

## Historic transfer of forest reproductive material in the Nordic region: drivers, scale and implications

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Large-scale transfer of reproductive material is a common phenomenon in forestry and is not only limited to recent history. Here we review the historical transfer of forest reproductive material (FRM) in Fennoscandia, the directions, their drivers, and the reported consequences for adaptation and gene pools of key forest tree species. We find that large imports of non-native FRM occurred from the 19th century onwards, partly due to prior deforestations directly associated with charcoal production for mining, extraction of timber and production of tar and pitch which have historically been important export commodities for Sweden, Norway, and Finland. In Denmark, conversion to agricultural land and the use of forests for livestock feeding was similarly important. During the subsequent reforestation efforts in Denmark, the introduction and use of non-autochthonous FRM of beech, oak and Scots pine became prevalent. Norway spruce FRM was extensively introduced to Sweden and Norway, and Scots pine FRM was imported to Sweden. Finland, in contrast, has limited records of FRM introductions. The importation of conifer seed to Norway and Sweden was initially driven by demand for large quantities of seed associated with the practice of direct seeding which prevailed until the mid-20th century. Large-scale changes to land ownership appear to have facilitated the logging of forests and subsequent seed imports for regeneration. Awareness of provenance variation in adaptive traits emerged gradually from the 19th century and led to more targeted imports of FRM to specifically improve climatic adaptation, trait qualities and growth, from the early 20th century. This, in turn, triggered the development of national regulations and guidelines from the 1930s to control the use of FRM, and marked a shift in forest legislation that had historically only been designed to control harvesting. Due to the geographical scales involved, transfers of FRM have unquestionably affected native gene pools, especially for species such as Norway spruce, Scots pine, beech, sessile and pedunculate oak, although relatively few examples of adaptive failures due to transfer have been reported.

**Keywords:** FRM, adaptation, gene pool, autochthonous species, forest trees

### Introduction

Forest products have been indispensable as sources of heat, construction materials, shelter and nutrient supply since the retreat of the ice glaciers (Steven and Carlisle, 1959). Even in the Nordic area with relatively low diversity of trees (Eiserhardt *et al.*, 2015), some species were sources of human food, including the fruits of hazel and rowan, and fodder for livestock such as the acorns of oak and beech, and leaves of lime and ash (e.g. Fægri, 1954).

Forests were mostly treated as an unlimited resource until the Bronze Age (6000–2800 BP), after which demand exceeded the local production (Fritzøger, 2005), and pollen maps have shown that large areas in western Denmark were already heavily deforested by 3000 BP (Nielsen *et al.*, 2012). The industrial use of wood for extraction of bog iron started later around 2000 years

BP and peaked at 1000 BP, leaving large areas deforested in sub-alpine regions (Solbraa, 1996). In more recent times the demand for timber, charcoal, pitch and tar increased among other factors as a result of population growth in central Europe from the 16th century. An uneven geographical distribution of forest resources, need for arable land and technological development along with an increasing demand for various forest products (Layton, 1993), led to deforestation trajectories peaking in Denmark and Norway in the 19th century (Solbraa, 1996; Rolstad and Storaunet, 2002; Fritzøger, 2005), and in mid- and southern Sweden in the 20th century (Josefsson and Östlund, 2011). Forest cover in Britain had been substantially reduced by a much earlier date (Sandmo, 1951; Steven and Carlisle, 1959). The actual reduction of forest cover varied considerably between countries and regions. In Sweden, forest cover never dropped below about 30 per cent

overall – but with deforestation that was extensive in the south and less in northern regions. Elsewhere, Iceland and Ireland became almost completely deforested (Bradshaw, 2004).

Natural regeneration was the usual means of renewing forests until the 19th century, when extensive imports of various seed sources started (Almäng, 1996; Larsen and Stupak Møller, 1997; Fritzbøger, 1999). This initiated a new paradigm for forestry where regeneration was not limited to local forest reproductive material (FRM), and FRM became a significant commodity that crossed the borders and climatic gradients of Europe. When reviewing past translocations of FRM, it is important to bear in mind that Scandinavia and Finland represent a wide range of growth conditions and potential for forest production, and this is reflected in the present distribution of forest resources (Table 1) and species of interest in the different countries.

Sweden is the biggest forest country in Europe after Russia by area, and its forestry is primarily based on native species (Anon, 2010). In contrast, Denmark has a modest forest cover, and the majority of contemporary forests are the direct result of prior large-scale reforestation activities where exotic species and foreign seed sources have played significant roles in replanting (Kjær et al., 2014). Thus, the proportion of the Danish forests which is based on foreign FRM is estimated to be as high as 65 per cent (Fritzbøger, 2005). The use of translocated FRM has varied among countries in the Nordic region, and significant knowledge on the suitability of different origins of FRM has been accumulated from practical experience as well as empirical data through systematic testing. Today it is well documented that introduced provenances do indeed differ genetically from autochthonous populations for the majority of forest tree species throughout the Nordic region. This includes Norway spruce (*Picea abies* L.), Scots pine (*Pinus sylvestris* L.) (Skrøppa, 1986; Almäng, 1996; Krakau et al., 2013), pedunculate oak (*Quercus robur* L.), sessile oak (*Q. petraea* L.) and beech (*Fagus sylvatica* L.) (Graudal et al., 1995). The geographic variation in the genetic make-up of these species implies a certain risk of poor adaptation when novel FRM replaces the autochthonous gene pool during a deforestation–afforestation event. We here review the historic supply and transfer of FRM in Scandinavia and Finland, with an emphasis on the last 150 years, with the aim of examining whether gene pools of the main autochthonous forest tree species are likely to have been

altered, primarily from an adaptive point of view. Large-scale spatial displacement of FRM can give very valuable information about robustness of species and populations of trees to climatic heterogeneity, as well as indicating their responses to future climatic changes. To put this work into an historical context, we start by analysing the main drivers and preconditions for the translocations, and review the actual transfers of Norway spruce, Scots pine, sessile oak, pedunculate oak and beech, as a basis for evaluating the effects on the gene pools of these species.

Drivers and important preconditions for the historical transfer of FRM

The economic and strategic significance of wood and timber in the region

Forestry has historically been an important business in the Nordic countries. It is likely that the timber trade started long before the Viking Age, and it has been verified that Norway supplied Iceland with round wood from about 900 A.D. and England with ship masts during the 11th and 12th century (Sandmo, 1951; Solbraa, 1996). From Medieval times the boreal forests of Fennoscandia became important in European trade. Norway and western Sweden were crucial for the timber markets in western Europe, particularly Britain and the Netherlands. From the 14th century, the timber trade had become a major income for Norway, and by the end of the 18th century timber exports provided about 25 per cent of the revenues of the state. Although Norway dominated the timber trade from about 1500 to 1850, it was exposed to a changing political landscape in Europe and there were severe depressions in the trade, for example during the war between England and Holland in the 1660s, and subsequently also during the Napoleonic wars, when Norwegian timber faced drastically increased tariffs on the English market (Sandmo, 1951). Duties from timber trade were one of the most important incomes of Norway already from the 14th century. Around 1630 Norway exported about 300 000 m<sup>3</sup> sawn timber to Holland, and possibly a similar amount to England (Sandmo, 1951). During the 18th century Norway became the largest source of timber on these markets, and timber became the most important export commodity in economic terms (Sandmo, 1951; Kent, 1955). Major river

Table 1 Basic figure on present forest resources in Scandinavia and Finland

	Total land cover (mill ha)	Total forest cover (mill ha)	Productive forest cover (mill ha)	Annual production (mill m <sup>3</sup> )	Standing volume (mill m <sup>3</sup> )					Reference
					Norway spruce	Scots pine	Beech	Oaks <sup>a</sup>	Total	
Sweden	41.3	28.4	22.9	120	1357	1299	18.2	42.8	3317	Lönnstedt and Sedjo (2012), Anon (2013)
Norway	27.5	12.2	8.2	25	335	226	0.5	6.8	745	Kucera and Næss (1999), Granhus et al. (2012)
Finland	30.4	22.8	20.3	104	703	1 157	–	–	2357	Anon (2014)
Denmark	4.6	0.61	–	6.9	22.7 <sup>b</sup>	8.7 <sup>c</sup>	33.3	12.4	128	Nord-Larsen et al. (2014)

<sup>a</sup>Both sessile oak and pedunculate oak.

<sup>b</sup>Not autochthonous in Denmark.

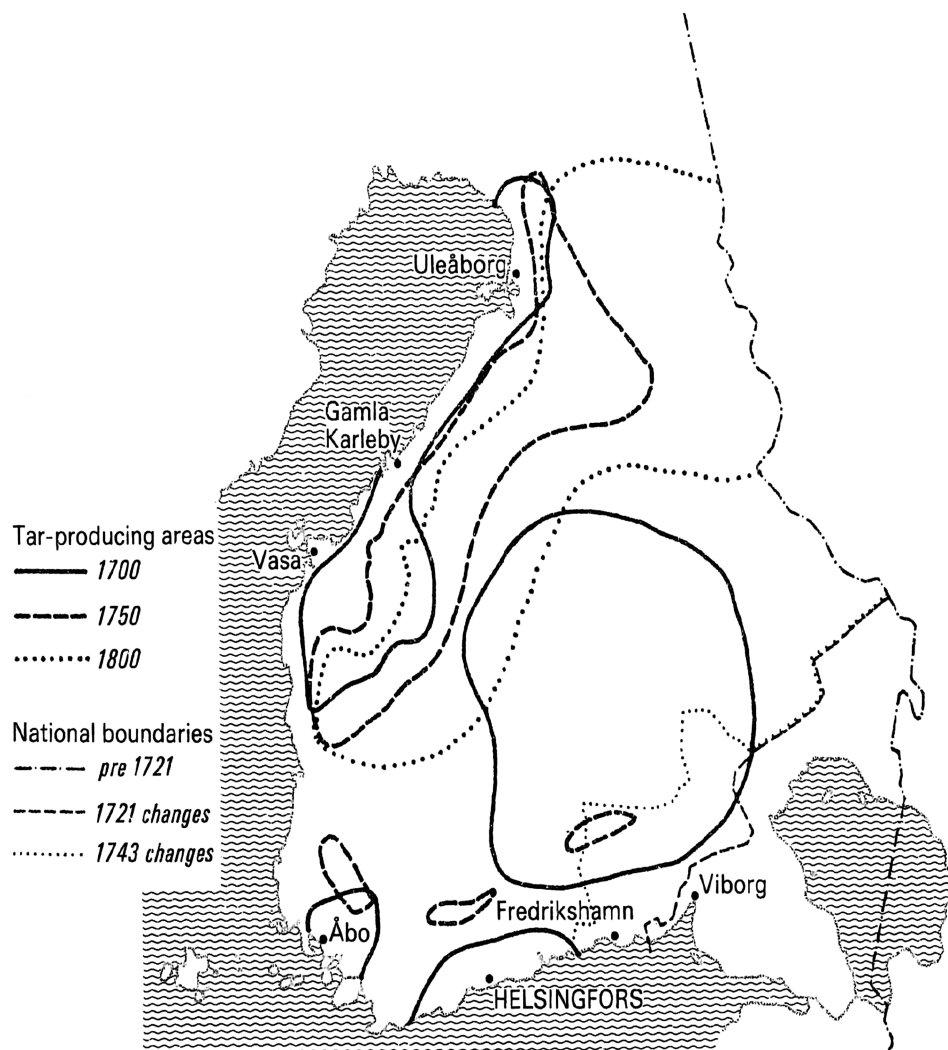
<sup>c</sup>All *Pinus* species.

systems and waterfalls close to the coast were necessary for running sawmills, and the shipments abroad were supported by a network of seaports and harbours along the Norwegian coast (Sandmo, 1951; Kent, 1955).

Sweden and Finland had less emphasis on the export of timber due to their dominance in the tar trade, and because supplies of charcoal were crucial for the iron industry. The main regions for tar production in the mid-16th century were in southern Sweden (Småland), and south-eastern Finland. About a century later tar production had increased sevenfold in these areas due to demand in Britain and the Netherlands, while supplies from Norway had tapered to become insignificant (Layton, 1993). The extensive tar burning in Sweden and Finland moved inland as the most accessible raw materials along the coastline and major rivers were depleted, a process clearly documented in Finland by 1750 and Sweden by 1822 (Figure 1) (Layton, 1993).

During the 17th century, the timber trade from the southern Baltic began to decline as accessible forests were exhausted, and focus moved to the northern and eastern Baltic. Sweden

experienced a boost in sawmilling during the industrial revolution as exports to the southern Baltic, and later to the Netherlands and Britain, became increasingly important (Layton, 1993). Mid- and northern-Sweden, termed 'Norrland', had become the major producer of sawn timber, and retained this position throughout the remainder of the century. Between 1750 and 1850 the population in northern Sweden had almost tripled (Östlund, 1995) and the increase in logging from about 1800 transformed Sweden from a peripheral country to an industrial nation (Josefsson and Östlund, 2011). Around 1870 Sweden was the world's biggest exporter of sawn wood products, with the vast majority originating from Norrland (Östlund, 2003), with wood products providing between 41.5 and 52.3 per cent of Swedish exports in the period 1880–1927. The proportion of sawn timber on the world market from Sweden was between 13 and 24 per cent in that same period, while the chemical and mechanical wood pulp ranged from 34 to 42 per cent and 23 to 29 per cent, respectively, between 1900 and 1927 (Björklund, 1988). Although the export of tar, wood and timber was fundamental for the Swedish economy, it was



**Figure 1** Spatial changes in the Finnish tar burning during the 18th century (Layton, 1993). This figure has been reproduced with kind permission from Franz Steiner Verlag GmbH.

modest compared with incomes derived from iron and copper mining, which themselves relied on domestic supplies of charcoal (Layton, 1993).

Finland has an entirely different history with strong influence of 'slash and burn' between the 12th and 20th centuries. However, regulations to limit this practice were introduced in the 1600s because of the mounting importance of wood use in ship building, mining and tar production. The role of firewood was fundamental before fossil fuels took over, and the overall consumption of firewood grew steadily concomitant with population growth until the 1950s. The war of 1808–1809 caused an economic depression, but the recovery after 1830 and associated demand for timber, ensured that the value of the sawmill industry permanently exceeded that of tar and pitch. By the end of the 19th and beginning of the 20th century the forest sector was a substantial employer, and in the 1950s about 7.5 per cent of the population of 4 million were employed somewhere in the forestry value chain (Tasanen, 2004).

The low percentage forest cover in Denmark indicates that forestry had not had the same strategic or economic significance as seen elsewhere in Scandinavia and in Finland (Fritzbøger, 1999). However, access to large size oak timber for battleship construction for the Danish Navy was of significant strategic importance. This appears to have been the driver behind plantations of oaks, often using the direct sowing method, in crown forests from 1800 onwards (Nielsen, 1975).

### Deforestation

Sweden can be divided into three regions with respect to human impact on forests. Southern Sweden, Götaland, is the most densely populated part of the country, covering approximately a fifth of the land area, and in which a large proportion of the forest was converted to arable land (Lämås and Fries, 1995). Deforestation that took place from about 1650 also left large areas of heathland, later to be reforested predominantly with Norway spruce and Scots pine of, for example, German and Polish origin (Almäng, 1996; Östlund, 1999). Reforestation at the time took place by direct seeding (Almäng, 1996), explaining the large importations seen in Table 2.

Svealand in mid-Sweden is of similar size to Götaland, and was heavily influenced by extensive charcoal production to support the copper and iron industries. Pine and spruce resources in the catchment areas of the mines were depleted in the 17th and 18th century (Layton, 1993). Norrland, mid- and northern-Sweden, was to become the main timber region of the country (Lämås and Fries, 1995). Initially, selective logging was prevalent in Norrland to supply the demand for large dimension timber, but this changed when the pulp wood industry was established and demand increased for smaller dimension logs. The rapid expansion of the sawmill industry in northern Sweden during the second half of late 18th and early 19th century (Östlund and Linderson, 1995), and the pulp wood industry in the 20th century came at a cost. A so-called timber frontier, starting in Norway in the early 19th century, quickly crossed the border to Sweden, driven by strong demand for various wood products from the industrialized western European countries (Östlund, 1995). Accordingly, the standing volume decreased steadily until c. 1940, and caused a fundamental change to the Swedish forest landscape (Josefsson and Östlund, 2011; Martinsson, 2011).

Norway also has a long history of overexploiting its forest resources. In addition to cutting for the tar and timber trade described above, firewood was used for the extraction of bog iron which peaked at about 1000 BP, for salt boiling along the coast before the 17th century, for dairy production in the alpine pastures and for production of charcoal. Excessive cutting around the centres of mining led to complete mine-centric deforestation. An example is the surroundings of the town of Røros, where Scots pine forests were depleted during the 17th century and have only started to recover in recent years. Livestock grazing hindered natural regeneration in many places, particularly in the lowlands near the coast that were exposed to grazing all year around (Sandmo, 1951; Solbraa, 1996). Forest resources were also eroded by selective cutting, which was a dominating harvest practice in spruce and pine forests until the 1920s (Solbraa, 1996). Despite the continuing overexploitation of the forest resources between the 16th and 19th century, the maintained export of timber reported above (e.g. Sandmo, 1951; Kent, 1955) implies that forest resources had not been depleted countrywide. The turning point was around 1920 when it was decided to control the harvest and ensure regeneration, and as a corollary of this, the National Forest Inventory was established in 1919 (Granhus et al., 2012). Production models were developed and harvests adjusted accordingly. From 1950 and onwards clear cuts and planting replaced selective logging and natural regeneration (Rolstad and Storaunet, 2002), and large-scale afforestation was initiated in coastal areas of western and northern Norway (Øyen, 2007). These forests started to expand both in terms of standing volume and coverage, a process which is still ongoing (Granhus et al., 2012).

By the beginning of the 20th century, 50–75 per cent the southern Finnish forests had been subjected to a regime of slash-and-burn, which had transformed the conifer woodlands to mixed forests or pure birch stands, particularly in east Finland (Tasanen, 2004). With the additional legacy of extensive tar-burning, the Finnish forests were in a poor condition. Although the turn of the century marked a change to the establishment of a forest industry, logging of the biggest trees significantly reduced the growth and quality of the remaining forests. Selective thinning from below became the prevalent management method from the last part of the 20th century (Tasanen, 2004), and is accepted as one of several management options in current forest legislation (Anon, 1996).

The deforestation in Denmark was caused by expansion of agriculture, demand for firewood and the need for liquidity among new landowners (Fritzbøger, 2005; Madsen et al., 2005). This led to an almost complete eradication of Scots pine, leaving Denmark without native conifers suitable for timber, and by 1820 the forest area was only about 2–3 per cent, compared with the present 13 per cent. However, the low forest area increased the political interest in reforestation. A lack of vegetation cover in coastal areas caused movement of sand dunes into fertile agricultural land that had catastrophic implications, including displacement of local inhabitants (Clemmensen et al., 2005). Also the abundant low productive heathland in large parts of Jutland further increased the public interest in reforestation in Denmark as part of rural development.

### Land tenure system and ownership patterns

A common feature of these countries is the large proportion of private forest ownership (Table 3). Delineation of the forest land



**Table 2** Sources of imported FRM for autochthonous forest tree species until 2014. Note that Scots pine is a native species of Denmark but was eradicated in mediaeval times

Country	Species	Time of introduction	Origins and amount of seed/seedling import	Conclusions	Area planted	Reference
Sweden	Norway spruce	First half of the 19th century to present	<u>Seeds:</u> 89 t 1889–1949 primarily from Germany (46%), Denmark (22%) and Finland (8%). 120 t 1950–1994, before 1970 primarily Czech Republic and Slovakia, after 1970 primarily Belarus and the Baltic States <u>Plants:</u> 605 mill 1950–1994, 46 mill 1994–2003	Belarus and Romanian provenances better than Swedish and central European provenances	Primarily southern Sweden	<a href="#">Almäng (1996)</a> , <a href="#">Hannerz and Almäng (1997)</a> , <a href="#">Laikre et al. (2006)</a>
	Scots pine	First half of the 19th century to present	> 40 t seed from c. 1800 to present (of which 26 t 1889–1949) from Finland (>65%), Russia, France, Norway, Poland and Germany	Poor performance of central European provenances		
Norway	Norway spruce	Late 1800 to present	Late 1800, seeds from Central Europe and Sweden. <u>Seeds:</u> 28 t 1952–2013 (mainly before 1970) from Germany (44%), Austria (39%), Sweden (4%), Czech Repl. / Slovakia (4%), Slovenia (3%), and other East European countries, Finland and Denmark (5%). Amounts to about 500 million seedlings planted in the forest and c. 16% of all seed sold in this period	German and Austrian provenances perform well on the west coast of southern Norway, poorer in inland	Western and south-eastern Norway	Norwegian Forest Seed Centre (pers. com.), <a href="#">Ording (1944)</a> , <a href="#">Skrøppa et al. (1993)</a>
Finland	Norway spruce	2005–2014	About 9 mill seedlings imported annually from Sweden/Estonia	Good performance when utilization areas properly defined. In southernmost Finland Estonian origin better than Finnish (less spring frost damage)		<a href="#">Rusanen et al. (2012)</a>
	Scots pine		Modest amounts, Swedish origin	Good performance when utilization areas are defined separately for each origin		
Denmark	Scots pine	1730 onwards	120 kg 1960–1980 from Norway (76%), Sweden (19%), Finland and West Germany 308 kg 1980–1995 primarily from western Norway	Best performance of provenances from adjacent areas (west coast of Sweden, southwest Norway, Scotland), but also from eastern Germany and the Baltic states		<a href="#">Larsen and Stupak Møller (1997)</a>
	Beech	1908 onwards	95 t 1960–1980 from Bulgaria (31%), Germany (30%), Romania (22%), the Netherlands (16%). France at an earlier stage. 155 t 1980–1995 from Germany (40%), Romania, Switzerland, Bulgaria, Belgium, Czech Republic, Slovakia, the Netherlands	Best performance of provenances from Switzerland (Zürich), Slovakia (Carpathians), secondly North Germany, the Netherlands and Denmark. Poor performance of French provenances		
	Pedunculate oak	1892 onwards	191 t 1960–1980 from the Netherlands (80%), West Germany (19%), Sweden 787 t 1980–1995 from the Netherlands (90%) Germany, Poland, Norway	Eastern Denmark: Best performance of Dutch and German materials		<a href="#">Larsen et al. (1997a)</a>
	Sessile oak		52 t 1960–1980 (origin not given) 368 t 1980–1995 from Norway (72%), Germany, France, Slovenia	Eastern Denmark: Norwegian and Dutch materials perform best Western/northern Denmark: Norwegian material perform best		

**Table 3** Current approximate distribution of forest ownership in Fennoscandia in % of forest cover

	Private	State/ municipalities	Industry/ companies	Other	Reference
Sweden	57	19 <sup>a</sup>	24	–	Eliasson (2011), Lönnstedt and Sedjo (2012)
Norway	81	13	2	4	Anon (2016a)
Finland	62	24	9	5	Anon (2016a)
Denmark	73	24	–	3	Anon (2016b)

<sup>a</sup>About 42 per cent of the forest land is owned by companies, of which one half belongs to the joint stock companies, with the state as the largest shareholder. This implies that the state forests to a large extent are privately owned in the form of a joint stock company (Lämås and Fries, 1995).

of northern Sweden began in the 18<sup>th</sup> century with the aim of clarifying ownership between the government and other owners, a process that was completed in the early 20<sup>th</sup> century (Östlund, 1995). Sweden stands out because of the high proportion of company-owned forests that dominates the northern and middle parts of the country (Lundgren, 2011), which resulted from companies established during the 19<sup>th</sup> century buying significant amounts of private forest. In contrast, the amount of company-owned forest is relatively insignificant in southern Sweden (Lönnstedt and Sedjo, 2012).

Norway has a larger proportion of private ownership than any other European country (Table 3), predominantly in southern and mid-Norway, with state ownership dominating in the north. Most private owners have small properties, and owners with areas >100 ha make up only 7 per cent, and own a total of 62 per cent of the forest area (Børset, 1985). In eastern Norway, communal forests (almenninger) also constitute a significant proportion, but such forests were much more abundant in the period prior to 1668 when a forest ordinance was issued, dividing the common forests between participating landowners (Fritzbøger, 1999). Crown land was also sold, particularly in the 17<sup>th</sup> century, but sales were modest compared with those in Denmark (Sandmo, 1951).

The large share of private ownership in Finland stems from the settlement starting in the 18<sup>th</sup> century (Tasanen, 2004). Currently the State owns 26 per cent of the forest land (Parviainen and Västilä, 2011).

In Medieval times, 15–20 per cent of the agricultural land was owned by the Crown of Denmark, about one-third each was owned by the aristocracy and by the church, and the remainder was owned by a small group of landowners. With the Reformation, the church lost the majority of its land to the Crown, and from 1800 onwards there were large-scale transfers of leased areas back into private ownership. From 1764 to 1774, the Crown sold most of its land to finance the potential threats of war. With increasing private ownership, the forests lost their legal protection against overexploitation, leading to a drastic reduction in the forest cover in subsequent decades (Fritzbøger, 2005).

### *Legally binding instruments to regulate the production, trade and use of seeds and plants*

Historically the development of forest legislation reflects the contrasting situations of individual countries regarding their own forest resources and exploitation. Norway, Sweden and Finland have had strong economic dependencies on the export of forest products, and their forest policies have generally been adapted to support free trade, at least until domestic availability was substantially threatened or depleted. Denmark, however, had insufficient forest resources to provide for domestic needs, and by around 1800, approximately one-third of Swedish timber exports were going to Denmark (Fritzbøger, 1999).

In Sweden, forest legislation from the 18<sup>th</sup> century gave the mining industry special privileges (Fritzbøger, 1999). From about 1850 there was also an emphasis on the sawmill industry, and the Floating law (1880) gave priority to the building of float-way structures for timber floating in watercourses. The largest river systems now became a central part of logging activities as they allowed floating of logs to downstream sawmills (Östlund, 1999; Törnlund and Östlund, 2002). Over several centuries, oak was protected and owned by the state because it was required for shipbuilding, especially by the Swedish navy. In the 19<sup>th</sup> century, Sweden and Norway (unified between 1814 and 1905) developed a more liberal approach, removing most restrictions on private forestry. An important consequence was that forest owners were allowed to establish commercial sawmills on their own land without restriction from 1818 onwards (Östlund, 1995; Fritzbøger, 1999). The first set of modern forestry laws in Sweden were passed in 1906 and specifically embodied 'sustainable forestry', although at the time this referred only to the sustainability of timber production, not the ecological values of forests. Ecological aspects of forestry were only considered in legislation of the late 20<sup>th</sup> century, when timber production and maintenance of biodiversity were given equal weighting (Östlund, 1995). The Swedish Forest Agency, along with other organizations, started the classification of seed stands in the 1960s (Werner, 2010), and regulations controlling the transfer and import of seed were adopted in 1980 (Skogstyrelsen, 1987).

In Norway forest overexploitation was reported frequently from the 16<sup>th</sup> century onwards, and as a result, a number of restrictions were placed on logging and the sawmill industry from the 17<sup>th</sup> century. In particular, oak, ash and beech forests in southern and southwestern Norway were protected for use in the shipbuilding industry (Solbraa, 1996). Regulations to support the mining industry were also implemented in the 17<sup>th</sup> century (Fritzbøger, 1999). Major deforestation that occurred during the union with Sweden in the 19<sup>th</sup> century (cf. Östlund, 1995; Fritzbøger, 1999, see above) was also related to the use of logging contracts from 1836 onwards. Timber buyers would overexploit forests for the duration of their contracts, which were awarded for anything between decades and several hundred years (Sandmo, 1951). The emphasis on documentation of provenances and origin of FRM are however relatively recent concerns. Formal seed collection zones for Norway spruce and Scots pine were not developed until 1939 in Norway (Skogdirektøren, 1957) and guidelines for the use of Norway spruce provenances in various parts of southern Norway were not adopted until the 1950s (Skogdirektøren, 1959, 1960). A specific regulation on the use of seeds and plants, anchored in the Forestry Act, was endorsed in 1965.

In Finland, the legal means to control expansion of settlements came in the 16th century (Tasanen, 2004). Increasing provision of timber for export, and to support mining, was at the expense of settlement expansion. Legislation of the 17th/18th century was developed with the intension of counteracting woodland clearance (Fritzbøger, 1999), and the 1734 Forest Act of Finland prohibited the burning of large trees for tar production (Tasanen, 2004). The Forest Act was revised in 1851 and was clearly influenced by the overall poor forest condition at that time. Various restrictions were included in this legislation, including control of the use of slash and burn, tar production, and specific controls of the sawmill industry. Nonetheless rights were maintained for private woodland use, provided that no harm was done. This was, however, replaced by stricter legislation in 1866 that exemplified a new direction in Finnish forest policy (Fritzbøger, 1999). The 1886 Forest Act unambiguously prohibited the 'ruining' of forests, clearly and specifically targeting long-lasting slash and burn practices. Although clear cuts were not forbidden, there was now an obligation to leave seed trees or foster regeneration, a principle that has been retained in more recent legislation. Substantial revision of the Finnish Forest Act was adopted in 2014. Whereas the previous legislation focused on timber production and benefits for the national economy, the updated act increased forest owners' freedom to manage and to set goals for their forests. The regulation of the use of seeds and plants is now based on the respective directives of the European Commission (Anon, 2000). In addition to legislative instruments, utilization areas are now given only as recommendations and are highly respected in current practice (Ruotsalainen and Haapanen, 2011).

The first Danish forest act of 1670 imposed silviculture and forest management (Tasanen 2004), but it did not prevent overexploitation during the succeeding centuries. In response to continuing deforestation in the 18th century, the Forest conservation act (Fredskovsforordningen) was adopted in Denmark in 1805 (Fritzbøger, 2005), and this terminated the split ownership of 'over-forests' and 'under-forest' (which are exposed to forest grazing), and decreed that all areas dedicated for forests should be fenced accordingly. This had immediate positive consequences, existing forests grew better and the forested areas increased steadily (Fritzbøger, 2005). The importance of selecting appropriate seed was recognized in the early 1900s, and the superiority of Dutch oak over Danish oak was demonstrated in the 1930s (Oppermann, 1932). Accordingly, the forest owners association organized a system for the approval of superior seed sources to keep track of origins in nurseries. The system was voluntary, but seedlings could only be traded as offspring from approved seed sources if they had been procured under the control scheme. The first list of approved seed stands for Denmark was issued in 1938 (Barner, 1980).

Forest administration and professional forest education was built up in the Nordic area in the 18th century. The forest administration was responsible for the control of felling and trade, tackling forest crime, performing state forest inventories, and promoting regeneration. A particular emphasis was placed on curbing illegal activities, and thus legal conflicts became a serious burden within the local and regional court systems (Fritzbøger, 1999). At the international level, the OECD scheme for FRM was established in 1967, with the aim of ensuring the documentation of origin and encouraging the production and eventual use of FRM. For member countries of, and those associated with, the EU, the trade in FRM

became regulated under a common set of EU rules (EC directive 1999/105). This regulation now controls approval and marketing, though not the subsequent use of FRM (FAO, 2014). The main purpose is to ensure compliance, while making sure that buyers get the necessary information for selecting suitable material for their purpose. Evidently, these national and international developments have contributed to an improved awareness of origin, adaptedness and the use of FRM, but detailed guidelines on how available seed sources are deployed remain national responsibilities.

## Transfer of FRM

The origin of reproductive material is relevant whenever forests are regenerated because the genetic background influences the growth and development of the trees (Kjær *et al.*, 2005). We regard autochthonous FRM as either natural regeneration and/or as artificially raised material from a local seed origin. However, the term 'local' is often ambiguous (Thomas *et al.*, 2014), and in the present review we therefore consider seed originating from the same provenance region to be local.

As shown in Table 2 non-autochthonous FRM has been crucial for Swedish forestry for about two centuries, and Norway spruce is the dominating species. In southern Sweden, the import of Norway spruce FRM has occurred over such long periods, and to such an extent, that it is now hard to identify autochthonous material with any confidence (Almäng, 1996). Even though the extent of use in Norway is modest compared with Sweden, introduced Norway spruce FRM is still important. The more open policy of Denmark with respect to non-autochthonous FRM, as well as non-native species, probably relates to prior deforestation history, and to the favourable growing conditions for a range of species (Kjær *et al.*, 2014). In fact, conifer forestry in Denmark is completely based on non-autochthonous FRM because no autochthonous seed sources are available (Larsen and Roulund, 1997; Larsen and Wellendorf, 1997). In contrast, in Finland, non-autochthonous FRM has virtually no significance, with the exception of modest amounts Estonian and Swedish Norway spruce material used in the southernmost parts of the country in recent years (Table 2). Swedish seed orchard material is also used in Finland after carefully matching the origin of the plus tree material with areas of utilization (Ruotsalainen and Haapanen, 2011).

## Norway spruce

Sweden experienced a deficit of Norway spruce seed by the 19th century, and large-scale importation took place from the 1890s, initially from Germany, Denmark and Finland. In the following century, Sweden imported more than 210 tonnes of seed and more than 600 million plants (Almäng, 1996; Laikre *et al.*, 2006). The peaks of import were primarily 1921–1923, 1974 and 1981 (Almäng, 1996), and the seeds were to be used in southern Sweden (Hannerz and Almäng, 1997). Regeneration of Norway spruce and Scots pine in Norrland following the 'timber frontier' in the 19th century was predominantly natural. During the 19th century, it became obvious that there were large variations among populations of Norway spruce and Scots pine in various adaptive traits. The central European provenances of Norway spruce used from the middle of the 19th century (Persson and Persson, 1992; and references therein) were found to be less frost

hardy and of poorer quality than autochthonous provenances, and were therefore discarded. On the basis of the results from research trials, interest shifted towards the eastern part of the distribution from the 1950s, particularly provenances from Belarus, but also Romania and the Baltic States (Almäng, 1996; Hannerz and Almäng, 1997) (Table 2). Tree breeding started in the 1940s with the selection of plus-trees and establishment of seed orchards. When irregular flowering in Norway spruce seed orchards resulted in a lack of seed in southern Sweden, it was compensated for mainly by import from Belarus. The general preference for Belarus provenances is due to their rapid growth, but also the late budburst that makes them less affected by late spring frosts (Hannerz and Almäng, 1997).

In Norway, the proportion of forest regenerated by planting and direct seeding was marginal until even-aged forestry was introduced in the 1920s and 1930s. Organized seed harvesting started in the 1880s, but seed was transferred more or less randomly across the country, prompting Ording (1944) to denote the period before 1930 as 'a dark chapter' for forest seed supply. Seed were also imported from Sweden and central Europe in this period (Table 2). Although information on provenance variation became available in the very early 1900s, this was not translated into guidelines for use in forestry until the 1930s due to the lack of organized forest research (Ording, 1944; and references therein). When clear-cutting and even-aged forestry became the prevailing practice from the 1950s, planting increased dramatically and peaked during the 1960s, when about 100 million seedlings were planted annually (Figure 2). About 20 per cent of the seedlings planted between 1952 and 1990 originated from imported seed, particularly of central European origin (Table 2). Seed consumption from the late 1980s onwards depended on seed sources from the Norwegian gene pool. In recent decades, imported seed has only been used for afforestation on the west coast of southern Norway.

During the 19th century and up to the 1950s, Norway spruce was almost completely naturally regenerated in Finland. After the Second World War planting expanded, notably due to the

higher demand for wood and increased logging, and required some imports from Estonia and Sweden (Tasanen, 2004; Rusanen *et al.*, 2012) (Table 2). Tree breeding started in the 1940s, and first generation, large-scale seed orchards were established in the 1960s and 1970s. However, the use of spruce seed orchard seed has so far been limited because of irregular flowering and insufficient seed production.

Norway spruce is not native to Denmark, but was extensively introduced from the 1760s and is presently a dominant species in Danish forestry (Larsen and Wellendorf, 1997).

### Scots pine

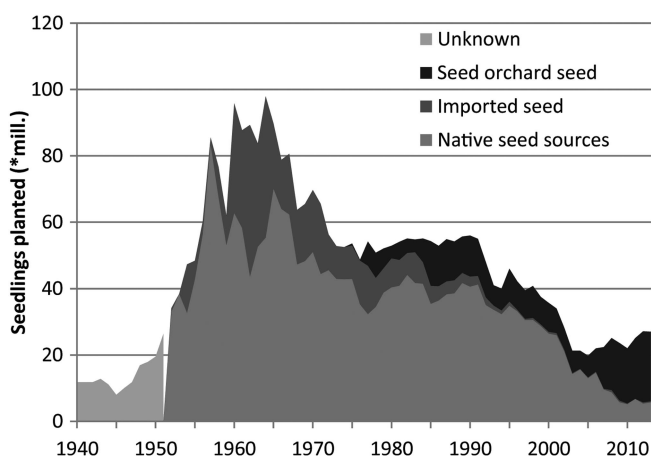
In Sweden, importation of Scots pine seeds began early in the 19th century, when it was no longer possible to satisfy the demand for seed using domestic supplies. Up to the present, more than 40 tonnes of seeds have been imported, and the period 1889–1949 represents a maximum in which 26 tonnes of seed were imported (Table 2). At least 65 per cent of the seeds had Finnish origin, but Russian, French, Norwegian, Polish and German sources were also used (Hannerz and Almäng, 1997). Seeds from Germany were used in southern Sweden early in the 19th century, but these were poorly adapted to the climate, resulting in the decline of about 20 000 ha of Scots pine forest, and a significant economic loss (Wibeck, 1912). During the early 1950s Wilhelm Eiche established a countrywide provenance series in Sweden with Scots pine, demonstrating that southward transfer of northern provenances could increase survival (e.g. Persson and Ståhl, 1993). Thus, translocation of Scots pine has been used actively to counteract climatic damage, e.g. by the use of Finnish provenances in northern Sweden (Hannerz and Almäng, 1997).

The import of Scots pine FRM to Norway has been negligible. Finland has introduced small amounts of Scots pine seed from Sweden (Table 2), and its use has been controlled by the authorities with the aim of matching FRM with the deployment areas in question.

Reintroduction of Scots pine to Denmark took place from about 1730, and later from 1900. The results depended strongly on the provenance, trait in question (stem form, growth potential) and growing site. Scots pine is prone to climatic injuries following transfers, even over short distances (Øyen *et al.*, 2006), and its performance in Denmark is usually best in provenances from the west coast of Sweden and southwest of Norway when grown on sandy soils, or from the Baltic area when grown on fertile soil (Larsen and Stupak Møller, 1997). Conversely, provenances from Finland, Scotland and Germany were less successful. The first clonal seed orchard based on selected trees of imported origin was established in the 1950s, and during 1960–1995 the domestic production of seeds amounted to 75–78 per cent of consumption. Import during this period was primarily from southwestern Norway (Larsen and Stupak Møller, 1997).

### Beech

In the Nordic region, beech has commercial relevance only in Denmark and, to some extent, in southernmost Sweden. Due to irregular seed years and inadequate seed storage techniques, it was for many years not possible to cover demand with domestic production in Denmark. Provenance trials indicated that sources towards the Carpathian Mountains would improve stem form



**Figure 2** Amount and origin of Norway spruce seedlings planted in Norway in the period 1952–2013. The seed orchards are primarily based on the native Norwegian gene pool. The total number of planted seedlings between 1940 and 1952 varied between 10–20 million, and the proportion of imported seed during this time interval is not known (The Norwegian Forest Seed Station, unpublished).



and production. Substantial imports of seeds from areas in Switzerland, Germany, Slovakia and the Czech Republic that had been tested under Danish conditions, as well as non-tested sources from eastern Europe, were therefore undertaken from the beginning in the 20th century (Table 2) (Larsen *et al.*, 1997b). During 1960–1980 and 1980–1995, imports constituted 86 and 74 per cent of the total seed consumption, respectively. The situation changed in the 1990s when new seed storage technology enabled storage of beech seed for multiple years, allowing domestic supply to be provided by seed collected during mast seed years (Ditlevsen, 1998). As a result, imports were reduced to less than 20 per cent of consumption during 1995–2008. However, a proportion of the seed collected from approved beech seed sources in Denmark do not represent the native genetic resource of the country, because many approved beech seed sources are based on introduced provenances. On the other hand, the overall impact of imports on the autochthonous gene pool in Denmark is less than the above data indicates, because a large part of the beech forest has traditionally been regenerated by natural seed fall rather than planting. In Sweden, local provenances and natural regeneration of beech have mostly been used, but in years with lower domestic availability, it has been necessary to import seed from neighbouring countries, especially Denmark, Germany and Poland, as well as the Netherlands and Switzerland.

## Oaks

In the Nordic context, oaks have commercial relevance only for Denmark and to a minor extent for Sweden. In Denmark, oaks are almost always regenerated by planting, and as with beech, production of oak timber has relied heavily on imports of seed to supplement domestic production. Imports took place from late in the 19th century, and during 1960–1980 and 1980–1995 imported pedunculate oak seed constituted 85 and 69 per cent of the total consumption, respectively. Provenances from the Netherlands and Germany dominated (Table 2). Several of the Danish approved pedunculate oak seed stands are of introduced origin, because many of the best Danish seed sources in terms of stem form are non-autochthonous (Larsen *et al.*, 1997c). For Sessile oak, imports accounted for approximately all seed consumption during 1960–1995, but were reduced to 55–75 per cent during 1995–2007 (Proschowsky and Jørgensen, 2015). The majority of the seed was imported to Denmark from Norway and Germany (Table 2), and Norwegian material is preferred due to good performance in Danish growth conditions (Larsen *et al.*, 1997c). Generally, the combination of seed deficit and a preference for non-autochthonous seed sources has led to a situation where a very large proportion of Danish oak forests are based on introduced FRM. In Sweden, some import of pedunculate oak seed has taken place from neighbouring countries during the periods of seed deficiency.

## Effects of translocations on the genetic resources in the Nordic forests

We have shown that deforestation events have long historical roots and have taken place to varying extents across Scandinavia and Finland. With the exception of Finland, the following reforestation efforts often involved large-scale use of introduced FRM, and the effect of these translocations on the native gene pool depends

on a number of factors, such as the amount and duration of introduction, and genetic distinctness of the translocated FRM. Also the regeneration method matters. Up to about 1950, seed was sown directly in the forest in Sweden, whereas planting dominated completely thereafter (Bradshaw, 2004), and while 1 kg seed is sufficient to regenerate 1–3 ha with direct sowing, 25–50 ha can be reforested by planting using the same amount of seed (Hannerz and Almäng, 1997). For Sweden the 1950s was therefore a watershed, with much higher genetic impact of the FRM used after than before this time. The majority of Norway spruce FRM imported to Sweden, and almost all imported to Norway, took place after planting had become the dominant regeneration method (Table 2, Figure 2). The genetic impact should also be considered in relation to this.

Norway spruce represents a special case as very large amounts of seed have been imported by Sweden and Norway (Table 2). Between 1964 and 1993 almost all FRM used in Götaland, southern Sweden, was imported, with the majority originating from Belarus (Hannerz and Almäng, 1997). Similarly, in Norway, 20 per cent of the seed sold between 1952 and 1990 was imported (Figure 2), of which more than 80 per cent originated from Germany and Austria (Table 2). Although this has indisputably influenced the gene pools and occasionally resulted in climatic injuries, there are no reports of major setbacks associated with transfers of Norway spruce in Fennoscandia (Skrøppa, 1986; Hannerz and Almäng, 1997). The negative effects of using sub-optimal FRM of Norway spruce may be reduced after the first generation, since epigenetic effects modify the growth rhythm of the next-generation making it more similar to the local provenances (Johnsen *et al.*, 2005; Kvaalen and Johnsen, 2008; Skrøppa *et al.*, 2010; Brautigam *et al.*, 2013). Thus, the plasticity of Norway spruce eases its translocation to new environments. Moreover, selection may have favoured adapted individuals, especially in the case of dense planting (often more than 4000 trees ha<sup>-1</sup>) or highly successful germination after direct seeding, as density-dependent selection and man-made thinning operations are likely to have improved the stand quality. Probably due to a combination of these factors, the negative effects of the early translocations of Norway spruce seem limited up to present from an adaptive point of view. The application of FRM from eastern Europe in Sweden, which generally has a later growth onset in spring (Jansson *et al.*, 2013), might even be beneficial in a climate change perspective in avoiding spring frost damage, as budburst has already advanced (Schleip *et al.*, 2008).

Scots pine represents a different case. The amount of import to Scandinavia and Finland has been far less, and the regeneration was, to a larger extent, based on natural seeding. This is fortunate, because initial imports showed much more sensitivity to translocation than in the case of Norway spruce (cf. Øyen *et al.*, 2006). By the 1840s it became clear that Scots pine seeds from Germany were not successful in Sweden (Wibeck, 1912; Almäng, 1996). Similarly, minor transfers of Scots pine plants of Siberian (Krasnojarsk) origin were undertaken to southwest Finland in mid-1960s. These plants grew well until 1980s when a significant proportion of the trees died as a result of *Scleroderris* canker (Tasanen, 2010). Thus, translocations from adjacent areas have given the best results (Table 2), but such long distance imports to Finland and Sweden constitute a limited proportion of the overall translocations (Table 2), and selection against poor performing FRM has probably been strong due to high mortality. Taken together, we assume that the legacy of

translocated Scots pine on the autochthonous gene pool is modest considering present-day adaptation and health condition of Scots pine. The large pollen flow in Scots pine (Lindgren *et al.*, 1995) may also have contributed to swamp the translocated FRM and limited the effect on the autochthonous gene pool of the species.

Translocation of the *Fagaceae* species has mostly relevance for Denmark due to the large quantity of distant FRM applied (Table 2). Predominant regeneration by planting combined with extensive import of acorns over centuries has created highly diversified gene pools. Danish oak populations have unknown and often non-autochthonous origin (Larsen *et al.*, 1997a, c). Introduced FRM are preferred by the commercial forestry industry due to stem form and growth being notably improved, at least when pedunculate oak is grown under protected conditions. Seed from mature, selected trees in Denmark is preferred where the offspring are likely to represent some degree of local adaptation, but comprehensive planting is still based on imported FRM due to insufficient domestic seed production. The southern and continental sessile oak provenances display earlier budburst than northern and western provenances (Liepe, 1993), and are therefore more prone to spring frost damage under Danish conditions. Indeed, the use of southern origins on sites exposed to wind and spring frost in central and western part of Denmark has reduced forest health (Jensen, 1993). Beech has the same geographic pattern in timing of budburst (von Wuehlisch *et al.*, 1995), and early flushing provenances from, for example, the lowlands of Switzerland and the Carpathians (Table 2) have better quality and height growth than domestic provenances when grown in mild climates. Beech is generally well adapted to Danish conditions, but spring frost can create severe mortality on trees planted on exposed sites, and on such sites seed sources of local origin are therefore recommended due to their later flushing (Larsen *et al.*, 1997b). The introduction of large amounts of beech FRM characterized by early budburst could therefore cause problems for future regeneration of beech on frost-exposed sites. However, the risk of damage from spring frost is reduced when beech is cultivated by natural seed fall, as the selection during the lifetime of the old plantations is expected to have favoured local adaptation.

The extensive translocation of FRM has without doubt changed the gene pools of the tree species covered by this review. For example, in southern parts of Sweden and Norway, FRM has been introduced from maternal genetic lineages separated during several consecutive glaciations (Tollefsrud *et al.*, 2008; Lockwood *et al.*, 2013). Similarly, re-colonization of the oaks in Europe after the last glaciation took place from several refugia in southern Europe with distinct genetic signatures (Petit *et al.*, 2002), and the various translocations have contributed to mixing of such genetic lineages in Denmark. This may be undesirable from a biodiversity perspective, but in terms of adaptation we note that up to the present day, severe negative effects on these species have rarely been reported in reforestation areas. With the exception of the first introductions of Scots pine to Sweden from Germany (Wibeck, 1912) and to Finland from Siberia (Tasanen, 2010), the main observation is therefore that the transfers have not led to major incidents of climatic injuries or dieback that can be ascribed to non-autochthonous genetic origin. This certainly also relates to the early recognition of the importance of genetic origin, the later provenances tests that have guided transfers, and finally, national legislation on the use of seed sources that have been effective for several decades.

The apparent robustness of these species may relate to their history. During repeated glaciations up to the late Pleistocene (11 700 BP), a high proportion of the European tree flora went extinct. The remaining tree species are therefore not a random selection of taxa, but rather a group of phylogenetically related and cold-resistant species which successfully tracked climatic oscillations across Europe for more than 2 million years (Eiserhardt *et al.*, 2015). The species' history before the era of modern forestry is therefore an unambiguous demonstration of robustness and the ability to cope with environmental heterogeneity, and as such an indication of adaptability needed to meet future climatic changes. As it is predicted that migration of trees will lag behind the pace of climate change, the substantial northward movement of provenances during the last century may support rapid adaptation to new future warmer climatic conditions in Scandinavia (cf. Williams and Dumroese, 2013). This is, however, very dependent on species and range of translocation, and increased winter temperatures could leave early flushing provenances of, for example, beech from southern and eastern Europe, more prone to spring frost damage in Scandinavia. The establishment of an extensive series of reciprocal field experiments along with high-resolution climate data would allow us to better evaluate the effects of future climate and to develop transfer guidelines, as has been done for Scots pine in Scandinavia (Kunskap direkt, 2015).

## Conclusion

The massive import of tree seeds to Sweden and Norway from the 19th century onwards was due to a combination of expansion of the wood-based industry, excessive logging, and a shift from natural regeneration to manual seeding (Almä, 1996; Hannerz and Almä, 1997). Finland, however, continued to follow a policy of natural regeneration by leaving seed trees after logging (Tasanen, 2010). Thus, adjacent countries with similar needs for seed supply had different strategies for meeting the prevailing demands and were differentially influenced by non-autochthonous FRM. For Denmark, the lack of effective seed storage techniques for beech and oak was an important driver in sustaining imports. Transfer of FRM in Scandinavia was not, however, only due to seed deficit, since recognition of geographic differences in adaptation, growth and stem straightness triggered import from sources proven superior to local supplies. The situation in Sweden, and partly Denmark, shows that a build-up of private and company-owned forests closely preceded, and was an important contributing factor towards large deforestation events. Although complex ownership patterns with many small owners, such as in Norway, did not prevent overexploitation in periods with high demand on the international market, it probably constrained effective harvesting before the 20th century, as it does today (SKOG22, 2014). Forest legislation was initially designed to regulate harvesting, which in turn influenced imports of FRM, but restrictions to logging were applied at late stages, when overexploitation had already taken place for centuries, as shown for Denmark and Finland. Movement and use of FRM is presently controlled effectively by specific national legislation, but such legislation did not appear until the 1930s when knowledge about provenance variation became available (cf. Ordning, 1944), and after massive imports of FRM to Scandinavia from various sources had already taken place. From the 1950s onwards, state-authorized bodies were established to control the seed

trade, and international and national regulations on FRM were developed. For Sweden, Norway, and to an extent Denmark, it appears that the most important preconditions for the build-up of forest resources from the 19th century were not specifically the actions of forest administrations and the legal instruments that control logging, but rather the shift from natural to artificial regeneration systems and the availability of translocated FRM. Undoubtedly, native gene pools of conifers have been most influenced by translocations in Sweden, followed by Norway, and have only been influenced to a limited extent in Finland. Autochthonous gene pools of deciduous species have been most extensively influenced for *Fagaceae* species in Denmark. However, over the long history of translocation of FRM in Fennoscandia, and within the scope of this review, we have found relatively few examples of distinct adaptation failures.

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## Conflict of interest statement

None declared.

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