blackburn, E.E. Dyer, P. Genovesi, P.E. Hulme, J.M. Jeschke, S. Pagad, P. Pyšek, et al. 2017. No saturation in the accumulation of alien species worldwide. *Nature Communications* 8: 14435. https://doi.org/10.1038/ncomms14435.
- Simberloff, D., J.-L. Martin, P. Genovesi, V. Maris, D.A. Wardle, J. Aronson, F. Courchamp, B. Galil, et al. 2013. Impacts of biological invasions: What's what and the way forward. *Trends* in Ecology & Evolution 28: 58–66. https://doi.org/10.1016/j.tree. 2012.07.013.
- Vilà, M., J.L. Espinar, M. Hejda, P.E. Hulme, V. Jarošík, J.L. Maron, J. Pergl, U. Schaffner, et al. 2011. Ecological impacts of invasive alien plants: A meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters* 14: 702–708. https://doi.org/10.1111/j.1461-0248.2011.01628.x.
- Ware, C., D.M. Bergstrom, E. Müller, and I.G. Alsos. 2012. Humans introduce viable seeds to the Arctic on footwear. *Biological Invasions* 14: 567–577. https://doi.org/10.1007/s10530-011-0098-4.
- Wasowicz, P., E.M. Przedpelska-Wasowicz, and H. Kristinsson. 2013. Alien vascular plants in Iceland: Diversity, spatial patterns, temporal trends, and the impact of climate change. *Flora Morphology, Distribution, Functional Ecology of Plants* 208: 648–673. https://doi.org/10.1016/j.flora.2013.09.009.
- Wasowicz, P. 2016. Non-native species in the vascular flora of highlands and mountains of Iceland. *PeerJ* 4: e1559. https://doi. org/10.7717/peerj.1559.
- Williamson, M., and A. Fitter. 1996. The varying success of invaders. Ecology 77: 1661–1666. https://doi.org/10.2307/2265769.

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

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