Review article

New arthropod herbivores on trees and shrubs in Iceland and changes in pest dynamics: A review

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ABSTRACT
This paper is a review of the history of the introduction of arthropod herbivore species to Iceland since the beginning of the 20th century. A total of 27 new arthropod herbivore species on trees and shrubs have become established in Iceland during this period. One of the introduced pest species, the pine woolly aphid, has been considered to be the major cause of the almost total eradication of the introduced Scots pine in Iceland. The rate of introduction was found to be highest during warm periods. Outbreaks of pests in birch woodlands were also found to be most severe during warm periods. Other pest species have shown changes in outbreak patterns since 1990. The consequences of these findings for isolated native forest ecosystems and a growing forest resource in Iceland are discussed.

Keywords: Birch woodland, climate change, insect outbreaks, introduced species, native forest ecosystems

YFIRLIT
Nýjar tegundir liðfætlna á trjám og runnum á Íslandi
Í þessari grein er rakin landnámssaga nýrra liðdýrategunda sem lifa á trjám og runnum á Íslandi. Frá byrjun tuttugustu aldar til ársins 2012 hafa alls 27 slíkar tegundir numið hér land. Ein þessara tegunda, furulús, er talin hafa verið meginorsakavaldur að dauða nær allrar skógarfuru hér á landi. Hraði landnáms reyndist vera mestur á hlýskeiðum og skordýrafaraldrar í birkiskógum reyndust einnig vera mestir á hlýskeiðum. Eftir 1990 hafa orðið verulegar breytingar á faraldsfræði annarra meindýra í skógum hér á landi. Í greininni er fjallað um hugsanleg áhrif nýrra meindýra og breytinga á faraldsfræði meindýra á innlend skógarvistkerfi og vaxandi skógarauðlindir landsins.

INTRODUCTION

In many countries range expansions and increased impacts of insect pests in addition to the ongoing introduction of new ones is a growing concern and likely to have a significant effect on agriculture (Cannon 1998) and forestry (Ayres & Lombardero 2000). This has partly been attributed to increased trade (Perrings et al. 2005) and partly to global climate change (MEA 2005). A review of climate change effects on North American forests indicates that insect outbreaks will intensify as the climate gets warmer (Logan et al. 2003). These changes are likely to be greatest close to the latitudinal and altitudinal distribution limits of forest pest species (Lindner et al. 2008, Netherer & Schopf 2010). In Scandinavia the distribution of important insect pests, such as *Operoptera brumata* L. and *Epirritia autumnata* L., has been extended further north and into formerly colder regions (Jepsen et al. 2008). Furthermore, the recent unusually large outbreaks of forest pests, such as the spruce bark beetle (*Dendroctonus rufipennis* Kirby) in Alaska and mountain pine beetle (*Dendroctonus ponderosae* Hopkins) in British Columbia, have been attributed to climate change (Wermelinger 2004, Kurz et al. 2008).

Environmental and ecological conditions in Iceland

Iceland is an isolated island in the North Atlantic Ocean between 63-66°N. The climate is oceanic with a mean annual temperature (MAT) in the lowlands (<400 m a.s.l.) of 0-4 °C (Icelandic Meteorological Office 2012). The MAT has increased since 1798 (Björnsson et al. 2008), similar to the patterns found for the northern hemisphere as a whole (ACIA 2005). The warming has not been steady, however, and in Iceland there have been interchanging warm and cold periods since 1900 (Jónsson 2013). However, since 2000, the MAT has increased by >1.0 °C compared to the 1961-1990 average in Iceland, resulting in many measurable effects on Icelandic flora and fauna (Björnsson et al. 2008).

The flora and fauna of Iceland are characterized by the isolation of the country and the environmental conditions of the island. Since the end of the ice age, downy birch (*Betula pubescens* Ehrh.) has been the only native forest forming species (Aradóttir & Eysteinsson 2005). Other native trees and shrubs are: dwarf birch (*B. nana* L.), rowan (*Sorbus aucuparia* L.), aspen (*Populus tremula* L.), tea-leaved willow (*Salix phylicifolia* L.), wooly willow (*S. lanata* L.), arctic willow (*S. arctica* Pall.), juniper (*Juniperus communis* L.), burnet rose (*Rosa pimpinellifolia* L.) and glaucous dog rose (*Rosa dumalis* Bechst.) (Kristinsson 2010).

Introduction of exotic trees and shrubs

The first continuous plantation of exotic tree species in Iceland was established in 1899. However, deliberate introduction of exotic trees started as early as in the mid-1600s when a local scholar named Gisli Magnusson tried to establish several species from seed sent from Denmark. Such early introductions were on a small scale, however, and mainly for use in gardening. Few were successful and the oldest exotic trees still remaining in Iceland were planted in the late 1800s. Approximately 150 different exotic species of trees and shrubs have been tried in Iceland by the Forestry Service alone (Blöndal & Gunnarsson 1999).

During the early 20th century, forestry efforts in Iceland focused on protecting the remaining downy birch woodlands and plantation of exotic trees was relatively uncommon (Blöndal & Gunnarsson 1999). By 1940s this policy changed, and since then exotic tree species have been preferred to native ones (Sigurdsson et al. 2007). After 1990 plantations have increased dramatically and since then approx. 1500-2000 ha have been afforested annually (Sigurdsson et al. 2007). The most commonly planted tree species during the past two decades have been: downy birch, Siberian larch (*Larix sibirica* Ledeb.), Sitka spruce (*Picea sitchensis* (Bong.) Carr.), lodgepole pine (*Pinus contorta* Douglas) and black cottonwood (*Populus trichocarpa* Torr. & Gray) (Sigurdsson et al. 2007).

Arthropod herbivores on trees and shrubs in Iceland

The total number of insect species recorded in Iceland is around 1200 (Ólafsson 1991) and relatively few native arthropod herbivores feed on woody plants in the country. According to Ottósson (1983), woody plants in Iceland by the late 20th century were hosts to a total of 61 arthropod species, of which 50 were native (Appendix 1). Since Ottósson´s (1983) review was published five species have been added to the list of native arthropod herbivores (Appendix 1). In addition, unidentified eriophyid gall mites are frequently found on native willows. However, three species listed by Ottósson (1983) as native, most likely are not: *Epinotia soladriana* L. was probably introduced (Wolff 1971); whereas *Agrochola circellaris* (Hufn.) and *Eupsilia transversa* (Hufn.) are considered to be vagrant (data not shown). The total number of native arthropod species feeding on woody plants in Iceland is thus 52 species.

Records on the introduction of new forest pests in Iceland trace back to the beginning of the 20th century. However, no comprehensive review has been published on the topic. Ottósson (1983) reviewed insects on trees and shrubs; Björnsson (1968) reviewed native insects on trees and shrubs; Koponen (1980) and Ottósson (1982) reviewed herbivorous insects on birch; Halldórsson & Sverrisson (1997) reviewed diseases and arthropod pests on trees and shrubs. In addition the Icelandic Institute of Natural History keeps a record of the introduction of new arthropod pests on trees and shrubs in Iceland.

The aim of the present paper is to provide a comprehensive overview of both native and introduced arthropod herbivores on trees and shrubs in Iceland. Furthermore, changes in insect pest dynamics are addressed to evaluate whether the occurrence of such pests has been increasing in the past few decades, as has been observed in North America and Scandinavia.

HISTORICAL OVERVIEW OF INTRODUCED HERBIVORES ON TREES AND SHRUBS

Since the beginning of the 20th century, a total of 27 arthropod herbivore species of trees and shrubs have been introduced into Iceland (Table 1). The largest groups are Hemiptera (12 species), Lepidoptera (6) and Coleoptera (4). Most of these new arthropod herbivore species feed on introduced trees and shrubs (16 species), some feed both on introduced and native trees and shrubs (9), and only two feed primarily on native birch (Table 1). The majority of these new herbivores feed on sap (12 species), eight feed on leaves/needles, three on roots, two on seeds in catkins, and one on wood (Table 1).

In most cases, the means of introduction is unknown. However, three species, the pine woolly aphid (*Pineus pini* Macquart), spruce spider mite (*Oligonychus ununguis* Jacobi), and the green spruce aphid (*Elatobium abietinum* Walker), are known to have been accidentally introduced on host plants (Blöndal 1995, Ottósson 1985). In order to hinder introduction of new pest species a regulation was issued in 1990, which contains a list of quarantine organisms and host trees which are prohibited from import (Reglugerð no. 189/1990), including seedlings of most species used in Icelandic forestry.

All herbivore species listed in Ottósson´s review (Ottósson 1983; Appendix 1) were rated according to the damage they cause. The same rating has been used for species added since that time (Table 1; Appendix 1). One-third of the new herbivore species cause significant damage, four species cause serious damage. and five cause moderate damage (Table 1). The most damaging pests belong to Hemiptera and Lepidoptera (Table 1).

Two of the Hemiptera species listed in Table 1 have caused serious damage in Icelandic forestry: the pine woolly aphid and the green spruce aphid. Both species can cause tree death. The former species is primarily found on Scots and mountain pine, but occasionally

Table 1. New arthropod herbivore species on trees and shrubs in Iceland, 1907-2012

First record	Species	*Hosts*	Food/substrate	Group	Damage	Icelandic name	Ref.
1907	*Epinotia solandriana*	*Betula (Salix)*	Leaves	Lepidoptera	****	Tígulvefari	1
1928	*Operophtera brumata*	Polyphagous	Leaves	Lepidoptera	****	Haustfeti	1
1937	*Pineus pini*	*Pinus*	Bark/sap	Hemiptera	****	Furulús	2
1947	*Rhopalosiphum padi*	*Prunus*	Leaves/sap	Hemiptera	*	Hafrablaðlús	3
1948	*Oligonychus ununguis*	*Picea*	Needles	Acarii	**	Köngulingur	4
1953	*Cryptomyzus galeopsidis*	*Ribes*	Leaves/sap	Hemiptera	*	Sólberjalús	3
1958	*Brachycaudus helichrysi*	*Prunus*	Leaves/sap	Hemiptera	*	Hegglús	5
1958	*Hyperomyzus rhinanthi*	*Prunus*	Leaves/sap	Hemiptera	**	Rifslús	5
1959	*Elatobium abietinum*	*Picea*	Leaves/sap	Hemiptera	****	Sitkalús	6
1961	*Cinara pilicornis*	*Picea*	Shoot/sap	Hemiptera	**	Grenisprotalús	7
1961	*Schizoneura ulmi*	*Ulmus*, *Ribes*	Leaves/sap	Hemiptera	***	Álmlús	7
1968	*Otiorhynchus singularis*	Polyphagous	Roots	Coleoptera	*	Trjákeppur	8
1980	*Barypeithes pellidus*	Polyphagous	Leaves	Coleoptera	**	Gljárani	8
1983	*Ribautiana ulmi*	*Ulmus*	Leaves/sap	Hemiptera	**	Álmtifa	4
1983	*Philaenus spumarius*	Polyphagous	Leaves/sap	Hemiptera	*	Froðutifa	4
1987	*Otiorhyncus ovaturovatus*	Polyphagous	Roots	Coleoptera	*	Eggkeppur	8
1992	*Zeiraphera grisana*	*Pinaceae*	Needles	Lepidoptera	***	Barrvefari	8
1994	*Acantholyda erythrocephala*	*Pinus*	Needles	Hymenoptera	**	Furuþéla	8
2001	*Tipula paludosa*	Polyphagous	Roots	Diptera	**	Folafluga	8
2002	*Cinara cuneomaculata*	*Larix*	Shoot/sap	Hemiptera	*	Lerkilús	9
2004	*Epinotia nisella Salix,*	Populus	Catkins/seed	Lepidoptera	*	Reklavefari	10
2005	*Heringocrania unimaculella*	*Betula*	Leaf miner	Lepidoptera	***	Birkikemba	8
2005	*Phratora vitellinae Populus,*	*Salix*	Leaves	Coleoptera	***	Asparglytta	8
2008	*Cavariella pastinacae*	*Salix pastinacea*	Leaves/sap	Hemiptera	*	Gljávíðilús	11
2010	*Nematus ribesii*	*Ribes*	Leaves	Hymenoptera	***	Rifsþéla	8
2011	*Urocerus gigas*	*Pinaceae*	Wood	Hymenoptera	*	Beltasveðja	12
2012	*Argyresthia goedartella*	*Alnus, Betula*	Catkins/seed	Lepidoptera	*	Elrispunamölur	8

* No record of damage ** Minor damage, ***Moderate damage, **** Serious damage, can cause tree death. Damage grading according to Ottósson (1983) and own observations (data not shown).

References: 1 = Wolff 1971; 2 = Blöndal 1986; 3 = Lambers 1955; 4 = Ottósson 1983; 5 = Prior & Stroyan 1960; 6 = Bjarnason 1961; 7 = Heie 1964; 8 = Data not shown; 9 = Data not shown; 10 = Mutanen et al. 2012; 11 = Skaftason, pers. comm..; 12 = Oddsdóttir et al. 2012.

also on lodgepole pine (Ottósson 1988, Halldórsson & Sigurgeirsson 1993). The green spruce aphid is a major pest on spruces, especially North American species, causing heavy defoliation and occasionally killing trees (Carter & Halldórsson, 1998). The currant root aphid, *Schizoneura ulmi* L., occasionally causes dieback of elm, *Ulmus glabra*

Box 1. Introduction of new herbivore species into Iceland.

Introduction of new herbivore species against time is shown in Figure 1a. In Figure 1a the period from 1900 until 2012 is divided into four interchanging warm and cold climatic periods, as described by Jónsson (2013, Table 2), and two distinct periods of low vs. high activity of planting of exotic tree species (Pétursson 1999, Sigurdsson et al. 2007, Table 2). The rate of introduction was calculated for different climatic periods and linear regression carried out for each period separately by SAS statistical software (Version 9.2, SAS Inc. Cary, NC). The difference in slopes was tested by comparing their 95% confidence intervals. The average rate of introduction during Period I was 0.08 species/year; for Period III 0.20 species/year; and for Periods II and IV 0.45 species/year (Figure 1b). The introduction rate for Period I was significantly lower than that of all the other periods. This was probably primarily caused by the lack of suitable hosts, as exotic tree species were at that time very rare in Iceland (Blöndal & Gunnarsson 1999) and the first part of the period was cold. No difference was found in the introduction rate between Period II and Period IV and the rate for these periods was significantly higher than that of Period I and Period III (Figure 1b).

Table 2. Planting of exotic species, MAT and new herbivores in Iceland, 1900-2012

Period	Planting of exotic tree species[1]	MAT[2]	No. of new herbivore species
Ia: 1900-1920	Very limited	Low	2
Ib: 1921-1945	Very limited	High	1
II: 1946-1963	Intensive	High	8
III: 1964-1994	Intensive	Low	7
IV: 1995-2012	Intensive	High	9

References: 1 = Pétursson 1999, Sigurdsson et al. 2007; 2 = Jónsson 2013

Huds. (Halldórsson & Sverrisson 1997).

The larvae of two Lepidoptera species listed in Table 1, *E. solandriana* and *O. brumata*, have caused serious damage to trees and shrubs in Iceland. The former species feeds primarily on downy birch and has caused total defoliation of large areas of birch woodland and contributed to tree death (Hallgrímsson et al. 2006). The larvae of *O. brumata* feed on various broadleaved trees and shrubs and can cause serious defoliation (Ottósson 1982). Two other Lepidoptera species are of some concern. The birch leaf miner (*Heringocrania unimaculella* Zetterstedt) has caused defoliation of downy birch in South and Southwest Iceland and sporadic outbreaks of the larch tortrix (*Zeiraphera grisana* Hübner) have occurred, primarily on lodgepole pine and Siberian larch (Sverrisson & Oddsdóttir 2009). The latter species is a well-known pest in mainland Europe causing regular defoliation of European larch (*Larix decidua* Mill.) in the Alps (Baltensweiler et al. 2008).

Three other introduced species have caused significant damage. The leaf beetle *Phratora vitellinae* L. has caused local dieback of willows (data

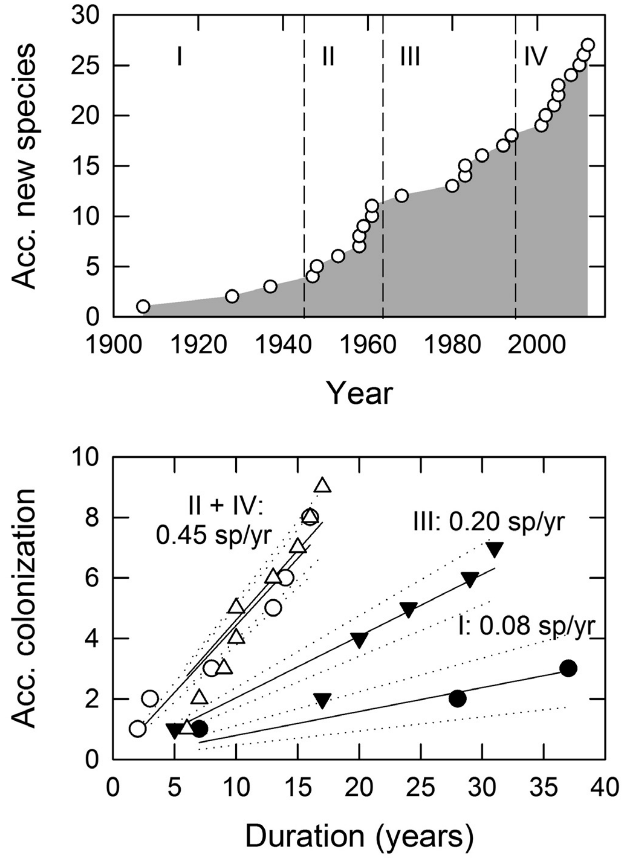

Figure 1. Upper panel: Accumulated number (open circles) of new arthropod herbivore species in Iceland, 1900-2012. Vertical lines separate four distinct periods based on forest history and climatic variation in Iceland (see text). Lower panel: Regression analysis (±95% confidence interval; dotted lines) of the colonization rate during the four periods. Average colonization rate (species/year) for significantly different periods also shown. Filled circles = Period I (degrees of freedom = 2; r^2 = 0.95; $SE_{estimate}$ = 0.007 spp/year).). Open circles = Period II (d.f. = 5; r^2 = 0.94; $SE_{estimate}$ = 0,044). Filled triangles = Period III (d.f. = 5; r^2 = 0.92; $SE_{estimate}$ = 0,024). Open triangles = Period IV (d.f. = 8; r^2 = 0.98; $SE_{estimate}$ = 0,026).

not shown); the gooseberry sawfly, *Nematus ribesii* Scopoli, has caused damage on *Ribes* spp. in gardens (data not shown); and the spruce spider mite, *Oligonychus ununguis* Jacobi, has caused damage in Christmas tree plantations (Halldórsson & Sverrisson 1997).

The rate of introduction of new herbivore species seems to be related to climate (see Box 1, Figure 1), as introduction during two warm periods was shown to be significantly higher than during colder periods. This was not unexpected as environmental conditions are one of the key factors for successful establishment of introduced species and range expansion of insects is expected to be one of the consequences of climate change (Cannon 1998). However, availability of suitable hosts and transport are also key factors in this process (Cannon 1998). Studies have shown that most introduced plant pests are introduced on host plants (Smith et al. 2007). However, changes in rates of importation of woody plant material to Iceland do not match observed changes in the introduction rate of herbivores, as the importation of woody plant material was less during 1945-1963 than during 1964-1994 (Hagstofa Íslands 1951, 1961, 1972, 1981, 1991), whereas the introduction rate of herbivores was higher during the former period (Figure 1). Therefore, we conclude that, although import of plant material is the most likely vector of introduction of new herbivore species, the observed fluctuations in the introduction rate of herbivores cannot be explained by fluctuation in import of plant material. Furthermore, only a fraction of new herbivores detected each year in Iceland become established (data not shown). Therefore, transport to Iceland does not seem to be the limiting factor for establishment of new herbivores.

Large scale planting of exotic tree species in Iceland started after World War II, and reached a level of 0.5-1 m seedlings/year around 1960 and continued at that level until 1990 (Pétursson 1999). After 1990 planting of exotic tree species increased to 2-4 m seedlings/year and have stayed at that level since then (Pétursson 1999, Sigurdsson et al. 2007). The area covered by potential host plants has therefore increased steadily since 1945 and changes in the availability of host plants must therefore be considered an unlikely explanation for the observed fluctuations in the introduction rate of herbivores.

Detection rates of introduced species may not necessarily reflect rates of introduction and establishment, as changes in the number of personnel working in forestry/entomology may affect detection rates. However, the authors are not aware of any such changes which might explain observed fluctuations in the detection of introduced herbivores.

CHANGES IN PEST DYNAMICS

Concurrent with establishment of new herbivore species since the beginning of the 20th century changes in insect pest dynamics have been observed in Iceland, both on native and introduced trees and shrubs, and both native and introduced pest species have been involved.

Insect outbreaks in the native downy birch woodlands have been known in Iceland for centuries and are frequently mentioned in old annals and institutional reports (e.g. Hallgrímsson et al. 2006). These outbreaks seem to be climate related, as 100 year records of outbreak history show that outbreak intensity has been highest during two warm periods, one during the 1920s to the 1950s, and the second after 1990 (see Box 2, Figure 2). The introduced green spruce aphid has also shown a very distinct change in outbreak patterns, which seem to be related to recently increased winter and spring temperatures (see Box 3, Figure 4).

Other native pest species have also shown changes in outbreak pattern and outbreak intensity. Since 1991 the introduced Nootka lupine *Lupinus nootkatensis* Donn (Sims) has been subject to large and prolonged insect outbreaks caused by the broom moth *Melanchra pisi* L. (Ólafsson 1999, Sigurðsson et al. 2003) and *Eupithesia satyrata* (Hübner) (Hrafnkelsdóttir et al. 2012). Concurrently, these two native insect species have been observed to

Box 2. Insect outbreaks in birch woodlands.

Insect outbreaks in birch woodlands in Iceland are described in reports of the Icelandic Forest Service. These reports describe the activities in the forest districts, tree growth, climatic conditions, insect outbreaks, etc. We used the annual reports of the forest district officer in East Iceland (Ársskýrslur skógarvarða á Austurlandi) to construct the history of insect outbreaks in the region during the period 1913-1996. However, no reports exist for six years: 1941, 1955, 1957, 1985, 1991 and 1992. Data for the first four years were supplied with information from the following annual reports of the forestry director: Bjarnason (1942; 1956; 1958) and Blöndal (1986). No data exist for the years 1991-92. By using other sources the outbreak history was constructed for the period 1997-2012, thus giving a 100 year history of outbreaks. For the period 1997 – 2004, we used outbreak data from Hallgrimsson et al. (2006) and for the period 2005-2011 from the Iceland Forest Service Annual Reports (Ársrit Skógræktar ríkisins). Similar data for other forest districts are more fragmented and therefore no attempt was made to reconstruct outbreak history for the whole of Iceland. The information given in these reports on insect outbreaks is verbal. Following is an example from the report for 1935: "Upp úr 20. júní komu mjög heitir dagar hér, braust þá maðkurinn þá út með svo miklum ákafa að stór svæði urðu lauflaus með öllu, og sýndust dökk tilsýndar sem á vetrardegi" [After 20 June the days here were very hot and then the larvae came out with such intensity that large areas became totally defoliated and looked from a distance as dark as on a winter day]. The major cause of damage during recent outbreaks has been the introduced *E. solandriana* and to a lesser extent the native *Acleris notana* (Don.) (Hallgrímsson et al. 2006). Other observations have also shown that since 1990 *E. solandriana* has been the major cause of defoliation in birch woodlands (data not shown). It is unknown which species were involved in earlier outbreaks.

These data were used to construct a score of outbreak intensity: Grade 0 = no herbivory observed; Grade 1 = some herbivory, no outbreaks; Grade 2 = small local outbreaks; Grade 3 = local intense outbreaks; and Grade 4 = widespread intense outbreaks, tree mortality observed. In most years some herbivory was observed, but mostly sub-outbreak level, i.e. Grade 1 (Fig. 2a). Outbreak frequency and intensity were low in the beginning of the 20th century, but increased in the 1930s and stayed at a relatively high level until the 1950s. During this period four years scored Grade 2, two Grade 3, and one Grade 4. Outbreak frequency and intensity were relatively low from 1960 until the 1990. During this period three years scored Grade 2 and one Grade 3. Outbreak frequency and intensity increased again after 1990 and has stayed high since then. During this period four years scored Grade 2, three Grade 3, and four Grade 4 (Figure 2a). The results coincide with fluctuations in temperature (Fig. 2b). The outbreak intensity was compared to mean annual temperature at the meteorological station at Stykkishólmur, West Iceland, by doing a non-parametric Spearman correlation with the SAS statistical software (Version 9.2, SAS Inc. Cary, NC). This station was chosen as it has the longest unbroken record in Iceland and is frequently used to represent long-term temperature development in the country (cf. Ólafsdóttir et al. 2001). Furthermore, no meteorological stations in East Iceland have unbroken records for the whole study period. In order to study the effect of long term climate changes on insect outbreak patterns we compared 5-year running averages of MAT to outbreak intensity and outbreak frequency.

The outbreak intensity in East Iceland was found to be highest during two periods: 1930-1947 and again during 1996-2011 (Figure 2a). This coincides with a period of relatively high MAT (Figure 2b). It was only during these two periods that the outbreak intensity reached Grade 4, i.e. widespread intense outbreaks where some tree mortality was observed. A significant correlation ($P<0.001$) was found between the 5-year running average of insect outbreak intensity and MAT in Stykkishólmur (Figure 2b). Using running averages in this kind of analysis is frequently done (Tenow et al. 1999) as it is a good way to relate different phenomena when there may be a lag phase between their responses, such as temperature and insect outbreaks. The length of the period used for the running average can have an effect on the result (cf. Levaniê & Eggertsson 2008), and in the present analysis a 5-year time step was selected after testing different lengths of periods (data not shown).

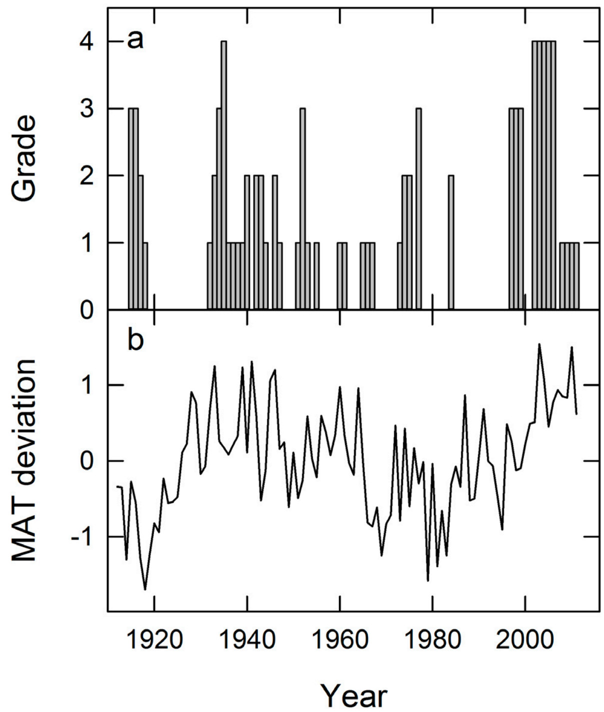

Figure 2. a) Insect pest outbreaks in birch in East Iceland (Grade 0-4). Grade 0 = no herbivory observed; Grade 1 = some herbivory, no outbreaks; Grade 2 = small local outbreaks; Grade 3 = local intense outbreaks; and Grade 4 = widespread intense outbreaks, tree mortality observed. b) Deviation from mean annual temperature in Stykkishólmur meteorological station during 1912-2011 (Icelandic Meteorological Office 2012).

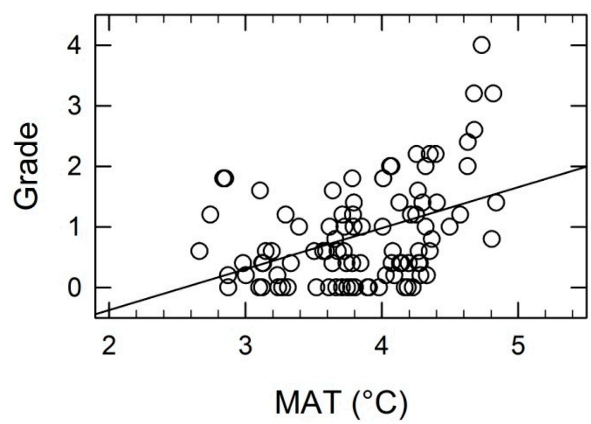

Figure 3. The relationship between outbreak intensity and mean annual temperatures during 1912-2011. MAT data from Stykkishólmur in West Iceland (Icelandic Meteorological Office 2012). Both variables are 5-year running averages. The line indicates the correlation between the two variables; Spearman r = 0.39, P<0.001, n=100.

cause significant damage on young tree plantations, especially the broom moth (Sigurðsson et al. 2003, Guðmundsdóttir 2008, Hrafnkelsdóttir et al. 2012). This is a significant change from Ottósson´s review (1983) where both species are listed as being of little importance (Appendix 1).

IMPLICATIONS OF NEW PEST INTRODUCTIONS INTO ICELAND ON FOREST ECOSYSTEMS

New pests and changes in pest dynamics can pose a serious threat to forest ecosystems, especially when new regions become open to forest pests (Cudmore et al. 2010). Since the settlement of Europeans in North America, over 450 non-indigenous insect pest species have colonized forests and urban trees in the United States (Aukema et al. 2010), inflicting significant damage on forests and forest ecosystems (Holmes et al. 2009, Aukema et al. 2010).

Icelandic ecosystems are isolated from other terrestrial ecosystems. Few native arthropod herbivore species are found on trees and shrubs (Ottósson 1983; Appendix 1) and the first grazing mammals were introduced to the island with the settlers in late ninth century AD (Blöndal & Gunnarsson 1999). In such isolated habitats, native hosts may not have evolved appropriate defenses and can be highly exposed to range shifting of herbivore species (Cudmore et al. 2010). There is some evi-

Box 3. Changes in the outbreak patterns of the green spruce aphid.

We reviewed outbreak history of the green spruce aphid in Reykjavík, as this area has the longest history of green spruce aphid outbreaks in Iceland. Up till now ten outbreaks have occurred in the Reykjavík area (Ragnarsson 1962, Ottósson 1985, Halldórsson & Kjartansson 2005, data not shown). Green spruce aphid populations have been shown to be positively related to winter and spring temperatures (Lima et al. 2008). Aphid populations are low during the summer due to the unfavorable nutritional status of host tree sap (Parry 1974) and pressure from natural enemies (Crute & Day 1990).

We compared outbreaks in Reykjavík during the period 1959-2012 to mean temperatures during Nov-April (Figure 4). All outbreaks occurred after a mild winter and spring. All outbreaks, until 2003, occurred during the autumn, whereas all outbreaks since 2003 occurred during the spring (Figure 4). Concurrent with the 2003 outbreak was a large production of alate aphids (data not shown), and high numbers of parasitized aphids were recorded (Halldórsson & Kjartansson 2005), both features hitherto almost unknown in Iceland. Average Nov-April temperatures for the autumn outbreak years were 1.6°C, for spring outbreak years 2.6°C, and for non-outbreak years 0.8°C.

Until the 2003 outbreak, outbreak patterns for Iceland differed from those of Europe where outbreaks occur during the spring (Bejer-Petersen 1962). However, outbreaks in the interior south-western United States occur during the autumn (Lynch 2004). It has been suggested that autumn outbreaks in Iceland were caused by the combination of a cool winter and spring, which hinders fast population build-up during the spring, and low summer mortality due to lack of natural enemies, which allows fast population buildup of the aphid during the autumn (Ottósson 1985, Austaraa et al. 1997). Therefore, increased winter temperatures would be expected to encourage spring outbreaks in Iceland. Recently observed parasitoid infestations in green spruce aphid in Iceland (Halldórsson & Kjartansson 2005) may, on the other hand, indicate increasing pressure from natural enemies on summer populations of the aphid, which would reduce the possibility of autumn outbreaks. If this is the case, outbreaks would only be expected after significantly milder winters and springs than before 2000. Outbreak history since 2000 suggests that this may be the case as mean Nov-April temperatures in non-outbreak years after 2000 have been 1.5°C, or similar to temperatures formerly triggering autumn outbreaks (Figure 4).

dence for this occurring in native Icelandic tree species. Studies in Finland showed that the Icelandic downy birch was more frequently attacked by mountain hares (*Lepus timidus* L.) than downy birch provenances from Finland or other birch species from Finland and Siberia (Bryant et al.1998). However, until now introduction of new species into Iceland that feed on the native birch has not had a major effect on birch ecosystems.

Introduced tree and shrub species in Iceland are also mostly free from pests that attack them in their natural habitats. In its native region lodgepole pine is host to more than 300 species of insects (Lindgren 1980), whereas only a few insect herbivores are found on lodgepole pine in Iceland (Table 1). Such systems can be highly vulnerable to the introduction of new pests and changes in pest dynamics (Lieutier 2008). There are also examples of this from Iceland. The most radical one is Scots pine, which was extensively planted in Iceland during the 1940s to 1960s (Pétursson 1999). In 1937 the pine woolly aphid was accidently introduced and spread subsequently throughout pine plantations in the country (Blöndal 1995). During the 1950s and early 1960s pine plantations in the country were devastated, leaving only a few thousand surviving trees out of 2-3 million tree seedlings that had been planted. This massive tree death has primarily been attributed to the pine woolly aphid (Ottósson 1988), but lack of suitable mycorrhizal symbionts and unfavorable climate may have also contributed to the devastation (Davíðsson 2007, Heiðarsson 2013). Similar pest-induced losses in pine plantations have been observed in East Africa and Hawaii, where the pine

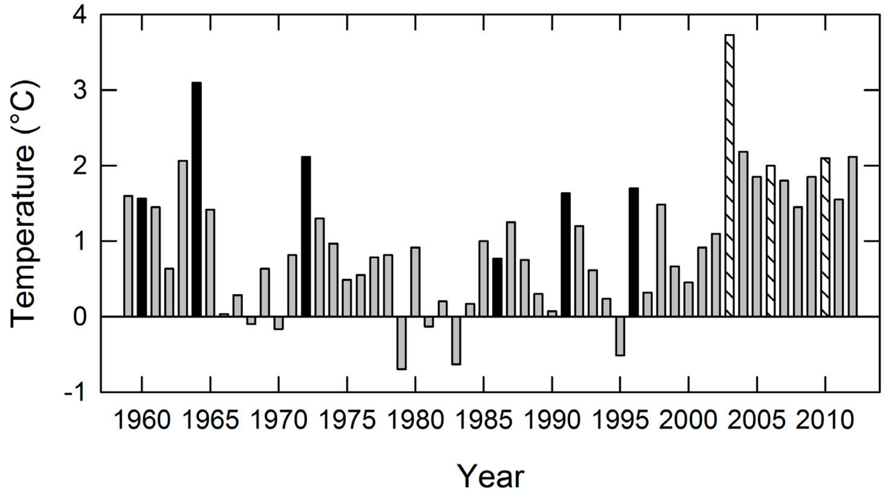

Figure 4. Green spruce aphid outbreaks and mean November-April temperature in Reykjavík during 1959-2012 (Icelandic Meteorological Office 2012). Vertical bars show mean temperature. Grey columns = no outbreak; black columns = autumn outbreaks; hatched columns = spring outbreaks.

woolly aphid has been introduced (Madoffe & Austarå 1990, Culliney et al. 1988).

The Scots pine is the only example where an exotic tree species has been more-or-less eradicated in Iceland by the introduction of an insect pest, but some introduced fungal pests have also had a major effect on the distribution of other exotic tree species. Siberian larch has been extensively planted in Iceland since the 1960s (Pétursson 1999) and is now the most common species in plantations in the country (Sigurdsson et al. 2007). Since 1990 high mortality in larch plantations in West and South Iceland has been observed. This has been attributed to the combined effect of frost damage caused by milder winters after 1985, followed by larch canker (*Lachnellula willkommii* (Hartig) Dennis) infections. It is mainly older plantations that have been attacked, and in some cases destroyed (Halldórsson & Sverrisson 1997). The Siberian larch has, however, been relatively problem free in inland North and East Iceland, where it has been most planted and the local climate is less oceanic and the winters subsequently cooler.

IMPLICATIONS OF CLIMATE-RELATED PEST DYNAMICS IN ICELAND ON FOREST ECOSYSTEMS

The MAT has increased by 0.7°C per century since 1798 in Iceland (Björnsson et al. 2008), even though the rate of increase has by no means been regular (Figure 2a). Cannon (1998), in his review on climate effects on insect pest species in the UK, stated that many pest species had shown a measurable change in their distribution and local abundance in warm years there, even if the change in availability of suitable habitats was also important.

We found clear indications for such climate related effects on the rate of introduction of new herbivores into Icelandic forest ecosystems and on outbreak patterns of native as well as introduced herbivore species. A higher MAT may also allow the establishment of forest pest species, which hitherto have been hindered in doing so by the cool climate of the island. Secondly, changes in outbreak patterns of native herbivore species may affect Icelandic ecosystems. Climate related changes in outbreak intensity in downy birch woodlands have caused significant tree death and may have substantial implications for birch ecosystems, as has been suggested for similar changes in arthropod herbivory in northern Fennoscandia (Jepsen et al. 2008). The effects of observed changes in outbreak pattern of the green spruce aphid are presently not known. Increased winter and spring temperatures may increase the outbreak frequency, but presently there is not sufficient data to support this conclusion. Increased populations of native species affecting young plantations, primarily the broom moth, are of concern for afforestation programs in Iceland.

It should, however, be kept in mind that even if insect pest frequency has increased as climate has warmed in Iceland, so has the productivity of both native and exotic tree and shrub species. Wöll (2008) showed manifold increases in downy birch productivity all around Iceland from the 1970s to the 2000s, when growing close to its altitudinal limit. Similarly, Levaniê and Eggertsson (2008) showed a significant relationship between June and July temperatures and a 110-year record of diameter growth of downy birch growing in the lowland in North Iceland. Such a positive relationship has also been found for the native rowan in North-west Iceland (Þórarinsson & Eggertsson 2012). Elevated temperatures have also been found to increase productivity of exotic trees used in Iceland, such as black cottonwood (Sigurdsson 2001) and Sitka spruce (data not shown).

Therefore, even if the negative effect of an insect pest can be substantial in the specific location where it occurs and its occurrence increases with higher temperatures (Figure 3), the positive effect of increased MAT on tree productivity is still is more important by far at a regional level. This statement is supported by a recent national estimate, which found that unmanaged downy birch forests and woodlands in Iceland are now on average accumulating dry matter at a relatively high rate (Hallsdóttir et al. 2012).

CONCLUSIONS

Our review showed increasing introductions of harmful organisms to Iceland and significant changes in herbivore dynamics and that both features seem to be climate related. This is of considerable concern. This may affect the growing timber resource, key native ecosystems and important ecosystem services such as carbon sequestration. These effects need to be counteracted. Such counteractions could involve using better adapted and genetically more diverse plant material in afforestation as well as combating introduction of new pest species. Iceland has followed a strict policy of preventing the introduction of new pest species. This includes a list of harmful organisms which may not be introduced, as well as a list of certain potential host plants which are also excluded from importation. Such limits of trade are subject to criticisms; however, Keller et al. (2007) found that there are potentially large long-term economic benefits for excluding destructive invasive species. This, together with the fact that the long isolation of native Icelandic woodlands may make them vulnerable to new pests, emphasizes the importance of combating any introduction of new forest pests to Iceland.

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Appendix 1. Native insect herbivores on trees and shrubs in Iceland

Species	Hosts	Substrate	Group	Damage	Icelandic name	Reference
Acleris maccana	*Vaccinium*	Leaves	Lepidoptera	**	Lyngvefari	1
Acleris notana	*Betula*	Leaves	Lepidoptera	**	Birkivefari	1
Apotomis sororculana	*Betula*	Leaves	Lepidoptera	*	Kjarrvefari	1
Epinotia caprana	*Salix*	Leaves	Lepidoptera	**	Blaðvefari	1
Matilella fusca	*Salix*	Leaves	Lepidoptera	*	Víðiglæða	1
Dysstroma citrata	*Vaccinium, Betula, Salix*	Leaves	Lepidoptera	*	Skrautfeti	1
Entephria caesiata	*Salix, Vaccinium, Empetrum, Calluna*	Leaves	Lepidoptera	**	Klettafeti	1
Erannis defoliaria	*Betula, Sorbus*	Leaves	Lepidoptera	**	Skógfeti	1
Eupithecia nanata	*Empetrum*	Fruit	Lepidoptera	*	Lyngfeti	1
Eupithecia satyrata	Polyphagous	Flowers, Leaves	Lepidoptera	*	Mófeti	1
Eupithecia pusillata	*Juniper*	Flowers	Lepidoptera	*	Einifeti	1
Hydriomena furcata	*Salix, Vaccinium*	Leaves	Lepidoptera	****	Víðifeti	1
Rheumaptera hastata	*Betula, Vaccinium, Salix*	Leaves	Lepidoptera	**	Birkifeti	1
Blepharita adusta	*Salix*	Leaves	Lepidoptera	*	Hringygla	1
Ceramica pisi	Polyphagous	Leaves	Lepidoptera	*	Ertuygla	1
Diarsia mendica	Polyphagous	Leaves	Lepidoptera	****	Jarðygla	1
Eurois occulta	Polyphagous	Leaves	Lepidoptera	*	Úlfygla	1
Euxoa ochrogaster	Polyphagous	Leaves	Lepidoptera	*	Brandygla	1
Syngrapha interrogationis	Polyphagous	Leaves	Lepidoptera	*	Silfurygla	1
Arctorthezia cataphracta	Polyphagous	Roots	Coccidea	*	Sekkskjalda	1
Acyrthosiphon brachysiphon	*Vaccinium, Arctostaphylos*	Sap	Aphidoidea	*		1
Betulaphis quadrituberculata	*Betula*	Sap	Aphidoidea	***	Birkiblaðlús	1
Betulaphis brevipilosa	*Betula*	Sap	Aphidoidea	*		1
Cavariella aegipodii	*Salix*	Sap	Aphidoidea	***	Svignalús	1
Cavariella archangelica	*Salix*	Sap	Aphidoidea	***	Slútlús	1
Cavariella konoi	*Salix*	Sap	Aphidoidea	***	Kvistlús	1
Ericaphis latifrons	*Vaccinium, Empetrum, Calluna*	Sap	Aphidoidea	*		1
Euceraphis punctipennis	*Betula*	Sap	Aphidoidea	**	Birkisprotalús	1
Pemphigus saliciradicis	*Salix*	Catkins	Aphidoidea	*		1
Pterocomma steinheili	*Salix*	Sap	Aphidoidea	*	Víðistofnlús	1
Egle minuta	*Salix*	Catkins	Anthomyiidae	*	Fræfluga	1
Egle pilitibia	*Salix*	Catkins	Anthomyiidae	*	Kólffluga	1
Pegomya fulgens	*Betula*	Leaves	Anthomyiidae	*		1
Semudobia betulae	*Betula*	Cones	Cecidomyiidae	**	Birkihnúðmý	1
Amauronematus amentorum	*Salix*	Cones	Tenthredinidae	**	Rekilþéla	1
Amauronematus variator	*Salix*	Leaves	Tenthredinidae	**		1
Pachynematus vagus	*Salix*	Leaves	Tenthredinidae	*		1
Pristiphora coactula	*Salix*	Leaves	Tenthredinidae	*		1
Pristiphora hyperborea	*Salix*	Leaves	Tenthredinidae	*		1
Nematus pavidus	*Salix*	Leaves	Tenthredinidae	*		1
Thrips vulgatissimus	Polyphagous	Flowers	Tripidae	*		1
Dorytomus taeniatus	*Salix, Populus*	Cones	Curculinidae	**	Víðirani	1
Otiorhyncus nodosus	Polyphagous	Roots	Curculinidae	***	Hélukeppur	1
Otiorhyncus rugifrons	Polyphagous	Roots	Curculinidae	*	Steinkeppur	1
Isochnus foliorum	*Salix*	Leaf miner	Curculinidae	*	Laufrani	1
Strophosoma melanogrammum	*Betula*	Roots	Curculinidae	**	Birkirani	1
Phratora polaris	*Salix*	Leaves	Chrysomelidae	*	Víðiglytta	1
Egle lyneborgi	*Salix*	Catkins	Diptera	*	Rekilfluga	1
Betulaphis pelei	*Betula*	Leaves/sap	Aphidoidea	*	Kvistlús	2
Orgya antiqua	Polyphagous	Leaves	Lepidoptera	**	Skógbursti	3
Otiorhyncus arcticus	Polyphagous	Roots	Coleoptera	***	Silakeppur	4
Hypnoidus riparius	Polyphagous	Roots	Coleoptera	*	Hagasmella	3

* No record of damage ** Minor damage, ***Moderate damage, **** Serious damage, can cause tree death. Damage grading according to Ottósson (1983) and own observations (data not shown).

References: 1 = Ottósson (1983); 2 = Halldórsson et al. 2002; 3 = Data not shown; 4= Halldórsson et al. 2000