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Non-native species in the vascular flora of highlands and mountains of Iceland

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ABSTRACT

The highlands and mountains of Iceland (defined here as areas located above 400 m a.s.l) are one of the largest remaining wilderness areas in Europe. The present study was aimed to provide the first comprehensive and up-to-date data on non-native plant species from these areas. The study was aimed to answer the following questions: (1) How many non-native vascular plant species inhabit highland and mountainous environments in Iceland? (2) Do temporal trends in alien species immigration to Iceland and highland areas differ? (3) Do human disturbed and undisturbed areas within Icelandic highlands differ in terms of alien species occurrence? (4) Is spread within the highland areas a second step in alien plant colonization? and (5) Can we point out hot-spots in the distribution of non native taxa within highlands? Overall, 16 non-native vascular plant species were detected, including 11 casuals and 5 naturalized taxa (1 invasive). Results showed that temporal trends in alien species immigration to Iceland and to highland areas are similar, but it is clear that the process of colonization of highland areas is still in its initial phase. It was evidenced that non-native plants tend to occur close to man-made infrastructure and buildings including huts, shelters, road network etc. Analysis of spatio-temporal patterns showed that the spread within highland areas is a second step in non-native plant colonization in Iceland. Several statically significant hot spots of alien plant occurrences were be identified using Getis-Ord Gi* statistic and linked to human disturbance. This research suggests that human-mediated dispersal is the main driving force increasing the risk of invasion in Icelandic highlands and mountain areas.

Keywords: non-native flora, Iceland, highland, mountain flora, invasive species, invasive plant species, tourism

INTRODUCTION

It is well known that the proportion of non-native species in polar regions is very low (Elven et al., 2011; Ellis et al., 2012; Alsos et al., 2015). The total number of alien plant species in the local floras may, however, differ considerably. In the Arctic, the number of both causal and naturalized aliens grows rapidly from polar arctic desert zone (where alien species are absent) towards low Arctic floras (S Greenland, N Scandinavia and Iceland) where the proportion of non-native taxa is high (Lassuy and Lewis, 2013; Wasowicz et al., 2013). Here, non-native plants introduced during centuries of human activity have significantly influenced both the composition of local floras as well as native vegetation patterns (Elven et al., 2011; Alsos et al., 2015).
The beginning of the human impact on the vascular flora of Iceland dates back to 874 AD when the island was first settled by Norse settlers migrating across the North Atlantic. It is sure that vegetation of Iceland has changed a lot since the time of settlement. Growing anthropogenic pressure and climatic changes during so called Little Ice Age (1600-1900 AD) have led to significant alteration in the vegetation cover mainly due to erosion and desertification. However, the composition of vascular flora remained, until recently, only lightly affected mainly due to isolation by the ocean and harsh climatic conditions (Wasowicz et al., 2013).

Recently published research on non-native flora of Iceland has shown that there are significant differences in the composition of the local floras in Iceland (Wasowicz et al., 2013). The results showed that while lowland floras host great number of imported taxa, highland and mountain areas seems to be almost free of alien species. The highlands and mountains of Iceland (defined here as areas located above 400 m a.s.l), which account for ca. 40% of the country, are some of the most pristine environments in Europe due to their remoteness and harsh climate (Einarsson, 1984). The central highlands are considered the largest territories in Europe south of the Arctic Circle that have never been permanently settled by humans (Vésteinsson, 1998). Recent research have also shown that these areas play a key role in maintaining natural plant distribution patterns for many native species in Iceland (Wasowicz et al., 2014). It seems that there are two main factors responsible for low rate of colonization of these areas by non-native species: low frequency of human-mediated dispersal and prevailing climate (see Supplemental Information 1) characterized by low temperatures (annual mean temperature below 0°C), long-persisting snow cover and shortness of the vegetation period (ca.2 months on average) (Thorhallsdóttir, 1996; Thórhallsdóttir, 1998). These two constraints, however, are rapidly changing due to unprecedented increase in human activity within the highlands (Sæþórsdóttir and Saarinen, 2015) and ongoing climate warming (Wasowicz et al., 2013). Therefore the establishment and spread of alien species in the Icelandic highland areas may be expected to escalate dramatically in the near future, what may lead to a major environmental change. It has been shown that the combined effects of non-native species and climate change on biodiversity and ecosystem function can be significant and include i.a. alteration of the community composition and structure, alterations in trophic pathways and interactions, changes in native species distribution, habitat structure as well as in the evolutionary processes of native species (Mooney and Cleland, 2001; Hellmann et al., 2008; Rahel and Olden, 2008; Lassuy and Lewis, 2013).

Future changes in the flora of highland areas of Iceland will be best understood only if measured against a credible baseline. Given the fact that no attempts have been made hitherto to summarize existing data concerning non-native plant species in Icelandic highlands the present study was designed and aimed to answer the following questions:

1. How many non-native vascular plant species inhabit highland and mountainous environments in Iceland?
2. Do temporal trends in alien species immigration to Iceland and highland areas differ?
3. Do human disturbed and undisturbed areas within Icelandic highlands differ in
4. Is spread within the highland areas a second step in alien plant colonization?

5. Can we point out hot-spots in the distribution of non-native taxa within highlands?

MATERIALS & METHODS

Definitions used
The study is focused on non-native plant species as defined by Pyšek et al. (2004), which represent taxa whose presence in a given area is due to intentional or unintentional human involvement or which have arrived there without human intervention from an area where they are alien. Non-native species are further subdivided into two categories: casual and naturalized species. Casual species were defined as alien plants that may flourish and even reproduce occasionally outside cultivation in an area, but that eventually die out because they do not form self-sustaining populations, and rely on repeated introductions for their persistence. Naturalized species on the other hand, were defined as alien plants with self-sustaining populations for at least 10 years without direct human intervention (or in spite of human intervention), but rather by recruitment from seed or ramets (tillers, tubers, bulbs, fragments, etc.). Invasive alien species were included under naturalized taxa, and defined as taxa that form self-replacing populations over many life cycles, produce reproductive offspring, often in very large numbers at considerable distances from the parent and/or site of introduction, and have the potential to spread over long distances (Pyšek et al., 2012).

Plant distribution data
Data were obtained from the Icelandic Institute of Natural History. The institute has the largest repository of biodiversity data in Iceland, containing over 500,000 georeferenced records of plant species distribution. Only records of non-native taxa (Wasowicz et al., 2013) were considered for the study. Overall, 9,396 records collected between 1840 and 2014 were examined, including vouchered specimens deposited in AMNH and ICEL herbaria, field observations and literature data records (Supplemental information 2).

Spatial analyses
All georeferenced data from the database were converted into shapefiles using QGIS (QGIS Development Team, 2015). Elevation data were retrieved from digital elevation model of Iceland (20 m per pixel) downloaded from The Icelandic geoportal (http://gatt.lmi.is). Elevation in meters was then assigned to each data point using point sampling tool in QGIS. A database was developed that contained georeferenced species occurrences and elevation data. This database was queried to identify records with an altitude of ≥ 400 m a.s.l. (124 in total; Supplemental information 2).

Checklist
A checklist of non-native taxa was developed, summarizing information on taxonomy, time of residence, naturalization status, biogeographical affinities and a life form (Raunkiær, 1935). Native distribution of alien taxa was recorded at a continent scale. If the taxa were present in two continents, they were included in both totals.
Spatio-temporal trends in colonization

The year of first observation for each species record was retrieved from the database and cumulative number of species introduced and number of observations were plotted against time. Curves were plotted in SigmaPlot (Systat Software, San Jose, CA) using locally weighted regression - LOESS (Cleveland, 1979), using a sampling proportion of 0.1 and polynomial degree set to 1. Distribution maps were plotted in QGIS (QGIS Development Team, 2015).

Hot Spot Analysis

The Hot Spot Analysis (Mitchell, 2005) was employed to identify statistically significant spatial clusters within the analyzed data set. The analysis uses the Getis-Ord Gi* statistic (Ord and Getis, 1995) for each feature in a data set. The analysis works by looking at each feature within the context of neighboring features and is able to determine whether a cluster of species observations (feature with high value) is statistically significant (surrounded by other features with high values). The local sum of feature and its neighbors is proportionally compared to the sum of all features. Statistically significant Z score results when the local sum is much different than the expected local sum, and that difference is too large to be result of random chance. The Getis-Ord local statistic is given by the following equation:

\[
G^*_i = \frac{\sum_{j=1}^{n} w_{i,j} x_{i,j} - \bar{X} \sum_{j=1}^{n} w_{i,j}}{S \sqrt{\left[ \frac{\sum_{j=1}^{n} w_{i,j}^2 - (\sum_{j=1}^{n} w_{i,j})^2}{n-1} \right]}}
\]

where \(x_i\) is attribute value for feature \(j\), \(w_{i,j}\) is the spatial weight between feature \(i\) and \(j\), \(n\) is equal to the total number of features and

\[
\bar{X} = \frac{\sum_{j=1}^{n} x_j}{n}
\]

\[
S = \sqrt{\frac{\sum_{j=1}^{n} x_j^2}{n} - (\bar{X})^2}
\]

The \(G^*_i\) statistic calculated in this way is a z-score (no further calculations are needed). In case of statistically positive Z scores, the higher the Z score is, the more intense the clustering of high values (statistically significant hot spot).

10x10 km grid used in Iceland to record and map plant occurrences (Wasowicz et al., 2014) was used in hot spot analysis. Only polygons containing areas located above 400 m a.s.l. were taken into account. Number of alien species records was aggregated using Spatial Joint tool and the main analysis was performed using Hot Spot Analysis tool. All calculations were carried out using ArcGis 10.2. (ESRI, 2013) Z values for each 10x10 polygon were visualized on a map.
Spatial patterns

Presence or absence of non-native plant species in each grid cell (10 x 10 km) was determined using QGIS software (QGIS Development Team, 2015) as well as the presence/absence of human-made infrastructure (buildings, roads etc.). $\chi^2$ test was used to test whether disturbed and undisturbed grid cells differ in terms of alien species occurrence. Distance from species occurrence point to the nearest man-made object was also calculated (using QGIS software) and compared between the analyzed taxa using Kruskal-Wallis test and Nemeyri post-hoc test (Pohlert, 2014). Statistical analysis was performed using the computing environment R (R Development Core Team, 2013). GIS layers with the data concerning spatial distribution of man-made objects and roads were downloaded from The Icelandic geoportal (http://gatt.lmi.is).

RESULTS & DISCUSSION

The number of non-native taxa and their origin

Overall, 16 non-native plant taxa were recorded in the Icelandic highlands and mountain areas between 1840 and 2014 (Table 1). According to the criteria proposed by Pyšek et al. (2004), 11 taxa (69% of total non-native flora) were classified as casual aliens, while 5 taxa (31% of non-native flora) were classified as naturalized. Based on the criteria by Pyšek et al. (2012), only Lupinus nootkatensis can be classified as an invasive plant. Comparison of the geographic origin of non-native plant taxa showed that most have an European origin, constituting 66% of all non-native flora in the highlands, and 49.2% of all non-native plants in Iceland (Wasowicz et al., 2013). Also taxa of Asian and Northern American origin scored high in both in the highlands and the country as a whole. In the highlands, non-native plants from Asia accounted for 55% all alien flora, while 33% of them were from North America. The percentage of non-native plants from North America in the Icelandic highlands is significantly greater than that seen for the entire country (8.9%, Wasowicz et al. (2013).This is due to the fact that several non-native species from Northern America have been deliberately introduced into the highlands, becoming naturalized at a faster rate than other non-native species. Plants such as Lupinus nootkatensis, Deschampsia caespitosa subsp. beringensis and Salix alaxensis are good examples of this. All three species have their native range in Northern and North Western part of Northern America, where they reach sub-alpine and alpine zone as well as the arctic part of N America and inhabit environments highly similar to those found in Icelandic highlands (Argus et al., 2002; Douglas et al., 1999, 2000, 2001). Given the high level of environmental matching, these species are most likely to spread quickly and effectively in the highlands.

Currently, Alaska lupine (L. nootkatensis) is the most widespread and invasive non-native plant in the Icelandic highlands. Due to the presence of nitrogen-fixing bacteria in the roots, the species is able to increase the availability of this nutrient in the soil, which otherwise is low, like in most of arctic environments (Dowdall et al., 2005; Forbes and Jefferies, 1999; Liška and Soldán, 2004). Lupine-induced change in nutrient content may further exacerbate the problem of alien species invasion. Several experimental studies have shown that alien species are favored when an increase of nutrients are added to nutrient poor soil (Aber et al., 1989; Chapin et al., 1986). Given the fact that
native species are adapted to nutrient poor conditions in Arctic environments (Dowdall et al., 2005; Liška and Soldán, 2004), they may possess poorer competitive qualities than non-native species when faced with the increase in soil nutrient availability (Chapin et al., 1986).

Temporal trends in alien species immigration to Iceland and to highland areas

The cumulative number of first taxa records was plotted against time to examine temporal trends in alien taxa immigration to the highlands and mountain areas. The analysis showed that the trend recorded for the highlands and mountain areas is very similar to the overall trend of non-native species immigration to Iceland (Fig. 1a). It seems, however, that a steady, linear increase in the number of non-native taxa records started much later in highlands than in Iceland as a whole (Fig 1a). The same pattern is clearly visible when the number of observations of non-native plant taxa is taken into account (Fig. 1b). A clear growth trend is seen in the highlands a few decades after it started in the lowlands or Iceland as a whole. The curve for the highland areas seems to be a lot steeper than the curve plotted for the entire country (Fig. 1b). General trends characterizing non-native plant colonization show clearly that the process is still in its initial phase. Relatively low number of non-native plant species was recorded in the highland areas when compared to the rich alien flora in the lowlands (16 vs. over 300 taxa) (Wasowicz et al., 2013). This suggests that further colonization may occur, especially if climatic constraints are significantly reduced or even removed by climate change, which has been suggested by recent modeling experiments (Wasowicz et al., 2013). A sharp increase in the number of species observations after 1960, may be indicative that construction of the first large hydropower plants in the central highlands in the mid-1960s contributed to an increase alien plant colonization. The construction of these hydropower plants involved significant improvements in road infrastructure, making some areas more accessible (Sæþórsdóttir and Saarinen, 2015).

Do human-disturbed and undisturbed areas differ in terms of alien species occurrence?

χ² test confirmed that human-disturbed (with the presence of man-made objects such as roads, huts, etc) and undisturbed areas (10×10 km polygons) differ in terms of the occurrence of non-native species (χ² = 26.3301, df = 1, p < 0.001). All investigated non-native species showed clear tendency to occur within ca. 5 km from man made objects (huts, small buildings etc.) and roads (fig. 2A and 2B). It was showed that investigated taxa differed in terms of the distance from the closest man-made object (Kruskal-Wallis test chi squared = 14.2016, df =3, p = 0.002643). Phleum pratense was found to occur in the closest proximity of such infrastructure (median distance 1361 m, Fig. 2A ). Analyzed species differed also in terms of their proximity to roads (Kruskal-Wallis test chi-squared = 37.6923, df = 3, p<0.001). Deschampsia caespitosa subsp. beringensis was found to occur in the closest proximity to roads and tracks (median distance 353 m, Fig 2b).

It is clear that the distribution and spread of non-native plants is the result of complex interactions between species and environmental conditions (Richardson et al., 1994; Thomas and Moloney, 2013). Apart from adaptations to effective spread and
reproduction, potential for invasion is also determined by ecosystem conditions and human-mediated disturbance (Beans et al., 2012; Catford et al., 2012). It has been also shown that human activities as well as the density of human occupancy have positive associations with invasive plant distributions (Decker et al., 2012). Results presented here confirm these findings by showing that areas disturbed by humans differ in terms of the occurrence of non-native taxa from the areas that have not been disturbed. The presence of association between human-disturbance and the distribution of non-native plants was already suggested from the Arctic (Elven et al., 2011) but the present study is the first one showing evidence for this relationship. Icelandic highlands offer an unique perspective for research focused on interaction between human disturbance and colonization by non-native taxa for several reasons: (1) the area have never been settled by humans; (2) the impact of non-native taxa on local flora is still minimal (very limited number of alien species that are not widespread) (3) there are processes underway (see below) that are likely to change the pattern of human disturbance. Given that the present study creates a baseline for the research on non-native plants in Icelandic highlands, forthcoming changes in local flora and species distribution recorded in this area can be identified easier and analyzed closer that in many other regions of the world.

Is spread within the highland areas a second step in alien plant colonization?

Taxa naturalized in highland environments (Alopecurus pratensis, Deschampsia caespitosa subsp. beringensis, Lupinus nootkatensis, Phleum pratense and Salix alaxensis) were analyzed in order to test the hypothesis that colonization of highland habitats in Iceland can be considered as a ”second step” in the process of colonization of the island by non-native taxa. Results showed that species naturalized within highland areas, were first well established in lowland areas and subsequently started to spread within highlands (Figs.3-6). This clear spatial and temporal trend was present in all analyzed cases (4 taxa). Furthermore, all taxa naturalized in highlands and mountain areas have been recorded as naturalized in the lowlands (Wasowicz et al., 2013) and most of the casual taxa in the highlands are already naturalized in the lowlands (Wasowicz et al., 2013). This shows that colonization of highland environments in Iceland is a “second step” in the process of naturalization of the species within the country. There is no evidence available so far showing a different direction of naturalization process (i.e. a species naturalized in highlands and spreading down into lowlands). It seems that climate is one potential factor that may explain the low rate of colonization success among non-native plants in the highlands. With very few exceptions, most of the highlands and mountain areas in Iceland have a mean temperature in July less than 10°C (Einarsson, 1984), and thus can be treated as Arctic areas based on climatic criteria (Przybylak, 2002). Modeling experiments carried our recently have shown that these unfavorable conditions with low temperature and very short vegetation period restricts the growth of many species in the Icelandic highlands and mountain areas, including native (Wasowicz et al., 2014) and non-native taxa (Wasowicz et al., 2013).

Can we point out hot-spots in the distribution of non-native taxa?

Hot-spot analysis was used to identify statistically significant spatial clusters with high number of non-native species records. The analysis showed that at lest four
main spatial clusters can be identified (Fig. 8): (1) areas around Mývatn lake including Rejkjahlíð, Namafjall, Krafla volcano and north of it, (2) area of Viðidalur and Vegaskarð, (3) areas W from Vatnajökull glacier (including i.e. Landmannalaugar and Jökulheimar) as well as (4) highland areas bordering with the S part of Skagafjörður in N Iceland. Apart from these clusters a general tendency can be observed that most of non-native plants occur within the central highland, while highland and mountain areas in other parts of the country still remain almost free of non-native taxa (Fig. 8).

Fairly accessible highland areas close to Mývatn Lake (North-Eastern Iceland) have been strongly influenced by naturalized alien plant species. The climatic conditions in the north-eastern part of the country allowed human settlement and farming activities above 400 m a.s.l, facilitating the introduction of non-native plants. In contrast, areas located above 400 m a.s.l. in other parts of Iceland (e.g. the Western Fjords and Eastern Fjords) appear to be almost free of non-native plant species. This pattern of spatial occurrence can be explained by human-mediated dispersal. A closer examination of places with very high numbers of non-native species records shows that they are mostly found in areas with tourist attractions such as hot springs (e.g. Hveravellir, Laugafell) and areas with geothermal activity (e.g. Reykjahlíð, Námafjall and Krafla volcano), as well as near hiking huts and shelters along the highlands (e.g. Jökulheimar).

The road network into the highlands is another source of propagules and is accelerating the spread of non-native plants into these areas. It is clear that all occurrences in spatial cluster covering areas of Viðidalur and Vegaskarð are related either to propagule transport along the road network or to direct spread of species used for restoration purposes along roads (e.g. *D. caespitosa* subsp. *beringensis*). The study seems to confirm that human-mediated dispersal along a road network is one of the most important factors contributing to plant dispersal (von der Lippe et al., 2013).

Only one spatial cluster identified during the present study (areas around S part of Skagafjörður) seems to depart from what was said above. This cluster contains mostly occurrences of grass species commonly used in Iceland as fodder: *Alpocurus pratensis* and *Phleum pratense*. This may suggest that penetration of agricultural species into the highlands within this area might be more dynamic than in other regions.

**Future of the flora of Icelandic highlands**

In recent years Arctic wilderness environments have become a major tourist attraction, and the central highlands in Iceland are considered one of the largest remaining wilderness areas in Europe (Sæþórsdóttir and Saarinen, 2015). The increase in international visitors coming to Iceland is particularly high, where the number of tourists has grown from 72,600 in 1982 to ca. 1 million in 2014 (Sæþórsdóttir and Saarinen, 2015). It is estimated that about one third of tourists visit the central highlands (Icelandic Tourist Board, 2013). These values suggest that the influx of propagules carried on the clothing, gear and vehicles of visitors to the central highland is very likely higher than ever before and will probably continue to grow with increasing tourism. Recent studies in Antarctica and the Arctic have shown that this type of plant propagule transfer should be considered as very important source of propagules of non-native species (Whinam et al., 2005; Lee and Chown, 2009; Ware et al., 2012; Chown et al., 2012; Huiskes et al., 2014). It is highly likely that increased propagule pressure will contribute to more secondary invasions
of existing non-native species through facilitated seed transport along road networks
(von der Lippe et al., 2013), as well as through the arrival of new alien species brought
by tourists from lowland areas and abroad. An example of this is Digitaria ischaemum
(Poaceae), which seems to have spread between thermal areas in southern Iceland
via the hiking shoes of visitors. Future actions to facilitate travel through the central
highlands (e.g. construction of new road tracks or improvement of existing routes), will
inevitably increase the number of visitors, leading to a greater inflow of seeds and other
plant propagules of non-native taxa and a higher risk of invasion.

Increased colonization due to increased propagule transfer, may be further facilitated
by climatic changes. It has been shown that climatic niche of many non-native species
in Iceland will increase dramatically in forthcoming decades (Wasowicz et al., 2013).

The genetic effects of alien species are a special case of interspecific interactions,
where the alien species can transfer genes and therefore change the genetic constitution
of a native species (Gederaas et al., 2012). It seems that the contribution of hybridization
to the displacement of native by alien species is little studied. In Iceland gene transfer
between native (D.caespitosa subsp. caespitosa) and non-native (D. caespitosa subsp.
beringensis) taxa is also likely given the fact that hybridization in grasses is very common
(Stebbins, 1956). The extent of genetic contamination from foreign species in this case
has never been studied, but is probably considerable.

CONCLUSIONS

1. The presence of 16 vascular plant taxa was evidenced within Icelandic highland.

2. Temporal trends in alien species immigration to Iceland and to highland areas are
similar, but it is clear that the process of colonization of highland areas is still in
its initial phase.

3. Non-native plants tend to occur close to all types of man-made infrastructure and
buildings including huts, shelters, road network etc.

4. Spread within highland areas is a second step in non-native plant colonization in
Iceland.

5. Several statically significant hot spots of alien plant occurrences can be identified
and linked to human disturbance.

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Icelandic Institute of Natural History that was analyzed here.
<table>
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<tr>
<th>Species</th>
<th>First record</th>
<th>Last record</th>
<th>Naturalization status</th>
<th>Life form</th>
<th>Origin</th>
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<tr>
<td>1 Alnus viridis ssp. sinuata</td>
<td>2005 (1996)</td>
<td>2005</td>
<td>CAS (NAT)</td>
<td>N</td>
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<td>2 Alopecurus pratensis</td>
<td>1963 (1902)</td>
<td>2007</td>
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<td>15</td>
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<td>3 Avenula pubescens</td>
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<td>1978</td>
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<td>H</td>
<td>Eu, Asi</td>
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<tr>
<td>4 Claytonia sibirica</td>
<td>2004 (2004)</td>
<td>2004</td>
<td>CAS (CAS)</td>
<td>H</td>
<td>Asi, NAm</td>
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<td>5 Deschampsia cespitosa subsp. beringensis</td>
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<td>2012</td>
<td>NAT (CAS)</td>
<td>H</td>
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<td>1988</td>
<td>CAS (CAS)</td>
<td>T</td>
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<td>8 Lepidotheca suaveolens</td>
<td>1969 (1902)</td>
<td>1999</td>
<td>CAS (CAS)</td>
<td>T</td>
<td>Eu, NAm, Asi</td>
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<td>9 Lolium perenne</td>
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<td>10 Lupinus nootkatensis</td>
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<td>H</td>
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<td>H</td>
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Table 1. Checklist of non-native vascular plants in highland and mountain areas of Iceland. **First record** - year of the first record of the species within highland areas, year of first record in Iceland was given in brackets; **Last record** - year of the last record of the species within highland areas; **Naturalization status** given for highland areas, status in Iceland (Wasowicz et al., 2013) was given in brackets: CAS - casual, NAT - naturalized, INV - invasive; **Life form** - assigned according to Raunkiær (1935): G - geophyte, H - hemicryptophyte T - therophyte N - nano-phanerophytes P - phanerophytes; **Origin** - geographic origin of the species: Eu - Europe, Asi - Asia, NAm - North America, cult - cultivated taxon; **N** - total number of examined records.
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Figure 1. LOESS curves showing dynamics and temporal trends in non-native flora of highland and mountain areas of Iceland (1840-2014) - LOESS curves. Left Y axis (red) corresponds to the highland areas, right Y axis (blue) to the whole country. A - number of observations, B - number of species. Cumulative numbers were calculated on the basis of *per annum* new taxa records/observations.
Figure 2. Distances from the place of occurrence to the closest A. man-made objects B. roads. Statistical significance (denoted by letters) was tested using Kruskal-Wallis and Nemeyri post-hoc test
Figure 3. Distribution and temporal trends in *Alopecurus pratensis*: A. occurrences from 1902 (first record in Iceland) to 1963 (first record in highland areas), B. present-day distribution (2015), C. Loess curves showing cumulative number of observations (unique records) in Iceland and in highland areas. Left Y axis (blue) corresponds to the whole country, right Y axis (red) to the highland areas.
Figure 4. Distribution and temporal trends in *Deschampsia caespitosa* subsp. *beringensis*: A. occurrences from 1986 (first record in Iceland) to 1996 (first record in highland areas), B. present-day distribution (2015), C. Loess curves showing cumulative number of observations (unique records) in Iceland and in highland areas. Left Y axis (blue) corresponds to the whole country, right Y axis (red) to the highland areas.
Figure 5. Distribution and temporal trends in *Lupinus nootkatensis*: **A.** occurrences from 1967 (first record in Iceland) to 1980 (first record in highland areas), **B.** present-day distribution (2015), **C.** Loess curves showing cumulative number of observations (unique records) in Iceland and in highland areas. Left Y axis (blue) corresponds to the whole country, right Y axis (red) to the highland areas.
Figure 6. Distribution and temporal trends in *Phleum pratense*: **A.** occurrences from 1887 (first record in Iceland) to 1935 (first record in highland areas), **B.** present-day distribution (2015), **C.** Loess curves showing cumulative number of observations (unique records) in Iceland and in highland areas. Left Y axis (blue) corresponds to the whole country, right Y axis (red) to the highland areas.
Figure 7. Distribution and temporal trends in *Salix alaxensis*: **A.** occurrences from 1998 (first record in Iceland) to 2011 (first record in highland areas), **B.** present-day distribution (2015), **C.** Loess curves showing cumulative number of observations (unique records) in Iceland and in highland areas. Left Y axis (blue) corresponds to the whole country, right Y axis (red) to the highland areas.
Figure 8. Results of hot spot analysis showing statistically significant spatial clusters of non-native taxa within highland areas in Iceland (color scale - see details on the figure): 1 - around Mývatn lake including Rejkjahlið, Námafjall, Krafla volcano; 2 - Viðidalur and Vegaskarð, 3 - areas W from Vatnajökull glacier (including i.e. Landmannalaugar and Jökulheimar); 4 - highland areas bordering with the S part of Skagafjörður. Occurrences of non-native plant taxa were marked with green points.