

University of Alberta

**Developing seed transfer strategies for European Lodgepole pine reforestation
to address climate change**

by

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and

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Abstract

Lodgepole pine is an important commercial tree species both in its native North America and as an introduced and naturalized species in Europe. Particularly in Sweden, intensive lodgepole pine forestry systems have been developed to maximize productivity through tree improvement programs that select provenances and genotypes that are well adapted to the environmental conditions where the lodgepole pine is grown as an introduced species. The benefits of such efforts to optimize growth and adaptation are, however, threatened by observed and projected climate change, leading to physiological stress and potentially exposing them to novel disease agents. The objective of this thesis is to develop guidelines for regional use of lodgepole pine in Europe. Specifically, I contribute: 1) a comparison of Lodgepole pine growth observed in European provenance tests with growth performance of native tree species for different climatic regions of Europe; 2) an assessment of the potential pest and disease risks of lodgepole pine for different climatic regions of Europe based on a comprehensive literature review; 3) an evaluation of how previous work on bioclimatic envelope modelling of lodgepole pine in Europe can predict competitiveness and health of lodgepole pine plantations under future climate projections. This research suggests that the projections of the realized climatic niche of a species in conjunction with growth analysis of different populations in provenance trials can be useful tools in guiding future reforestation strategies.

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1. INTRODUCTION

The introduction of exotic tree species has an important history in forestry. The naturalization of many non-native species has led to varying opinions on what defines an exotic tree species. Some say that an exotic species is simply the opposite of native: a tree species introduced through anthropogenic activity. Other definitions exclude exotic species that have become “fully naturalized”, distinguishing those with a long-standing history as an introduced species (Bradshaw, 1995).

Historically, introduced trees satisfied aesthetic desires and human interest. However, large-scale reforestation initiatives started in the 19th century in Europe and led to an increase in the global use of exotics (Moore 2005). They have displayed impressive growth performance, high environmental tolerance and a resistance to disease and pests (Mead 2013). However, there are several risks associated with introduced species that must be considered. They can become invasive and reduce biodiversity, alter surrounding ecosystems and potentially hybridize with local native species (Jäger et al. 2009; Richardson and Rejmanek 2011; Le Maitre et al. 2002; Moore 2005). The risks and benefits associated with introduced species calls their future usefulness in climate change mitigation and adaptation into consideration.

Provenance trials, often referred to as common garden experiments, are large-scale plantation experiments. Seeds are collected from a specified range of their native habitat and systematically planted elsewhere. Traditionally, provenance trials were predominately used to inform seed transfer guidelines and to identify superior seed genotypes for a region (Leites et al. 2012). However, provenance trials also provide realistic, large-scale monitoring opportunities to observe the effects of climate conditions and seed type on tree productivity. Typically, trees species that have been deemed valuable both economically and ecologically are studied under provenance trials (Mátyás 1996). With growing concern regarding the impact of climate change on forestry, provenance trials are become increasingly valuable. Now, provenance trials can be used to evaluate a species response to climate change.

In addition to provenance trials, species distribution models (SDMs) have become common tools used to assess potential impacts of climate change on species range (Beaumont, 2008). Guisan and Zimmerman (2000) defined a species distribution model as “an empirical model relating to field observations of environmental predictor variables based on statistically or theoretically derived response surfaces”. Common applications of SDMs are selecting conservation areas, predicting the effect of climate change on species range and assessing the risk of a species invasion (Gomes et al. 2018). SDMs estimate the best match between observed species distributions and multivariate climatic variables to project potential suitable habitat (Araujo and Peterson 2012). While SDMs are valuable tools, they can often be misinterpreted or misused. Comparing theoretical distributions with observed growth performances is a very powerful model validation method.

Provenance trials are an excellent source of data that may be used to validate SDMs. Once an SDM is used to produce a predictive map, suitable habitat predictions can be compared against observed population performances recorded from provenance trials. This can assess the true growth potential of a species in current and future conditions.

Lodgepole pine (*Pinus contorta*) is a highly prized tree species both to its’ native North America and as an introduced and naturalized tree species in Europe. It is of regional importance for the European forestry industry, which has placed long-term investment in plantation establishment. The growth potential and habitat suitability has been evaluated through provenance trials across Europe. There have been many trials established for Lodgepole pine across North America and Europe, a testament to its’ societal and economic importance.

Herva (2016) conducted a study assessing the suitability of a species distribution model in predicting Lodgepole pine reforestation stock in Europe under climate change. In this study, Herva (2016) sought to examine whether a species distribution model accurately predicted suitable habitat for Lodgepole pine in Europe under current and future climate conditions. The study found that the model was able to reasonably predict best growing populations in European regions. However, strong growth was observed outside of the predicted habitat, questioning the accuracy of the model. Comparatively, lower growth performance was observed in areas of high SDM suitability.

I would like to reassess the validity of the SDM model. I believe the model was highly accurate in predicting best growing populations of Lodgepole pine in European regions. The conclusions made by Herva (2016) did not consider the influence of potential competition and pest outbreaks. Despite strong growth observed outside the predicted habitat, Lodgepole pine may not be the strongest reforestation stock in those regions. The relative growth performance of Lodgepole pine to other local species must be considered. Also, introducing Lodgepole pine to new environments comes with the risk of novel insect and pest outbreaks. Assessing the potential outbreak severity both inside and outside the predicted habitat will also provide important context in validating the model.

The two hypotheses that were tested in this study were: 1) Lodgepole pine was outcompeted by other local tree species in areas of low SDM suitability; Lodgepole pine was a strong competitor with other local species in areas of high SDM suitability; 2) There is a higher risk of pest outbreaks on Lodgepole trees planted outside the predicted habitat. Ultimately, this study aimed to support the theory that SDMs can be used to guide human-assisted migration of trees under climate change.

2. LITERATURE REVIEW

2.1. History of introduced species

Global native forests are increasingly threatened by accelerated rates of forest degradation and land conversion in the past century (Brown and Lugo 1990). According the United Nations Food and Agriculture Organization (FAO 2016), global forest area has decreased by an annual average of 3.3 million hectares from 2010 to 2015. Africa and Latin America are very concerning, with an annual forest loss rate of 0.54% and 0.43% respectively (EFI 2018). Forestland is primarily cleared for ranching purposes in Latin America; forests are cleared for agricultural land in Africa (Chapman and Chapman 1996). Forests play an important role in local and national economies. Fuelwood is the prime source of energy in most developing countries. Non-timber forest products such as fruit, nuts and fibres contribute to the livelihood of rural communities around the world.

While resource exploitation is the greatest threat to tropical and subtropical forests, the potential impact of climate change is a major concern for boreal and temperate forests. Soja et al. (2007) concluded that the projected climate-induced landscape-scale changes in the boreal forest are currently underway. Species compositions may be altered by disturbances, pest infestation, or unfavourable growing conditions (Dale et al. 2018). The growing demand of forest-based products and the climate-induced physiological stress on trees shows that sustainable forest management and long-term planning is crucial. For many years, international forestry research circles have been interested in introduced species and the role they may play in the future global forestry industry.

Tree planting has a long history stemming from eastern Asia. However, large-scale non-native plantations did not emerge until the late 19th century in Europe (Zobel et al. 1987 as cited in Richardson 1998). Afforestation using introduced species increased mid-20th century. Large-scale planting of North American Radiata pine (*Pinus radiata*) began in Chile in 1970 and quickly spread to other South American countries (most notably Argentina and Brazil) as well as other tropical and subtropical regions (Le Maitre 1998). Between 1970 and 1996, ~ 4 million hectares of Radiata pine had been planted (Lavery and Mead 1998). As of 2005, 7% of the

Earth's forest coverage was composed of non-native forest plantations (Evans 2009). Shifting biomes and climate –induced stress on native species will likely lead to non-native forest plantation coverage to increase from 7% to approximately 20% soon (Brockerhoff et al. 2006 cited from Valduga et al. 2016).

Introduced species provide several socio-economic, environmental and human health benefits to both forestry professionals and surrounding forest-dependent rural communities (Moore 2005). Zobel et al. (1987) and Mather (1993) summarized seven reasons for using exotic trees in afforestation programs:

- 1) There is a need for conifer species in areas that lack them. Coniferous trees produce important fibers and solid wood products.
- 2) Exotic species often grow faster than native species.
- 3) Exotic species can be easier to manage. Widely planted exotic species that are well studied and well documented make silvicultural and breeding decisions easier on foresters.
- 4) Native seeds can be hard to obtain, however exotic species (often genetically-enhanced) are more readily available.
- 5) Many exotic species have shown strong growth performance in degraded forest land where native species have struggled to establish themselves.
- 6) Current forest markets favour pines and eucalypts, the two leading exotic plantation genera.
- 7) Exotic species can be resistant to diseases or insects that have plagued native species in their native distribution.

Introduced species have helped many countries improve their forestry industries by providing a source for roundwood, pulp and fuelwood (Zobel et al. 1987) In addition to financial benefits, introduced species can provide several vital ecosystem services. They can combat desertification and protect soil. Conifers were first planted to stabilize sand dunes in Portugal in the 14th century and quickly spread to France and the Baltic shores (Richardson 1998). They can purify water and enhance carbon sequestration (Moore 2005). Maema et al. (2016) found rural communities in South Africa are dependent on exotic tree species to combat ailments. Contrary

to popular belief, introduced species can also maintain biodiversity (Daehler and Gordon 1997; Moore 2005).

2.2. Provenance trials

Provenance trials, or common garden experiments, are large scale planting experiments in which seeds are collected throughout a species native range and tested at planting sites. Randomized experimental designs and careful selection of planting sites are very important: constant environmental conditions infer any differences in observed growth performance are attributed to genetic differences in seeds. Strong genetic diversity and genetic adaptive capacity arise from a species' large geographic range and variety of growing climates (Wright 1976). Significant differences in growth performance can mean there is potential gain from selecting the correct seed source for the growing environment. Long-term observations are preferred, as they provide a realistic representation of the environmental conditions at a planting site.

The importance of using seed sources that are adapted to their introduced environments is a long-held principle in forestry. The genetic differentiation in a population arising from evolutionary adaptation to environmental conditions can be best described as a continuum, with significant genetic differences found at either extreme (White et al. 2007). Guidelines have been outlined to establish seed zones, inform seed transfers and reduce the risk of maladaptation (Hamann et al. 2011). A seed zone outlines the geographic area in which planting stock must remain; seed transfer guidelines specify maximum distances and elevations between a source location and potential planting site (Hamann et al. 2011). There are two different approaches to establish these guides: aiming to maximize tree growth and aiming to minimize risk (Hamann et al. 2011).

There is a strong need to use the wealth of existing data from provenance trials. Many of these trials are designed to specifically explore the influence of climate and seed origin on growth performance (Booth 2017). It is astonishing how little this information is used in climate change research. Often, poor provenance trials results go unreported or are discarded. However, poorly performing provenances are equally important as it may be useful in predicting how natural stands may respond under climate change (Booth 2017).

2.3. Successful introductions

Eucalyptus spp.

Eucalyptus spp. is a fast-growing, tropical forestry genus endemic to Australia, Indonesia, the Philippines and New Guinea (Paine et al. 2011). The *Eucalyptus* genus has over 500 different species and is the most widely planted exotic tree in the tropics. The most commonly introduced species are *Eucalyptus grandis*, *Eucalyptus paniculata*, *Eucalyptus globulus*, *Eucalyptus saligna* and *Eucalyptus citriodora* (Eldridge et al. 1994). *Eucalypt* plantations are the fastest growing sector of world forestry (Turnbull 1999). Research efforts focused on improving genetics and silviculture has doubled productivity of these plantations every 10-20 years (Binkley and Stape 2004). Many species can grow in various soils and climates, are easily managed through coppicing, are not palatable to grazing animals and produce both valuable wood and non-wood products (Turnbull 1999). A study conducted by Richardson and McMahon (1992) showed *E. nitens* was successfully grown in South Africa where the climate was much warmer and drier than its' native Australia. The Centre for International Forestry Research (CIFOR) suggested that exotic *Eucalyptus* plantations suffer from much less pest damage than its' native plantations and natural forests (Nair 2001). Essentially, exotic eucalypts have an increased chance at regeneration.

Large eucalypt plantations have been established in over 80 countries (Floyd et al. 1998) and successfully introduced to numerous tropical and sub-tropical regions. *Eucalyptus* spp. has been intensively planted and successfully cultivated in India (~1 million ha), China (~600 000 ha), Portugal (~550 000 ha) and Morocco (~200, 000 ha; Kumar 1991; Leuning et al. 1991; Gazarini et al. 1990; Marien 1991 cited from Turnbull 1999). Most eucalypt plantations are established to produce pulpwood because of its' availability and price; however smaller-scale eucalypt plantings can be used as windbreaks, for land reclamation and for leaf-oil production (Turnbull 1999). Brazil is the largest producer of *Eucalyptus* pulp, with over 3 million hectares of predominately *E. grandis* plantations. While other Brazilian commodity prices have decreased with time, the global pulp price has continued to increase and benefit pulp producers (Campinhos 1999).

In addition to industrial purposes, eucalypts play an important role in rural areas. Eucalypts can be used to make tools and poles, to extract essential oils and tannins and to support honey production (Turnball 1999). Zheng (1988) reported that eucalypts have improved the quality of life of many Chinese farmers. Many people in Ethiopia are dependent on single plantings of *E. globulus* for fuelwood and construction material (Turnball 1999). West African countries have been able to incorporate *E. camaldulensis* into their agroforestry practices.

Pinus radiata

Radiata pine (*Pinus radiata*), indigenous to California and Mexico, is a medium density, fast-growing conifer that can tolerate a wide variety of climates (Mead 2013). Similarly, to other popular exotic species, Radiata pine has been extensively studied and has a highly developed silvicultural regime used to obtain desirable lumber and pulp qualities. Although Radiata pine has little commercial value in its native range, it has become a very valuable exotic timber species. In fact, Radiata pine is the most widely planted pine species in the world and referred to as the “best expatriate of the North American conifers” (Mead 2013). It is the leading introduced species in Australia, New Zealand and Spain. Largest exotic plantations are in New Zealand (~ 1.5 million ha), Chile (~1.5 million ha), Australia (~ 0.77 million ha) and Spain (0.29 million ha). It is also a very commonly planted species in plantations across Argentina, Uruguay, Kenya and the Republic of South Africa (Mead 2013).

Radiata pine was first introduced to New Zealand in the mid-19th century (Wu et al. 2007). Large-scale plantations did not begin until the late 1950’s and soon established the longest-running forest tree breeding program (Burdon et al. 2008). The forestry industry is based on exotic plantation forests and contributes 3% of New Zealand’s Gross Domestic Product (GDP); Radiata pine currently makes up 90% of total exotic plantation coverage (New Zealand Government 2018). After three generations of undergoing selective breeding programs, Radiata pine in New Zealand was recorded to have increased volume production by 33% (Mead 2013). Not only is Radiata pine an excellent example of successful tree introduction, it represents an important case in the domestication of forest trees using provenance trial data.

Chile has developed a strong vertically integrated industry around Radiata pine. Forestry accounts for 7.4% of Chile's GDP and Radiata pine accounts for 65% of total plantation coverage (Mead 2013). Chile has a substantial amount of protected native forest; Radiata pine is predominately planted on degraded agricultural land where other native species are incapable of establishing themselves.

In addition to economic benefits, Radiata pine provides ecosystem services such as erosion control, slope stabilization and maintain biodiversity. Radiata pine was introduced in the coastal range of Chile to remediate a highly eroded coastal range (Mead 2013). Mature Radiata pine plantations have been home to several endangered species including the brown kiwi in the New Zealand falcon and the native frog (O'Loughlin et al. 2005; Brockerhoff et al. 2008 as cited in Mead 2013).

Pinus caribaea

Caribbean Pine is a widely planted tropical pine tree. Native to parts of Central America and the Caribbean, Caribbean pine has intentionally been introduced to Asia, Africa and Australia (Salazar and Joker 2000) and used for its pulp, fuelwood, poles and sawn lumber (Plumber 1988 as cited in Wadsworth 2008). Caribbean pine is characterized by its rapid rate of growth, wide resistance to pests and ability to be highly productive in various environments (Berlyn et al. 1991). Caribbean pine was first introduced to Fiji in the mid-1950s and has remained the most suitable exotic softwood species (Cown and McConchie 1981). It was an important forestry species for Puerto Rico because of its ability to naturally regenerate, saving the Puerto Rican government money on replanting costs (Francis et al. 1991). Caribbean pine can also grow in all types of soil conditions across Puerto Rico, including the moist areas. Today, it is primarily used for erosion control and ornament.

Caribbean pine has been at the centre of a massive reforestation program in Sri Lanka. Lamb (1973) found that Caribbean pine can improve soil nitrogen status. While it may not be an ideal plantation species given its inability to produce viable seeds in moist climates, this property makes Caribbean pine appealing as a reforestation species as it reduces the possibility of

invasiveness. Prior to the reforestation initiative, vast areas of Sri Lanka were degraded and severely eroded. By 1987, ~ 25 000 ha of degraded land was reforested with Caribbean pine (Pereira 1988).

2.4. Failed introductions

Pinus strobus L.

Weymouth pine (*Pinus strobus*) is a conifer native to North America and introduced to France in the mid-16th century. The introduction of Weymouth pine was first considered a success because of its ability to grow more rapidly than native conifers (Karlman 1981). By the 19th century, large-scale planting of Weymouth pine has spread from France to Germany and Austria (Schmitt 1972). However, Weymouth pine stands were suddenly damaged by blister rust caused by *Cronartium ribicola* a pathogenic fungal species. These stands were very susceptible to this pathogen and spread over all of Europe within 30 years. The damage caused by this fungus was catastrophic; German inventory showed 90% of the plantation had been injured (Radu 2008). Studies suggest that the original host of this pathogen was Swiss pine (*Pinus cembra*), a pine species native to Europe (Karlman 1981). The disaster did not end there: the pathogen was then introduced to the United States of America from Germany and to Canada from France. Unfortunately, this also caused heavy loss of Weymouth pine in its native distribution (Van der Plank 1975). Blister rust was and continues to be a major limiting factor for potential expansion of Weymouth pine (Radu 2008).

Dothistroma Needle Blight

Dothistroma needle blight (*DNB*) caused by fungus (*Dothistroma septosporum*) is considered one of the most important foliar diseases of pines in the world (Barnes et al. 2004). DNB occurs in almost every country where a susceptible host is found, with an impressive climatic range spanning from tropical to subarctic (Watt et al. 2009). In the 1960s, extreme outbreaks were only observed in the southern hemisphere. Exotic pine plantations, predominately Radiata pine, in

New Zealand, Australia, and Chile suffered severe economic loss from *Dothistroma* outbreaks (Bradshaw 2004). DNB limited expansion of exotic pine plantations in East Africa (Gibson 1974 as cited in Drenkhan et al. 2016) and India (Bakshi and Singh 1968 as cited in Drenkhan et al. 2016) and continues to be a limiting factor in New Zealand. DNB, an exotic pest attacking an exotic plant host, provides an excellent example of the risk associated with species introduction.

Dothistroma is native to North America and historically, damages to native pine trees in the northern forests have been low (Woods et al. 2005). The past two decades have seen an increase in prevalence and severity of DNB outbreaks in North America and Europe (Bradshaw 2004; Hanso and Drenkhan 2008; Hamann et al. 2011; Solheim and Vuorinen 2011). Some studies link the rise in outbreaks to global climate change: North America and Europe are experiencing higher temperatures and significant changes to annual precipitation patterns (Hanso and Drenkhan 2013; Woods et al. 2016).

2.5. Lodgepole pine and its' introduction to Europe

Ecology and Range

Lodgepole pine (*Pinus contorta*) is a coniferous tree species, native to North America. It has wide ecological amplitude, both in the context of climate and biotic conditions. Lodgepole pine has a wide distribution, starting from mid Yukon, down the west coast until Baja, California (Karlman 1981). No other tree species has a similar altitudinal range. Despite this impressive distribution, Johnstone and Chapman (2003) suggest that Lodgepole pine is lagging its potential range into colder environments.

Lodgepole pine trees can grow under various environmental conditions from semi-desert, to mountainous ranges and wetlands. Critchfield (1979) identified four subspecies of Lodgepole pine that differ in dimension, needle size, cone form, serotiny, branchiness, among other characteristics.

1. *Pinus contorta ssp. latifolia* “The Rocky Mountain inter-mountain race”. This is the most commonly planted and harvested Lodgepole pine subspecies. It can be found from the central Yukon Territories, to eastern Oregon and down to Southern Colorado. Lodgepole pine can only be found in scattered, discrete populations across northern Alberta and southern North Dakota. This subspecies is an aggressive pioneer, with serotinous cones and rapid growth performance during establishment that allows it to dominate areas prone to forest fires.
2. *Pinus contorta ssp. murrayana* “The Sierra-Cascade race”. As the name suggests, this subspecies can be found in the Cascade Range and Sierra Nevada mountains of southern California. Although *murrayana* is slower growing than *latifolia*, it has a larger trunk diameter. This subspecies has relatively broad leaves and a thin, scaly bark.
3. *Pinus contorta spp. contorta var contorta* “Shore pine”. Shore pine can be found on the Pacific coast of North America stretching from Alaska to northern California. This subspecies has a restricted coastal range, is low growing and develops a heavily branched, twisted trunk.
4. *Pinus contorta subsp. bolanderi* “Mendocino White Plains”. *Bolanderi* is low growing in its natural distribution but grows to a relatively reasonable height when planted outside of its’ range. This subspecies is found in soils with low pH (2.8-3.9).
5. *Del norte* is an uncommon subspecies that is limited to a coastal region of mountainous north-west California.

Lodgepole pine is a highly prized forestry species in its’ native North America. Historically, Lodgepole pine was particularly import to Indigenous peoples: it was used as structural poles for tipi shelters and as a traditional medicine to remedy ailments (Government of Alberta 2018). In the early 1900s, Lodgepole pine was used to make railway ties. It plays an important role in both the Canadian and American forestry industry and is manufactured to serve many uses including: structural poles, plywood and pulp (Government of Alberta 2018).

Introduction to Europe

Lodgepole pine was first introduced to Britain in 1853, with disappointing results. Large-scale plantations were introduced to Sweden in the late 19th century and spread to other European countries shortly thereafter (Elfving et al. 2001). Interest in Lodgepole pine as an exotic forestry species led to more plantations being established. Little progress was first observed with provenance trials. Up until 1953, Sweden had only considered using provenances south of 55 Degrees N (Karlman 1981). Failed trials had led to the understanding that incorrect provenances were being selected for the region; stands were often subjected to snow thrust, damaged from windthrow and pest outbreaks (Elfving et al. 2001). Breeding programs in Sweden ventured further out and tested provenances as far north as 63 Degrees N (Karlman 1981). Guidelines were published to help inform provenance selection in Sweden (Remrod 1977; National Board of Forestry 1979 as cited in Karlman 1981).

Today, Lodgepole pine is planted extensively in Sweden and in Great Britain. Lodgepole has also been introduced to climatically harsh, nutrient poor soils in Ireland (Gallagher et al. 1987) and Scotland (Lines 1996), sand fields in Denmark (Larsen 1980) and in Finland (Weissenberg 1977). An international network of Lodgepole pine test plantations was established by the International Union of Forest Research Organizations (IUFRO; Lindgren et al. 1994). This network set out to test growth performance of seed origins in various climatic conditions. The most important finding of these provenance series was that seed origin selection is of the utmost importance in determining the success of an introduced species.

Lodgepole pine has been somewhat successful as an introduced species in Europe. It has outperformed other exotic conifers introduced to Sweden. Studies show that Lodgepole pine can produce 40-70% higher yield per ha than Scots pine (*Pinus sylvestris*), a conifer native to Sweden (Hägglund et al. 1979 cited from Karlman 1981). In addition to higher yields, the optimal rotation period for Lodgepole pine is approximately 15 years shorter than Scots pine (Remrodd 1977 cited from Karlman 1981). Most importantly, studies show that Lodgepole pine is resistant to *Melampsora* rust and *Lophodermella* needle cast, two fungal pathogens that have devastated Scots pine plantations across Sweden (Karlman 1981).

However, Lodgepole pine has also been referred to as one of the most aggressively invasive plantation species (Pena et al. 2008; Ledgard 2001). It was first introduced to New Zealand in 1880. By the mid-20th century, there were 10,000 hectares of Lodgepole pine stands (Miller and Encroyd 1987). Unlike Sweden, Lodgepole pine in New Zealand had been outperformed by other introduced forestry species. Due to slower growth, uncertain market acceptance and concern about natural generation, Lodgepole pine stand establishment ceased by 1980 (Ledgard 2001). However, Lodgepole pine was able to aggressively regenerate, referred to as a phenomenon called “wilding spread” (Ledgard 2001). Lodgepole pine can spread more vigorously than other introduced conifers in New Zealand, threatening native biodiversity, landscape values and farming productivity. Over 150,000 hectares have been impacted by the natural generation of Lodgepole pine, with concern over further spreading (Ledgard 2001). Today, Lodgepole pine is the most targeted pest in New Zealand and is banned from sale, propagation and distribution.

Risks with introduction

There are a few risks associated with introducing an exotic species. Despite the vast amount of available information, species introduction is still a poorly understood phenomenon. The greatest risk one faces is invasion. As seen by Lodgepole pine in New Zealand, self-dispersal is concerning. Natural regeneration will occur if all factors are present: plentiful seed, low predators, good germination and ideal settings for seedling establishment (Engelmark 2001). The risk of pathogen introduction and spread of diseases should also be considered. Pests can be carried from one continent to another through seeds, plants and timber (particularly unbarked timber). Another concern is maladaptation. A tree that was a strong forestry species in its’ native habitat could display low tree vigour in its new habitat. Risk can be minimized by taking the following precautions: 1) Avoiding monocultures when possible to reduce widespread outbreak of a pathogen with a mixed stand and 2) careful site selection with respect to climatic and biotic conditions.

2.6. Global climate change

Global climate trends

Greenhouse gas emissions have significantly altered the global climate, with increased global surface temperature change of $+0.5^{\circ}\text{C}$ recorded since 1970 (IPCC 2007). While the Earth has historically experienced fluctuations in mean surface temperature from natural phenomenon such as volcanic eruptions and solar activity, the pace of current changes is unprecedented and certainly attributed to anthropogenic activity (IPCC 2013). Global mean temperature has increased by $+0.13^{\circ}\text{C}$ per decade since 1950; this is twice as fast as the previous century (IPCC 2007). Even under the most conservative projections and changes to current industrial practices, future climate change will very likely consist of: increase in mean surface temperature, increase in frequency and intensity of droughts and more frequent heat waves and floods (IPCC 2007). The Intergovernmental Panel on Climate Change (IPCC), the leading international body for climate change research, established four future emission scenarios in the IPCC fourth assessment called the Special Report on Emissions Scenarios (SRES):

- 1) A1- future world of very rapid economic growth and introduction of new and more efficient technologies with a strong emphasis on capacity building and decrease in regional per capita income.
- 2) A2- heterogeneous world with a fragmented economic growth and technological advancement
- 3) B1- rapid economic growth with emphasis on improved equity and global solutions to economic, social and environmental sustainability.
- 4) B2- like B1 scenario but with a local and regional scope, as opposed to the global emphasis.

The IPCC has since replaced these future climate trajectories with the Representative Concentration Pathways (RCPs) in their fifth assessment that outlines revised climate scenarios projected until 2100. The RCPs were developed with the collaborative effort of integrated assessment modellers, climate modellers, terrestrial ecosystem modellers and emission inventory

experts (van Vuuren et al. 2011). Although relatively similar, the RCPs predict an additional +0.5 to 1°C increase in surface mean temperature from 2016-2035 (IPCC 2013).

Climate change in Europe

Despite the overall increase in global mean surface temperature, the increase will not be uniformly experienced. Higher latitude regions, such as Northern and Central Europe, will experience higher temperatures during the winter months; southern Europe will experience higher temperatures during the summer months (IPCC 2013). Extreme projections suggest that summer temperatures in the Iberian Peninsula and France may increase by + 6°C by 2100 from the reference period temperature (IPCC 2007). Nonetheless, the entire continent of Europe will experience more frequent and extreme heat waves and is predicted to be above the global mean (Christensen et al. 2013).

Precipitation is difficult to predict, and so projections have greater uncertainty. Annual precipitation is likely to increase in most of northern Europe and decrease in most of the Mediterranean. Precipitation is likely to increase in winter months and decrease in the summer in central Europe and the Mediterranean (Christensen et al. 2007). Lower annual precipitation and increased mean surface temperature leaves central Europe and the Mediterranean more vulnerable to frequent summer drought spells.

Forests and climate Trends

Although trees have an inherent capacity to deal with changing environments, they are highly sensitive to changes in temperature, precipitation and atmospheric carbon. One of the greatest issues facing future health and productivity of forests is climate change. Climate change is causing significant habitat change throughout the life of a tree, putting them through physiological stress and potentially exposing them to novel insect and disease agents (Allen et al., 2010; Gray et al. 2011). Unfortunately, trees are limited in their ability to migrate and

therefore cannot adapt to rapidly changing climates the way other species can. Thuiller (2007) estimated that +1°C can result in a required latitudinal ecological zone shift of 160 km or 100 m change in altitude. Optimal habitat range for some North American conifers is predicted to shift ~ 100 km every decade (Hamann and Wang 2006). Unfortunately, trees have the migration capacity of 100 m per year (Aitken et al. 2008). Increased annual temperatures are having a palpable effect on tree phenology and vigour. A study by Beaubien and Hamann (2011) found that *Populus tremuloides* and *Anemone patens* bloom dates had advanced two weeks in the past seven decades, causing increased exposure to late-spring frost in western Canada.

Future drought conditions are of concern in Europe. Changes to snowfall patterns and increased temperature in winter months can affect the seasonal availability of water. In 2003, a severe summer drought was experienced that resulted in a sharp decrease in forest productivity in central Europe (Ciai et al. 2005 as cited in Bolte et al. 2009). An increased sensitivity of *Picea abies*, *Larix decidua* and *Pinus sylvestris* (three of the most important European forestry species) to lower precipitation and late-summer drought is currently being observed in the alpine region of Norway (Cermak et al. 2017).

The impact of climate change on Norway spruce is alarming; it is an incredibly valuable forestry species that has been widely planted across Europe. Hanenwinkel et al. (2012) reported that Norway spruce will be restricted to northern Sweden, Finland, Norway and high elevations in central Europe by 2100. Broadleaves such as oak and beech are also predicted to shift and expand from today's range in Western Europe to more central and northern Europe (Hanenwinkel et al. 2012).

European forests are predominantly maintained to support a valuable timber industry. Climate change will cause a shift in suitable forestry species. Unfortunately, the increased temperature and decreased annual precipitation will reduce the range of cold-adapted species like Norway Spruce for drought-adapted species like oak. By 2100, 21 to 60% of European forest land will be suitable for Mediterranean oak. This change can result in income losses and a reduction of raw materials (Hanenwinkel et al. 2012). Oak has a lower economic return and a reduced carbon sequestration capacity, which will affect forest owners and reduce the potential for climate change mitigation. To compensate for these losses, other species need to be introduced from outside Europe (Hanenwinkel et al. 2012).

Moving planting stock that is adapted to anticipated climate conditions has been proposed as a potential climate change mitigation strategy (Gray et al. 2011). Such assisted migration prescriptions, defined as the “human-aided translocation of species to areas where climate is projected to become suitable” have been proposed in the context of species conservation, but are also suitable in forestry (Mueller and Hellman 2008).

2.7. Species distribution models and their uses

Guisan and Zimmerman (2000), two leading climate- species modelling researchers, defined a species distribution model (SDM) as an “empirical model relating field observation to environmental predictor variables, based on statistically or theoretically derived response surfaces”. Also known as ecological niche models or bioclimatic envelope models, SDMs seek to explain observed patterns of species occurrences. SDMs are based on the fundamental vs. realized niche concept outlined by Hutchinson (1957). The fundamental niche represents the broader range that a species can survive in without competition (Austin, 2007; Soberon and Nakamura 2009). Hutchinson argues that species are excluded from part of their fundamental niche by non-climatic variables, thus occupying their realized niche. Observed distributions are constrained by non-climatic variables and therefore SDMs are quantifying Hutchinson’s realized niche of species.

SDMs are used to address a wide range of theoretical and applied research objectives (Guisan and Thuiller 2005). These include: analyzing the potential spread of a disease/pest (Peterson et al. 2002), evaluating established reserves and their ability to maintain species habitat (Araujo 2004) and to inform potential habitat selection for assisted migration (e.g. Vitt et al. 2010, Gray and Hamann 2013). Most recently, SDMs have been used to predict future impacts of climate change by combining present day distributions of species and climatic variables to project future species distributions (Araujo et al. 2005). This approach was pioneered by Busy (1988) who used an SDM to analyze likely climate change impacts in Australia on two animal species and a tree species. Improvements to climate projections have increased the likelihood of accurate potential habitat projections.

Assumptions and critiques

Despite their usefulness, there are a few critiques against SDMs. Uncertainty comes from the combination of different possible analyses, varying spatial resolutions and scales, variety of modelling techniques and validation methods. Failing to acknowledge the limitations and underlying assumptions of a model can lead to misinterpreted or misinformed results.

A key assumption of an SDM is the current distribution of a species provides an accurate estimate of their climatic requirements (Booth 2017). SDMs ignore the inherent adaptive capacity of a species. This assumption has been challenged by results from commercial plantation trials that show species growing successfully outside their native climatic range. Provenance trial data can be particularly important in these cases. Growth performance from trials outside a species natural distribution should be collected and considered in conjunction with SDM predictions when possible. Along these lines, it is also assumed that if an SDM can accurately display population distributions under current climates, then it will also be able to do so for sure future climates (Lawler et al. 2006). However, evolutionary processes and non-climatic conditions, two variables that can alter a species' distribution, are not accounted for in an SDM. Competition is also an important theoretical factor that is absent from most examples of SDM research (Guisan and Thuiller 2005).

A controversial assumption of an SDM is that a species is in equilibrium with its' environment (Guisan and Thuiller 2005). This means that a species occupies its' entire habitable range. This assumption is unrealistic and problematic because dispersal can be constrained by anthropogenic intervention and biotic interactions (Svenning and Skov 2004; Araujo and Pearson 2005). While this assumption is necessary to consider for SDM applications that extrapolate into space and time, one must be cognizant of the risk. The physiological tolerance of species to novel climates can be estimated by a model but should be validated by experimentation (Araujo and Peterson 2012).

Multi-collinearity of predictor variables is an important factor that can affect model selection and lead to erroneous model projections (Guisan and Thuiller 2005). Models must be based solely on

the biologically significant predictor variables. Determining significant environmental variables can be difficult and may lead to one of two outcomes: 1) Model selects most significant predictor variables that best describe population distribution and provides an accurate projection or 2) Model selects insignificant, highly correlated predictor variables that result in an under or over estimation of potential population distribution (Gray 2011).

3. METHODS

3.1. Provenance data

Provenance data was obtained from Herva (2016). Herva (2016) conducted a literature review to create a comprehensive list of Lodgepole pine provenance trials across Europe. Twelve conference proceedings and technical reports (Fryk 1980, Larsen 1980, Lindgren and Lindgren 1978, Lines 1996; Madsen 1992, Magnesan 1992; Orlic and Gracan 1992; Persson 1979; Pfeifer 1992; Ruotsalainen 1992; Stephan et al. 1992; de Vries 1992), unpublished data of six German provenance trials from the von Thünen Institut, and five Swedish trials from the Siljanfors Experimental Forest (Hagner and Fahlroth, 1974; Karlman 2014) were compiled and used to create the provenance dataset for this study.

In total, 72 sites across Europe had suitable data to be used in this analysis. I classified the sites into different regions in Europe. Except for Scandinavia, each country was used for a regional summary. This is because most provenance trial series are national efforts, with the same provenances replicated in multiple sites within each country. For Scandinavia, the environmental gradients were too large for national summaries, however, so another region “Northern Scandinavia” was created for regional summaries (Fig 1).

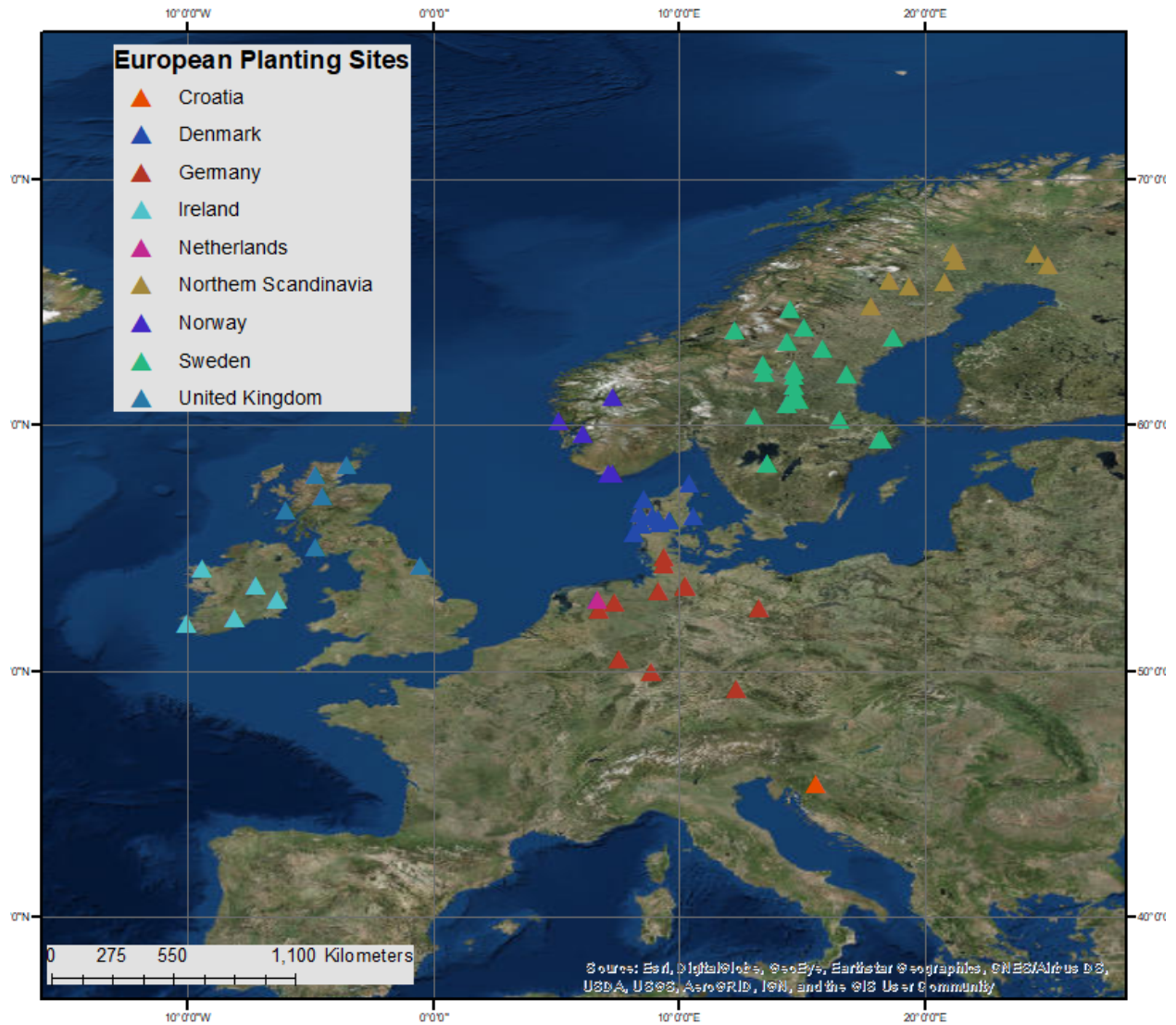


Figure 1. Map of 72 European Lodgepole pine provenance trials sites sorted into 10 European regions

Across the 72 sites, 223 North American provenances were tested. Provenance locations from North America were also grouped into different regions of origin by an ecological classification system: Boreal, Cascades, Central Coast Wet, Central Coast Dry, Northern Coast, Southeast Interior, Southern Coastal, Southern Interior and Sub-Boreal (Figure 2).

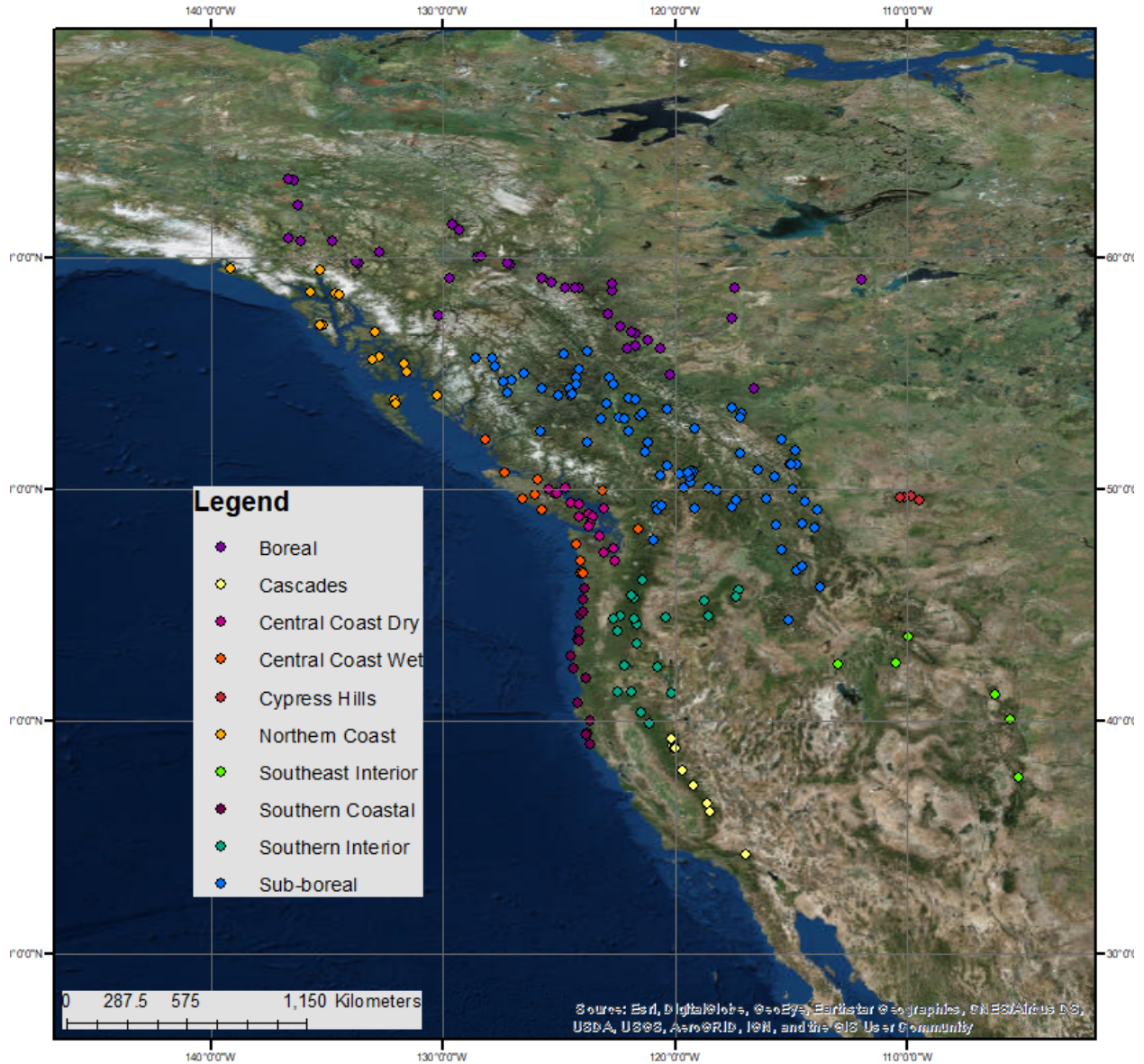


Figure 2. Lodgepole pine seed source collection sites in its' native North America sorted by seed origin type.

Height was used to measure provenance performance because it was uniformly reported across all provenance trials. Height data was normalized for each planting site to account for different test site age and different site factors. This allowed for environmental factors to be excluded and to only consider genetic influences on provenance performance.

3.1.1. Analysis of lodgepole pine growth data in provenance trials

To assess consistency of provenance performance within sites and within European regions, site height means were calculated using the *plyr* package for the R programming environment. Percent deviation (%) of each seed origin from site mean was calculated to compare seed origin performance across trials of different ages.

3.1.2. Estimating origin means by European region

To estimate the height means by region, a mixed model with fixed effects was run on provenance data using a combination of the *lme4* and *lsmeans* packages for the R programming environment. The *lmer* function provides Best Linear Unbiased Estimates (BLUEs), a preferred method to estimate means for experiments by different researchers that have accumulated over years. The site means were then recalibrated to set the average of all origins for a country to zero.

3.1.3. Estimating provenance performance at age 30

One of the objectives is to compare the performance of Lodgepole pine provenance data with other species in the same general region where Lodgepole pine was tested. To compare Lodgepole pine provenances to other species, we used a site index curve to derive absolute values for a uniform age. Using a site index equation for interior Lodgepole pine developed by the B.C. government (Thrower et al. 1994), we fitted non-linear regressions to height data from best performing seed origin of each European region to obtain growth estimates at age 30.

Site Index Curve Equation:

$$H = 1.3 + (S - 1.3) \left(\frac{b1}{b2} \right)$$
$$b1 = 1 + \exp[7.815 - 1.285 \ln 50 - 1.007 \ln(S - 1.3)]$$
$$b2 = 1 + \exp[7.815 - 1.285 \ln A - 1.007 \ln(S - 1.3)]$$
$$y_{tb} = 5.6 + (42.64/S)$$

Where:

H= height (m) of best performing seed origin in European region

S= site index (height at 50 years breast-height age)

A= breast-height age (years)

y_{tb}= number of years to reach breast height (1.3 m)

3.2. Competition analysis using site index curves

Next, we want to compare absolute growth performance of Lodgepole pine provenances with other local species. Using the same approach as above, we use published site index curves for a comparison at age 30. Site index curves are usually generated from forest inventory data. Here we report site index values for sites classified as poor, medium or high (Assmann 1970, Forestry Commission 1920, Gustavsen 1980, Hägglund 1974, Hägglund 1980, Johansson 1994, Karlberg 1961, Karlsson 1999, Karlsson 2000, Lewkadi 2012, Liziniewicz 2016, Nord-Larsen 2009, Vuokila 1972). For other publications, site quality was not specified (Bradley 1966, Nord-Larsen 2009, Pretzch 1996, Pretzch 1997).

3.3. Inventory data

As an additional competition comparison, I selected growth data from a European inventory plot database (van der Maaten et al. 2017) that were collected within a buffer zone of 300 km around each provenance trial (Figure 3). Four forestry species were selected to represent local competition (*Picea abies*, *Pinus sylvestris*, *Pseudotsuga menziesi* and *Quercus petrae*). Local European forestry species that were found within each buffer zone were deemed regionally comparable to its' respective provenance trial and extracted.

The local species growth data extracted from the ArcGIS layer was separated by region and species. Height was averaged between 25- 35 years to obtain a 30 year midpoint average for each species to compare against growth data obtained in section 3.4 and 3.5.

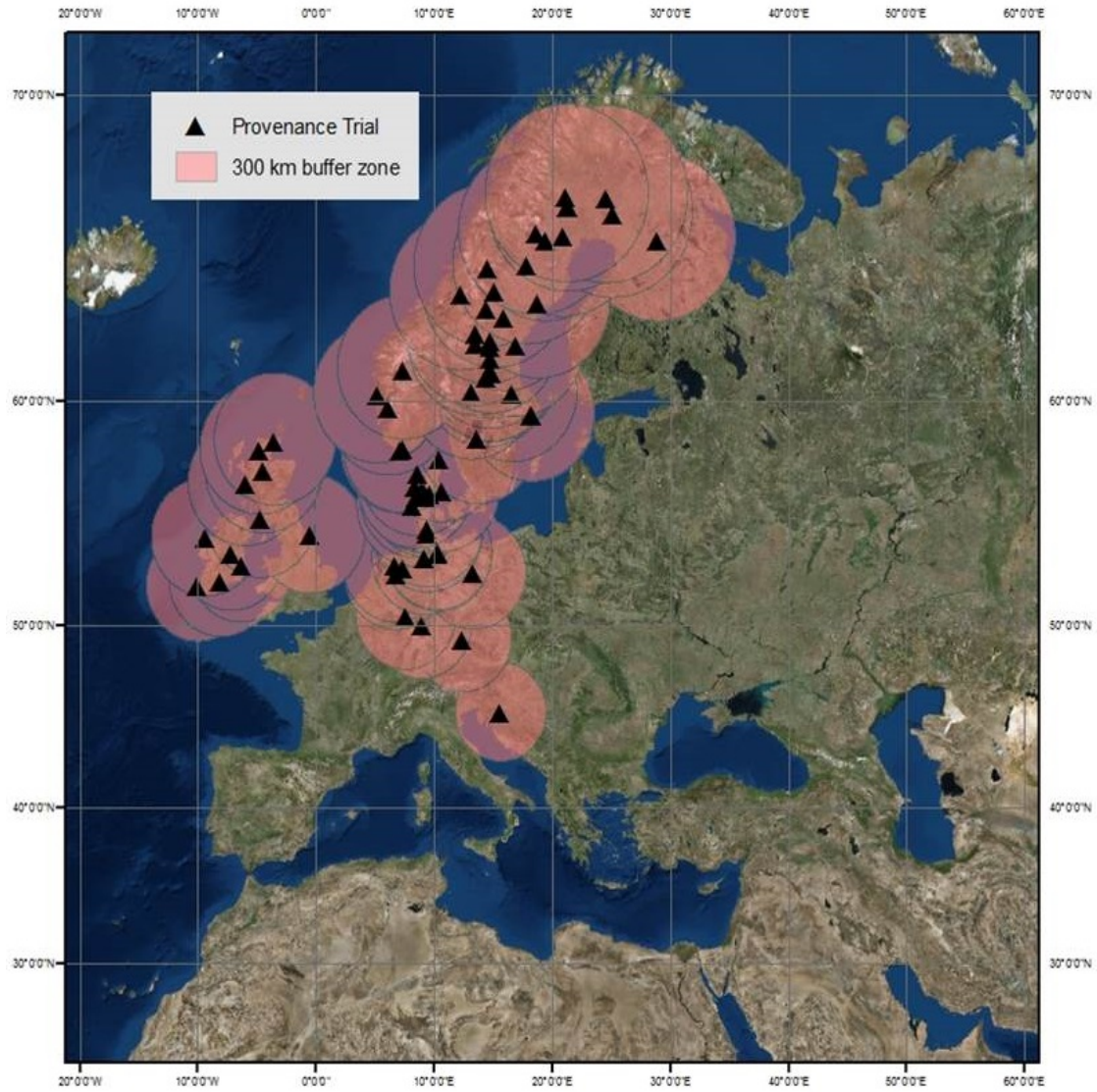


Figure 3. Map of 72 Lodgepole pine provenance trial sites in Europe with a 300km buffer

3.4. Disease and pest data literature review

Besides a growth comparison, we also want to evaluate potential risk factors for planting an introduced species within or beyond their realized climatic niche. An extensive literature review was conducted to document pest and disease outbreaks on Lodgepole pine trees across Europe. Peer-reviewed literature following strict search syntax (Table 3) was obtained using the following databases: CAB eBOOKs, Agriculture & Environmental Science Database, Google Scholar and Web of Science. The University of Alberta Discovery Service (EBSCO) was used to obtain multiple IUFRO conference proceedings and non-digitized peer-reviewed journal articles. Grey literature including unpublished data in journal articles for Ireland and the United Kingdom were obtained via email. Government reports were obtained through Google Search Engine and Open Grey, a database for grey literature in Europe.

The literature review retrieved an impressive 54174 sources across all databases. Almost half of the searches were briefly screened for relevance. Many of the retrieved articles were not relevant or made no mention of a pest outbreak on Lodgepole pine trees or a European country. Once the rigorous screening process was complete, over 98% of the retrieved articles were discarded. The remaining 243 were carefully evaluated for specific information on: pest/disease name, location of outbreak, extent of damage, comparative analysis to other local species and susceptibility of different provenances. This evaluation process further reduced articles from 243 to 39 unique sources with detailed accounts of pest outbreaks and a general measure of outbreak severity.

The final 39 outbreak reports were summarized and separated into seven countries: Croatia, Denmark, Finland, France, Germany, Netherlands, Sweden and the United Kingdom. Each outbreak was given a severity score from 1-5 (Table 1).

Table 1. Descriptions of each severity score assigned to reported pest outbreaks on Lodgepole pine trees across Europe from 1 (lowest) to 5 (highest)

Severity Index	Literature Descriptors
1	<ul style="list-style-type: none"> ▪ Very low susceptibility ▪ Negligible/ non-significant damage reported ▪ Rarely occurs
2	<ul style="list-style-type: none"> ▪ Less susceptible than other provenances ▪ Some localized damage reported ▪ Only one field trial found damaged
3	<ul style="list-style-type: none"> ▪ Most provenances considered slightly susceptible ▪ Some severe infections kill trees ▪ Provenance slightly more susceptible than others ▪ Small scale outbreak
4	<ul style="list-style-type: none"> ▪ Often severe outbreak ▪ Serious problem when outside specified range ▪ Can cause considerable damage
5	<ul style="list-style-type: none"> ▪ Affects all young shoots ▪ All provenances highly susceptible ▪ Very limited growth ▪ Damaged Lodgepole more than any other local forest species

4. RESULTS

4.1. Provenance data

4.1.1. Site-level analysis

Provenance data was first analyzed by seed origin performance at each site. This analysis showed the variability in Lodgepole pine response to different planting sites. Generally, European planting sites with similar climates to North American seed origin sites were best suited.

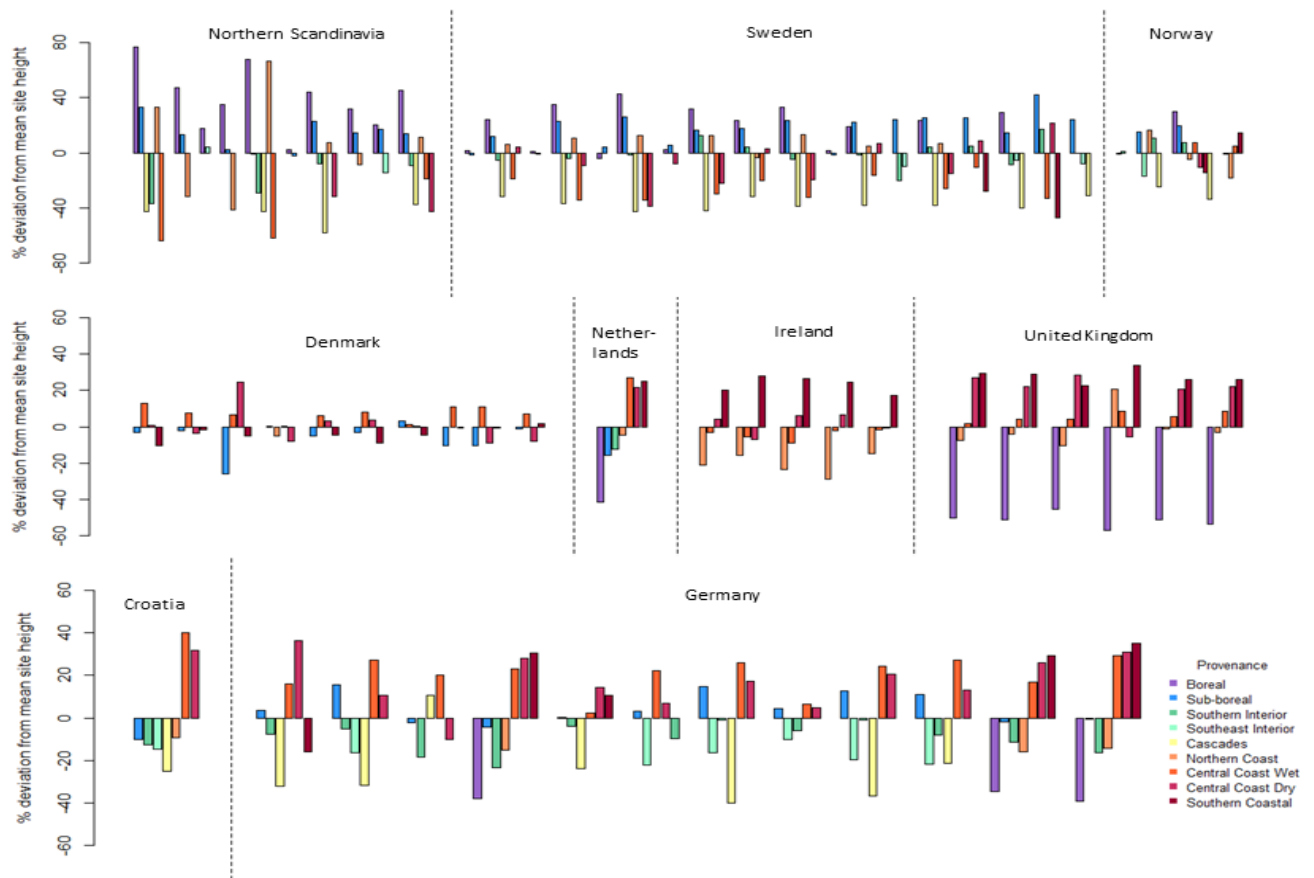


Figure 4. Percent (%) deviation from mean regional height of 9 Lodgepole pine seed origins in Northern Scandinavia (Finland and Northern Sweden), Southern Sweden, Norway, Denmark, Netherlands, Ireland, United Kingdom, Croatia and Germany.

Northern Scandinavia

Movement further south and west strongly affected the growth response of each origin in Northern Scandinavia. Boreal seed sources were the strongest performers in higher latitudinal planting sites (Figure 4). The largest deviations from site mean were observed in Northern Scandinavia. Lappeasuando, Sweden (67.05°N, 21.13°E) is the most northern provenance and has the strongest boreal performance (76.98% higher than site mean). Similarly, boreal provenance performance was 67.42% higher in Kompo, Sweden (66.73°N, 21.27 °E) and 47.14% higher in Kolari, Finland (67.02°N, 24.50°E). Conversely, Lappeasuando, Kompo, Kolari also had the weakest Central Coast Wet performances (-63.82%, -61.76% and -69.5% respectively).

Northern Coast performance was very site-dependent. Sites that were climatically similar such as Kompo, Sweden and Kolari, Finland yielded opposite results (66.74% and -31.58% respectively). It is interesting to note that most sites found in Finland showed very poor Northern Coast performance whereas the provenances found in northern Sweden did well.

Sweden

Southern Sweden followed a similar latitudinal pattern as Northern Scandinavia, with less variability within sites. At sites Backskogen (60.37°N, 13.43°E) and Skansen (60.27°N, 16.57°E) both boreal and sub-boreal were planted. In these milder temperature regions, we began to see sub-boreal provenances replace boreal as the strongest performing origins (25.1% and 22% respectively). Below 60°N, boreal origins were no longer tested in trials; sub-boreal continued to be the strongest origin. Central Coast Wet, Central Coast Dry and Southern Coast were the poorest performing provenances.

Norway

Norway's provenance analysis produced different results from both Finland and Sweden. Although relatively similar in latitude to Sweden, Norway's sites were along the coast whereas

Southern Sweden's planting sites were more continental. Central Coast Wet struggled to perform in Finland and Sweden, however it was 7.1% above the site mean in Erkheim, Norway (59.70°N, 6.08°E). Moving further south towards the most maritime site Kaofjord, Norway (58.05°N, 7.12°E), Southern Coastal became the strongest provenance performer (+14.6%)

Central Europe

Similar to Scandinavia, Southern Interior and Southeast Interior were poor performers across Germany and Croatia (Figure 4). Only one planting site was monitored in Croatia; however, this site followed a similar latitudinal pattern observed in Scandinavia. Southern provenances Central Coast Wet (+40%) and Central Coast Dry (31.7%) were the most successful.

Boreal shifted from the strongest provenance in Scandinavia to the poorest performer in Germany, most notably at the most southern German planting site Bodenworh (49.30°N, 12.33°E), where it was -39.2% below the site mean. Southern provenances Central Coast Wet, Central Coast Dry and Southern Coastal were the strongest performers across Germany. Central Coast Dry was 30.8% above site mean at the most southern planting site Bodenworh, but also 36.44% above site mean at the most northern site Eggebeck (54.63°N, 9.38°E;). Sub-Boreal provenances did not follow a strong latitudinal pattern as their performance varied greatly across all German sites.

Maritime Europe

Maritime European planting sites yielded opposite results to Scandinavia (Figure 4). Origin performances were very consistent across the United Kingdom and Ireland. Southern Coastal were optimal seed sources across these regions. Northern Coast was the most unsuccessful source in Ireland (- 14.8 to - 28.7% below regional mean) and a moderately poor performer in the United Kingdom (- 1.2 % to -10.23 %). However, at the furthest NW site Fiunary, UK (56.58°N, 6.02°W), Northern Coast was 20.5% above site mean.

Only one site was tested in the Netherlands; however, it yielded very similar results to other maritime European regions. Central Coast Wet was optimal (27% above site mean) followed closely by Southern Coastal and Central Coast Dry (25.1% and 21.7% respectively).

Origin performance in Denmark was very site-specific. Denmark is relatively small and there is not a significant change in latitude or elevation, which may attribute to lack of variability.

Langagergaard (57.64°N, 10.43°E) is the most northern planting site in Denmark and Vejers (55.63°N, 8.15°E) is the most southern site; sub-boreal was the poorest performer at both sites (-25.9% and -10.25% respectively). Central Coast Wet was the strongest performer at most sites (0.42% - 10.84), except at Langagergaard where Central Coast Dry was exceptionally strong (24.5% above site mean).

4.1.2. Regional analysis

Regional provenance analysis showed the different growth response of seed origins by climatic region. Generally, boreal and sub-boreal were optimal in northern planting sites; conversely, southern seed sources were optimal in southern regions (Figure 5). Central Coast Wet and Southern Coastal provenances were strongest in warmer, maritime regions like the United Kingdom and Ireland; Central Coast Dry was optimal for warm, continental regions like Croatia and Germany. Cascades provenances were poor performers in all European regions.

Northern Scandinavia and the United Kingdom had consistent results across their regions but showed large within-site variability. Seeds sourced from native range extremities of Lodgepole pine deviated greatly from site means. Provenance performance in other European regions was more site-dependent, strongly influenced by proximity to coast among other factors.

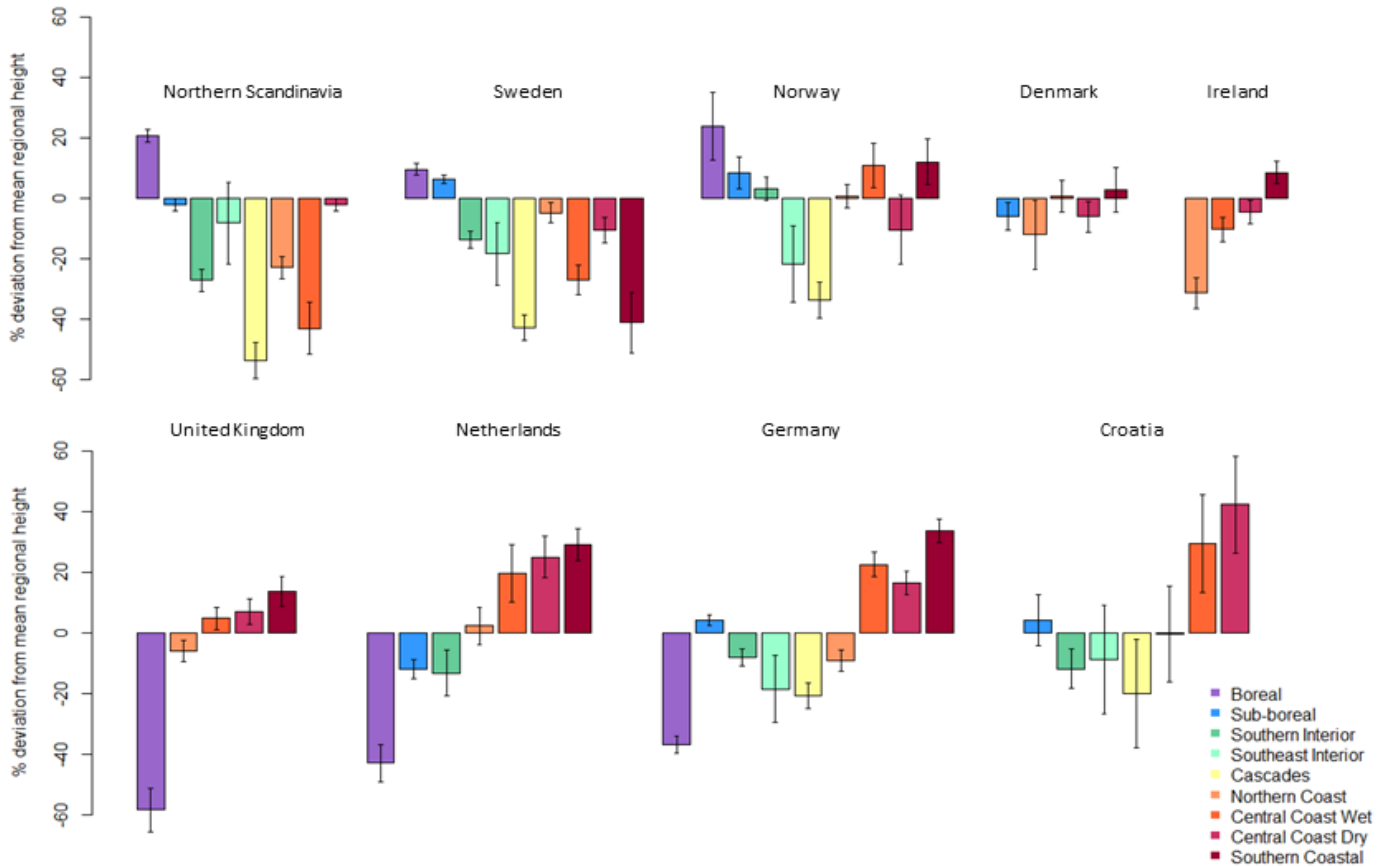


Figure 5. Percent (%) deviation from mean regional height of 9 Lodgepole pine seed sources in Northern Scandinavia (Finland and Northern Sweden), Southern Sweden, Norway, Denmark, Ireland, United Kingdom, Netherlands, Germany, Croatia

Boreal was the strongest seed origin across Scandinavia, ranging from +9.5% to 24.0% above than the region’s mean provenance height. The greatest difference in seed source performance across northern Europe was observed between Northern Scandinavia and Norway. Southern Interior and Central Coast Wet were very poor performers in Northern Scandinavia (-27.2% and -43.2% respectively); they both performed relatively well in Norway (3.2% and 10.9 % respectively).

Provenance performance was very consistent across central and coastal Europe (Figure 5). Boreal provenances were exceptionally poor performers in the United Kingdom (-58.5%), Netherlands (-43.0%) and Germany (-36.9%). Southern Coastal (2.9 %- 33.7%) was the strongest performing seed source. Denmark had the least variability across provenances. Aside from Northern Coast, provenance performance in Denmark did not significantly change across the region.

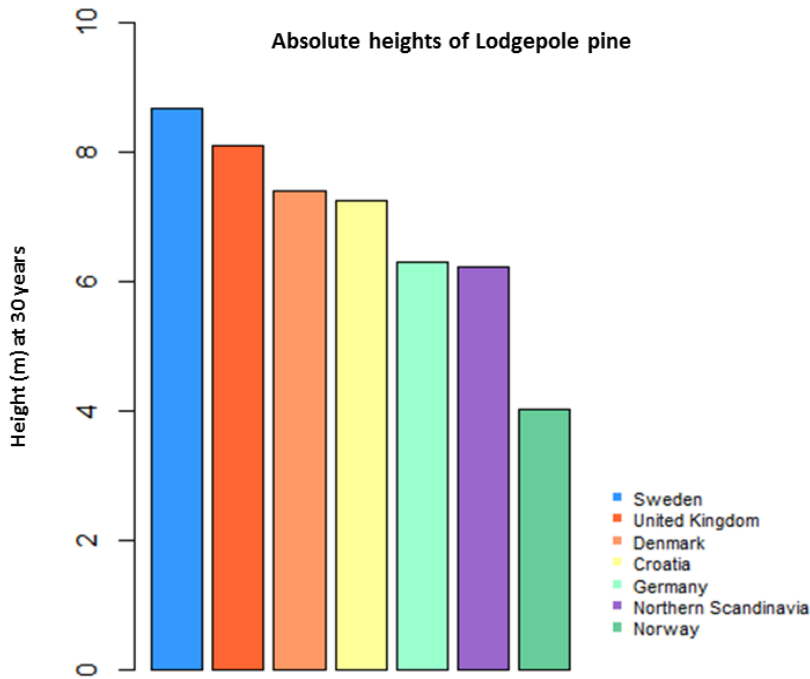


Figure 6. Absolute height (m) of Lodgepole pine trees derived from a site index curve equation (Thrower et al. 1994).

Absolute heights of Lodgepole pine trees at age 30 were calculated using a site index curve equation (Figure 6). Except for Sweden, the strongest Lodgepole pine height growth was observed outside of the realized niche. Absolute growth heights were lower within the realized niche (Northern Scandinavia and Norway).

4.2. Competition analysis

Growth performance of other forestry trees were compared against Lodgepole pine provenance trials to assess competition risk. Lodgepole pine was significantly outcompeted by other forestry species when planted outside of the realized niche.

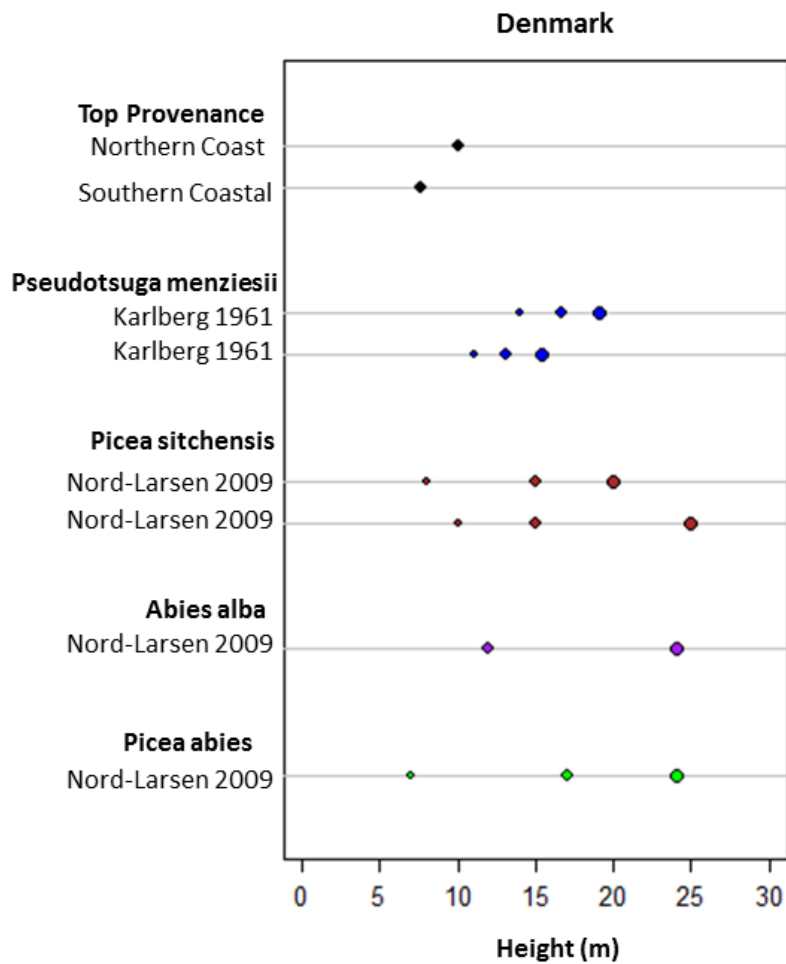


Figure 7. Height (m) of forestry species in Denmark at age 30 on poor (○), medium (◐), and high-quality sites (●).

4.2.1. Outside predicted habitat

Lodgepole pine was the poorest performing forestry species in Denmark (Figure 7). Common Danish forestry species Sitka spruce (*Picea sitchensis*) and Douglas fir (*Pseudotsuga menziesii*) significantly outcompeted Lodgepole pine. There was minimal overlap with Silver fir (*Abies alba*) and Norway Spruce (*Picea abies*) growing on poor quality sites.

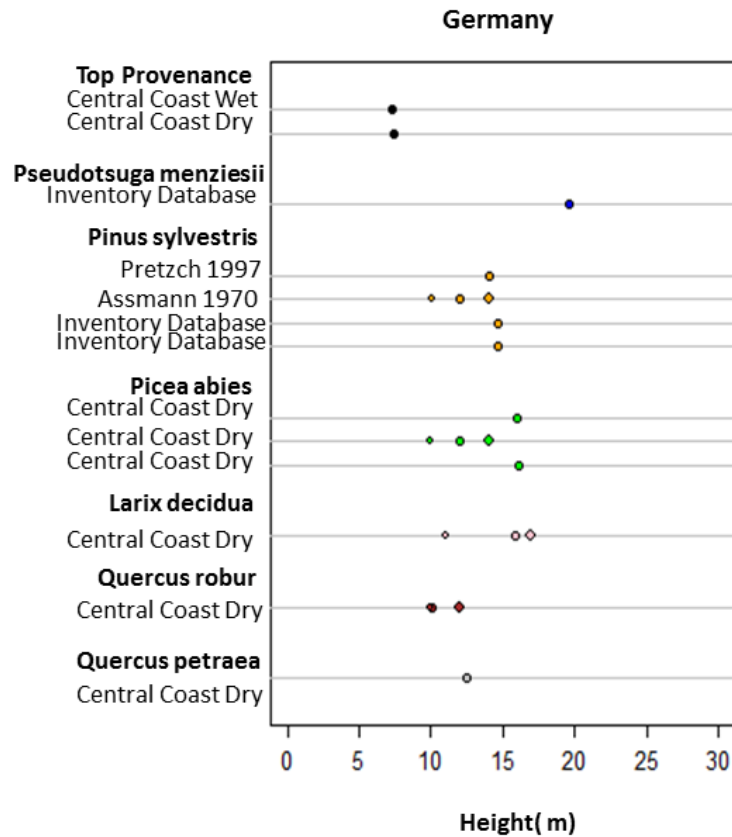


Figure 8. Height (m) of forestry species in Germany at age 30 on poor (○), medium (◇), and high-quality sites (●)

Lodgepole pine was the poorest performing forestry species in Germany (Figure 8). There was no overlap with other forestry species, leading one to believe that Lodgepole pine would be significantly outcompeted.

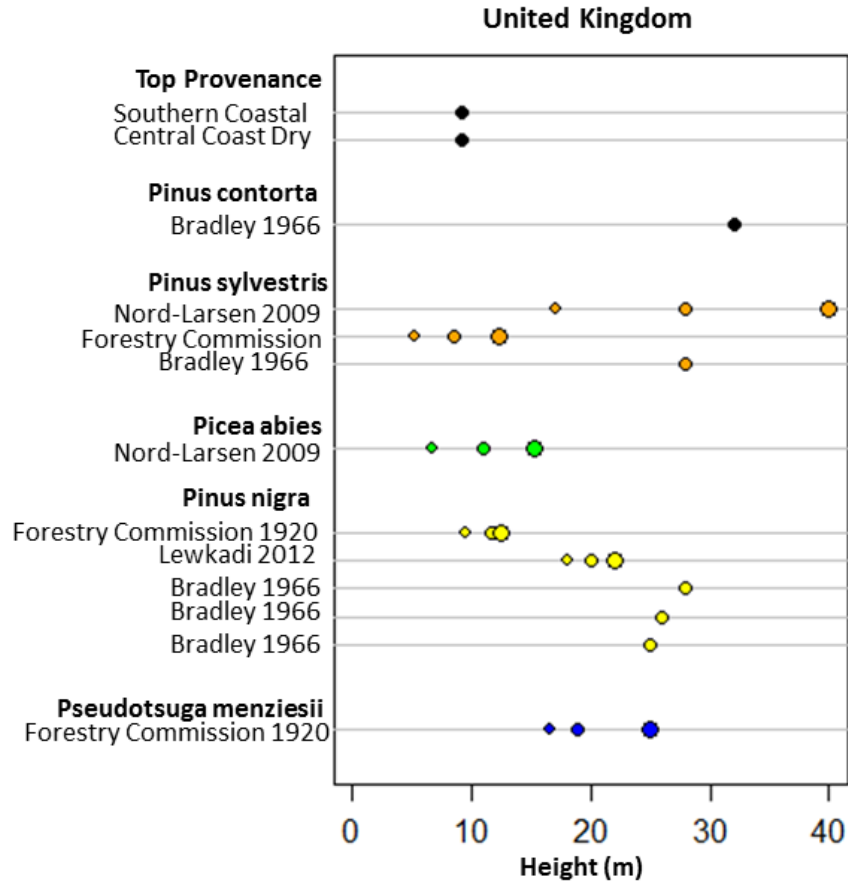


Figure 9. Height (m) of forestry species in the United Kingdom at age 30 on poor (◊), medium (○), and high-quality sites (●)

Lodgepole pine is moderately outcompeted by other species in the United Kingdom (Figure 9). There is some overlap with Norway Spruce, Black pine (*Austrian pine*) and Scots pine. While there are other local species such as Douglas fir and Black pine that display stronger growth potential, Lodgepole pine may be a competitor in the United under certain conditions.

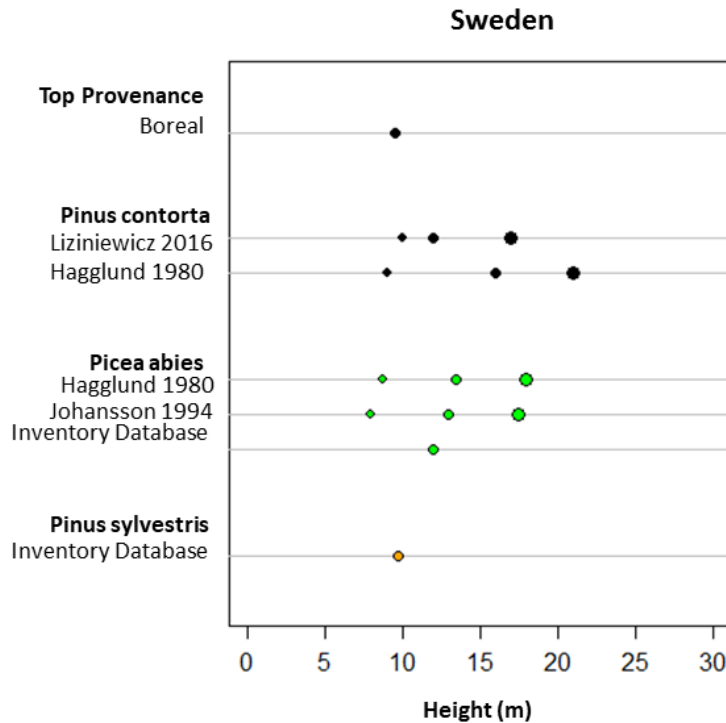


Figure 10. Height (m) of forestry species in Sweden at age 30 on poor (○), medium (◐), and high-quality sites (●).

4.2.2. Inside predicted habitat

Lodgepole pine is a strong forestry species in Sweden (Figure 10). Strong overlap was observed in growth performance among Norway Spruce and Scots pine, the two most important local forestry species in Sweden.

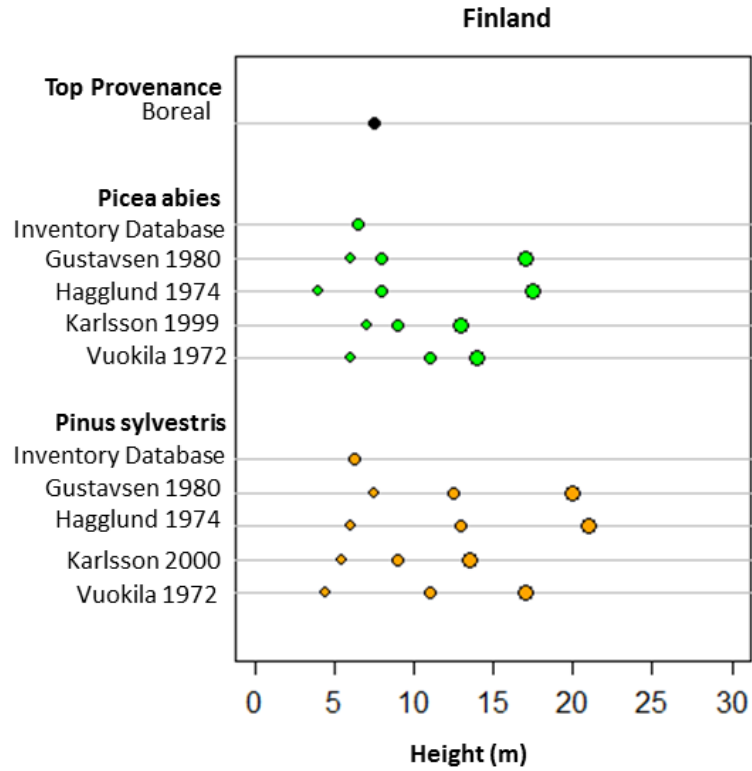


Figure 11. Height (m) of forestry species in Finland at age 30 on poor (○), medium (◐), and high-quality sites (●).

Lodgepole pine growth performance is comparable to Norway spruce and Scots pine in Finland (Figure 11). Moderate overlap indicates the competition potential of Lodgepole pine.

4.3. Pest and disease overview

Generally, Lodgepole pine trees planted in countries outside of the predicted habitat are at higher risk to pest and disease outbreaks (Figure 12). Pine shoot moth (*Rhyacionia buoliana*) is the greatest threat to coastal provenances planted in central and Western Europe. DNB (*Dothistroma septosporum*) is widely distributed across the United Kingdom and is the greatest threat to interior provenances. Countries found within predicted habitat have experienced moderate to negligible pest outbreaks. Sweden has recorded moderate outbreaks of Sclerroderris canker (*Gremmeniella abietina*) to which all provenances are susceptible. Finland and Latvia are the countries of least concern when examining historical pest outbreaks on Lodgepole pine.

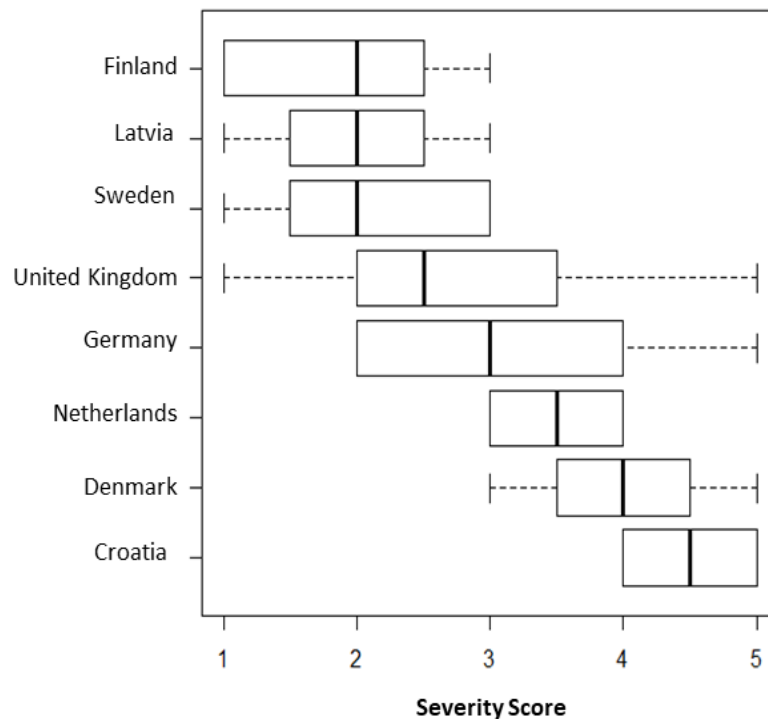


Figure 12. Summary of pest outbreak severity on European Lodgepole pine

4.3.1. Outside predicted habitat

Lodgepole pine trees are at high risk of a pest outbreak in Croatia (Figure 13). Most provenances in Croatia are highly susceptible to *Diorcytria splendidela*. All provenances are highly susceptible to pine shoot moth however Orlic et al. (1993) found that provenances from Idaho, California and Oregon suffered the most severe attacks.

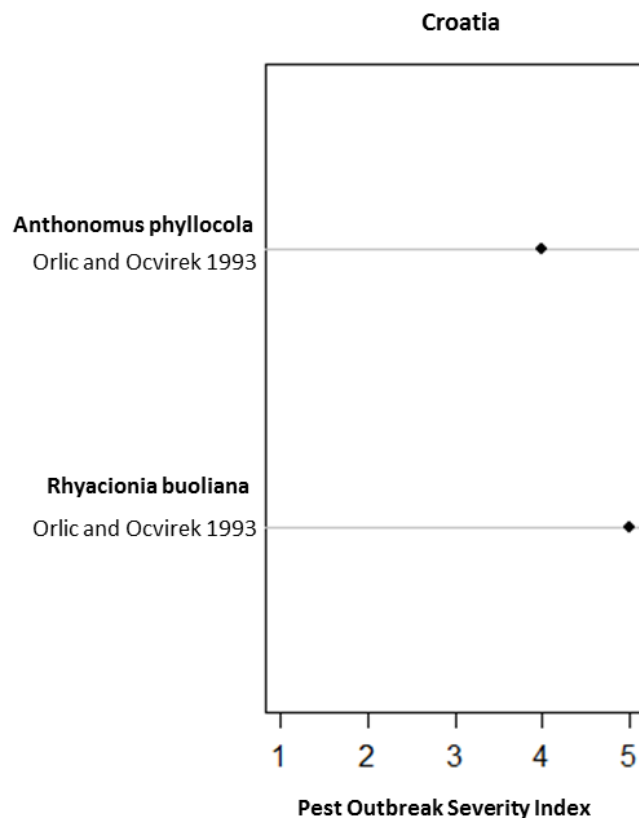


Figure 13. Pest severity outbreak risk on Lodgepole pine trees in Croatia ranked from 1-5 (low to high risk)

Lodgepole pine trees have been severely affected by pine shoot moth in Denmark (Figure 14). Esbjerg (1971) found that Lodgepole pine trees were attacked by pine shoot moth more severely than other common Danish forest species including Scots pine (*Pinus sylvestris*), Mountain pine (*Pinus mugo*) and Austrian pine (*Pinus nigra*). While many inland provenances were severely attacked, coastal provenances were the most susceptible to the pine shoot moth. Heavier infestations were recorded following drought years.

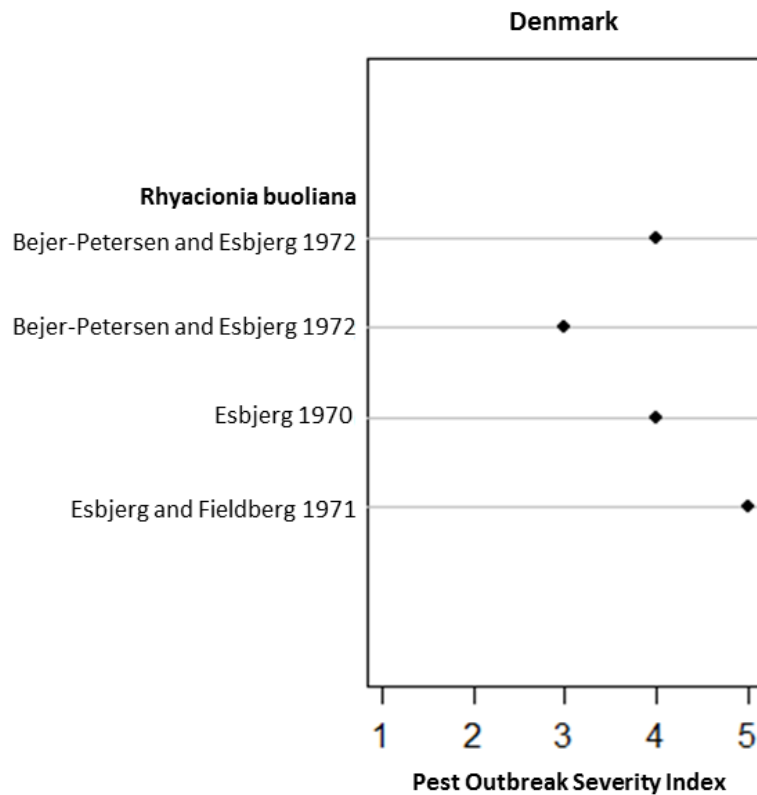


Figure 14. Pest severity outbreak risk on Lodgepole pine trees in Denmark ranked from 1-5 (low to high risk)

Susceptibility to pest outbreaks in Lodgepole pine stands in Germany is dependent on region and provenance (Figure 15). Pine shoot moth is the greatest threat to coastal provenances in Northern Germany; inland provenances were less impacted. However, both coastal and inland provenances in were less susceptible to pine shoot moth outbreaks in southern Germany. There have been a few low to moderately severe reports of *Crumenulopsis* pine dieback (*Crumenulopsis sororia*) in Germany. Wyoming and California are the most susceptible provenances across the country. Lodgepole pine was reportedly more susceptible to *Heterobasidion annosum* than neighbouring species Scots pine (*Pinus sylvestris*), however the outbreak was not widespread or significant. *Aarmillistirls mellae* has severely attacked and killed Lodgepole pine stands in western Germany.

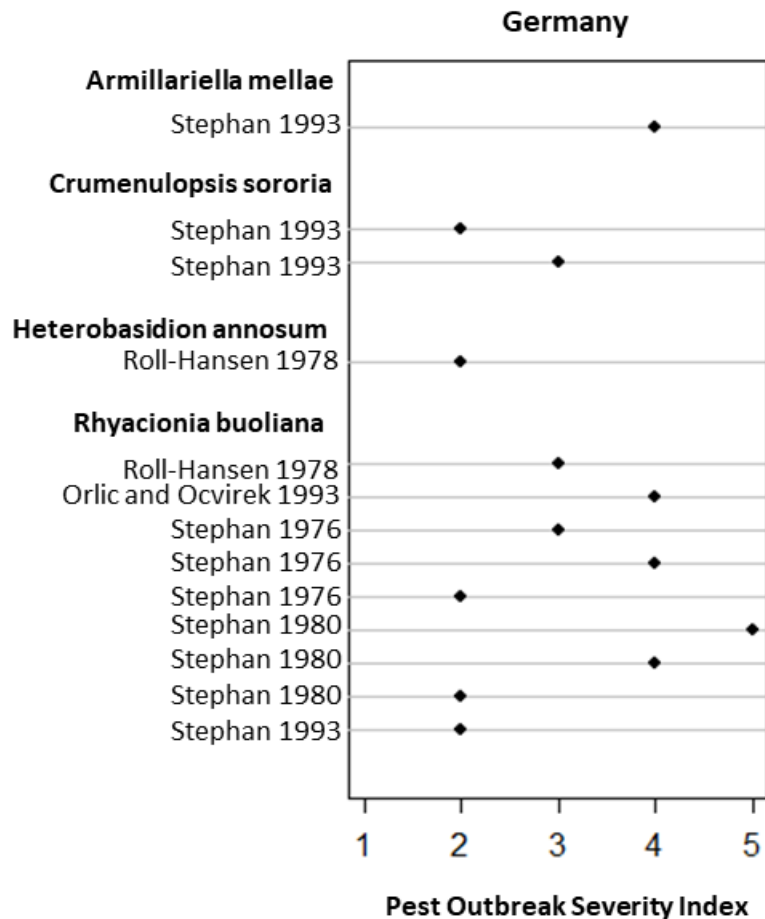


Figure 15. Pest severity outbreak risk on Lodgepole pine trees in Germany ranked from 1-5 (low to high risk)



Figure 16. Pest severity outbreak risk on Lodgepole pine trees in United Kingdom ranked from 1-5 (low to high risk)

There are several pests that have limited Lodgepole pine growth in the United Kingdom (Figure 16). The greatest threat to Lodgepole pine trees in the United Kingdom is Dothistroma needle blight (Dothistroma septosporum). Dothistroma needle blight (DNB) is widely distributed across Wales and England. It has been more closely monitored in recent years because DNB is becoming more widespread and severe. Interior provenances are extremely susceptible to DNB; coastal provenances are moderately susceptible and Alaskan provenances are least susceptible. Pine beauty moth (Panolis flammea) caused severe defoliation in northern Scotland in the late 20th century; recent reports show less damage linked to this pest. Ramichloridium shoot dieback (Ramichloridium pinide hood & rahman) occurs widely across the United Kingdom but causes considerable damage in western Britain. Ramichloridium shoot dieback infects young shoots

during the early ingrowing season; while most outbreaks damage shoots, some severe infections kill trees. Southern coastal provenances are more susceptible than northern coastal and interior provenances.

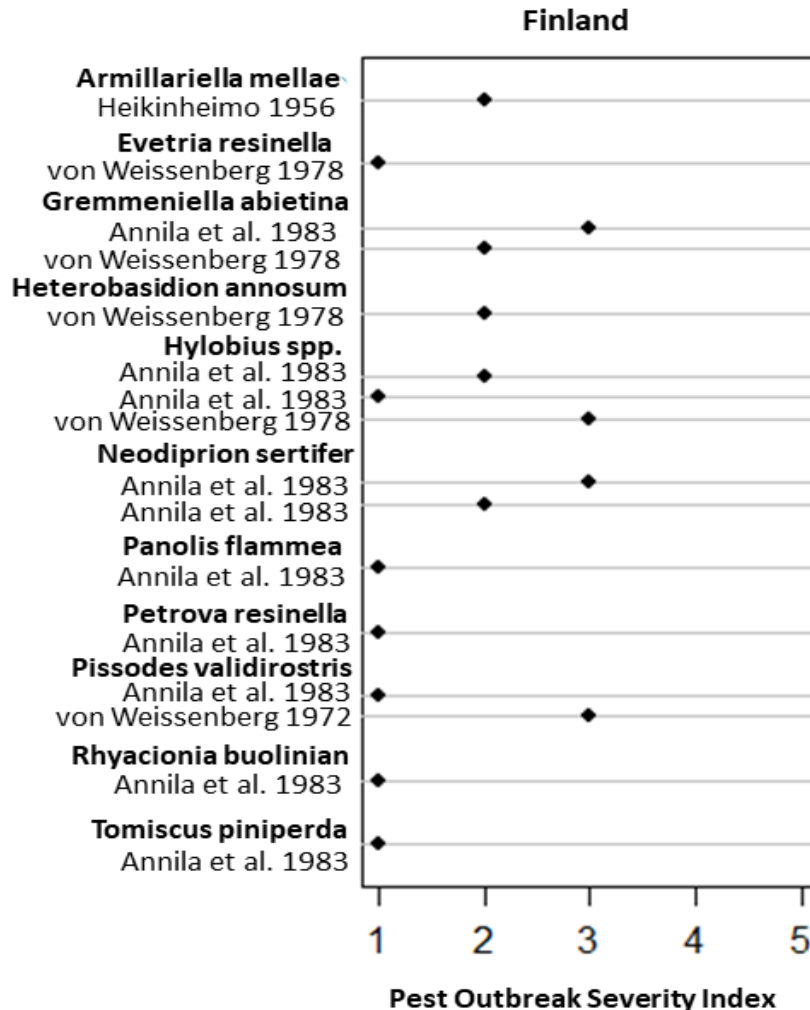


Figure 17. Pest severity outbreak risk on Lodgepole pine trees in Finland ranked from 1-5 (low to high risk)

4.3.2. Inside predicted habitat

All the pests reported in Finland are rarely found and are not alarming (Figure 17). Annosus root rot (*Heterobasidion annosum*) has the potential to cause the most damage to all stands, however it is not frequently found. European pine sawfly can cause severe defoliation in older stands; this

pest is less common in younger plants and in Cypress Hill provenances. Lodgepole pine and Scots pine are equally susceptible to honey fungus (*Armillariella melleae*); however Lodgepole pine is more susceptible to *Evetria resinella* than Scots pine.

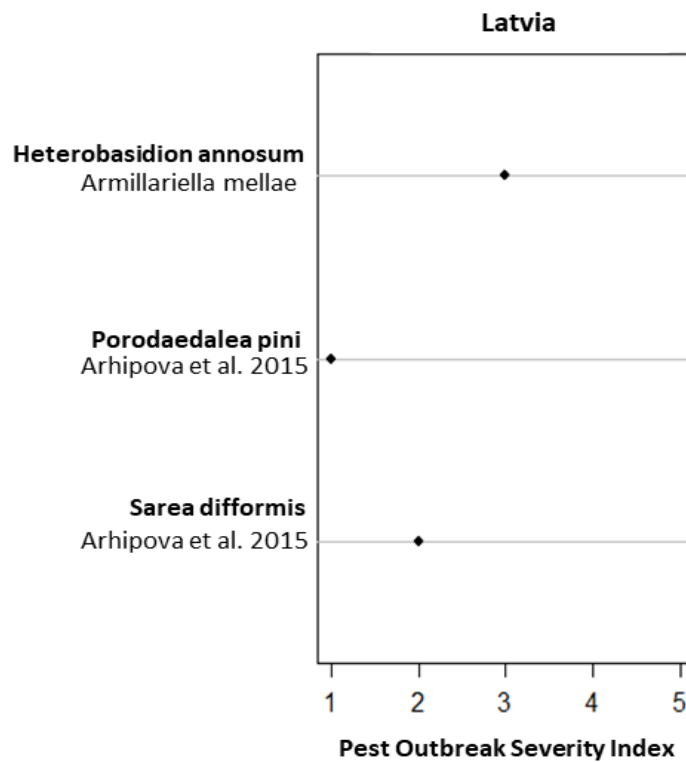


Figure 18. Pest severity outbreak risk on Lodgepole pine trees in Latvia ranked from 1-5 (low to high risk)

Lodgepole pine planted in Latvia is at low risk of a pest outbreak (Figure 18). Annosus root rot (*Heterobasidion annosum*) attacks Lodgepole pine more frequently than Scots pine in Latvia. Although *Sarea difformis* is the most common fungal isolation found on Lodgepole pine trees, it appears irregularly and typically does not cause significant damage. Red ring rot (*Porodaedalea pini*) is rarely found and remains dormant for years.

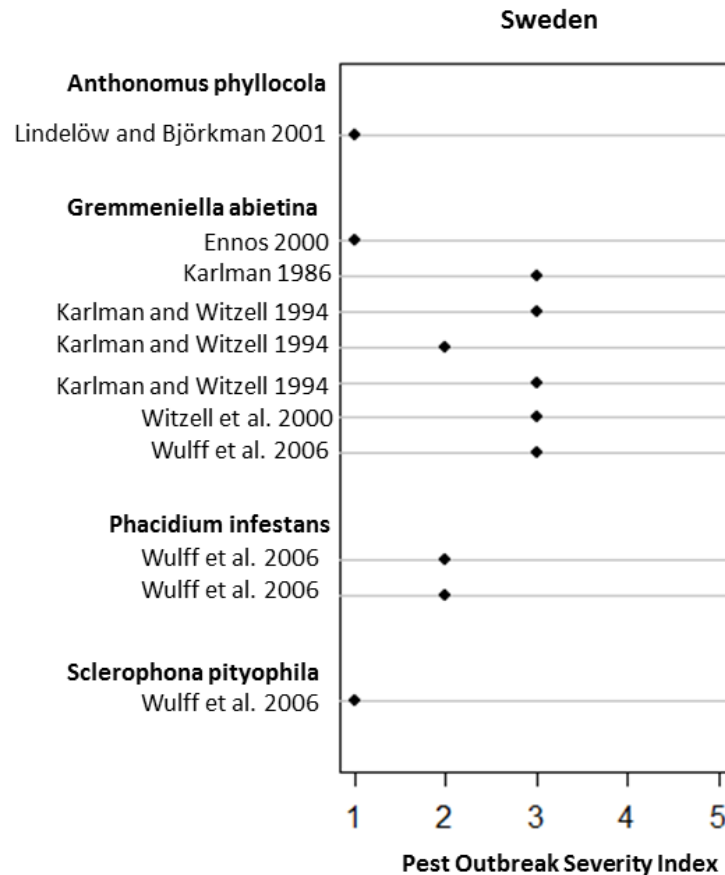


Figure 19. Pest severity outbreak risk on Lodgepole pine trees in Sweden ranked from 1-5 (low to high risk)

Lodgepole pine in Sweden is at moderate risk of a pest outbreak (Figure 19). The biggest pest outbreak on Lodgepole pine trees in Sweden was caused by the fungal pathogen Scleroderris canker (*Gremmeniella abietina*). While some provenances such as Northern British Columbia and Yukon have been impacted, southern provenances are the most affected. Southern provenances are also more susceptible to *Phacidium infestans* (snow blight). However, snowblight is a lower risk to Lodgepole pine than Scots pine due to its' rapid early growth. *Anthonomus phyllocola* and *Sclerophona pityophila* are considered secondary pathogens that are found on Lodgepole pine after weather damage or following a Scleroderis canker outbreak.

5. DISCUSSION & CONCLUSIONS

5.1. SDM predictions vs. observed growth

The species distribution model (SDM) developed by Herva (2016) predicted suitable habitat for Lodgepole pine in Europe, shown here for reference in Figure 20.

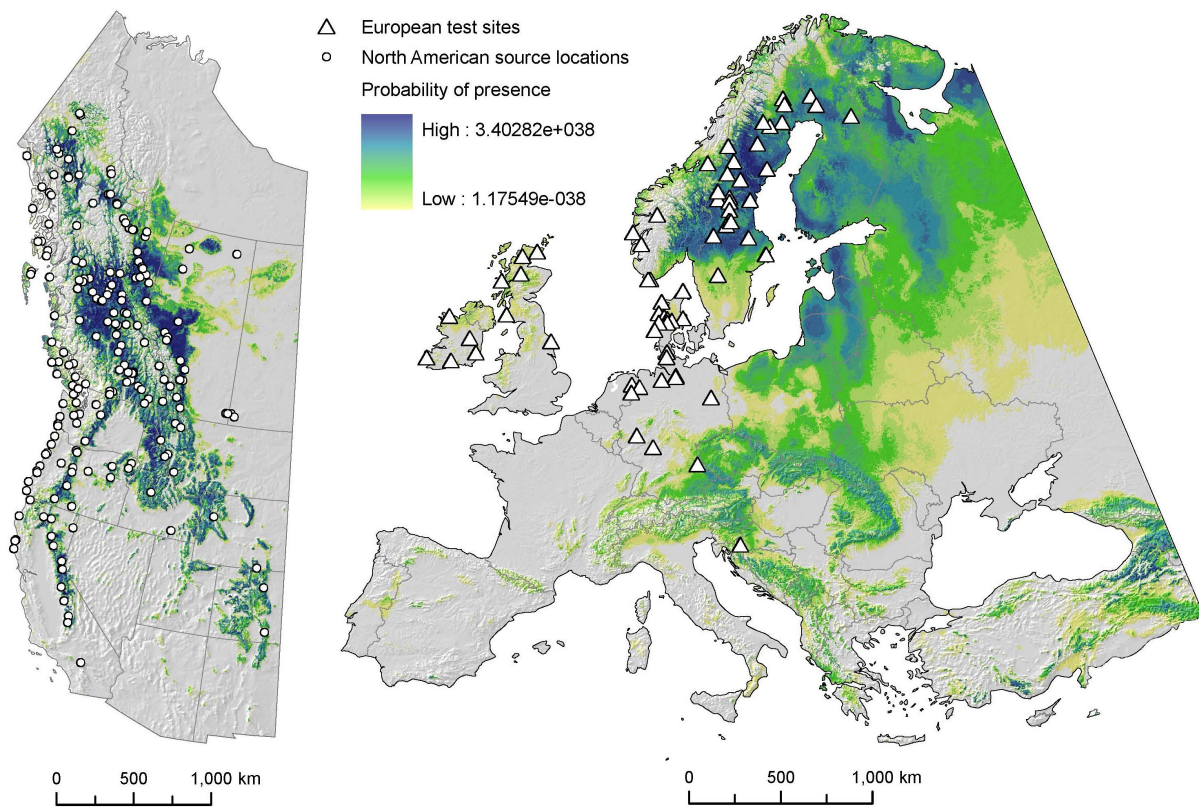


Figure 20. Lodgepole pine species distribution model output as probability of presence indicating the modelled suitable habitats of the species in both Western North America (left) and Europe (right). The white circles (○) represent seed collection sites and the white triangles (△) represent European planting sites (figure reproduced from Herva 2016).

5.1.1. Competition analysis

The competition analysis supported the SDM projections. Lodgepole pine was outcompeted by other local forestry species in European regions that were deemed unsuitable; however, Lodgepole pine was a strong contender in highly suitable European regions. Lodgepole pine was an excellent competitor to Scots pine, a valuable and native species to Northern Scandinavia (Northern Sweden and Finland). Studies support findings that exotic Lodgepole pine is superior to native Scots pine in both survival and stem growth in Sweden (Elfving and Norgren 1993). Fries et al. (2017) conducted a transcontinental reciprocal transplant experiment in which Lodgepole pine and Scots pine trees were observed in both their native and introduced habitats. Lodgepole pine was more productive than native Scots pine at one Swedish site, and equally productive to Scots pine at the other site. This study concluded that the higher success of Lodgepole pine in Sweden was due to the overall higher production capacity of Lodgepole pine as well as less damage observed by pests and pathogens.

There is also evidence that shows Lodgepole pine has a larger growth potential in Sweden than its' native Canada. Gundale (2016) found that Swedish soil provides better biota and has more nitrogen available for Lodgepole pine than in Canada, further supporting Lodgepole pine as a strong reforestation choice for Sweden.

It is important to note that the European Inventory Database was compiled in 2017 and the most recent growth values for European species in this study; growth curves found in literature date as far back as 1920. Site indices can change and may become less accurate with time. Spiecker et al. (1996) discovered an overall increase in productivity across 12 sites across Europe. This increase was attributed to a number of factors including: land use history and land use change, improved forest management regimes and climate change. Currently, Norway spruce and European beech stands in Central Europe exhibit significantly faster tree growth (+ 32 to 77%) than in 1960 (Pretzsch et al. 2014).

The competition analysis of the United Kingdom and Denmark relied exclusively on site index curves from literature (some values dating back almost 100 years) that were used in comparison to relatively recent Lodgepole pine provenance performances. These values may be conservative and underestimate the growth potential of key forestry species. The height difference between

local species and Lodgepole pine may be larger in current forests. Lodgepole pine, Scots pine and Norway spruce were planted more frequently in the United Kingdom in the early and mid-20th century. However, pest damage, lower productivity, and poor stem form of Lodgepole pine as well as limited site adaptability of Scots pine have significantly reduced forest coverage of these species. Forestry in the United Kingdom has shifted to superior Black pine and Douglas fir (Malcom 1997).

5.1.2. Pest analysis

The pest analysis moderately supported SDM projections; countries outside of the predicted habitats were more susceptible to large-scale pest outbreaks. Croatia, Denmark and the United Kingdom are at a moderate to high risk and Germany and Southern Sweden were at moderate pest outbreak risk; Northern Sweden, Finland and Latvia were of least concern.

Pine shoot moth (*Rhyacionia buoliana*) is the only significant threat to Lodgepole pine stands in central Europe, including Croatia, Germany and Denmark. The pine shoot moth causes severe infestations in pine trees, resulting in stem deformations and reduced product quality.

Overwintering pine shoot moths depend on snow cover for protection during cold winters (Miller et al. 1970). A decrease in snow cover can increase moth mortality; conversely drought conditions may exacerbate infestations. Central Europe is predicted to experience warmer and drier climates, reducing snow coverage but also increasing drought conditions. The future range and frequency of pine shoot moth outbreaks in response to climate change in Europe is uncertain, however the high susceptibility of all Lodgepole pine provenances in Croatia and Denmark put Lodgepole pine at a high risk of wide scale damage. De Vries (1992) reported that all the Lodgepole pine provenances in the Netherlands were also impacted by pine shoot moth. Germany was classified as a lower risk than other countries due to the provenance and region-dependent susceptibility.

Dothistroma needle blight (DNB) is the biggest threat to interior and coastal Lodgepole pine stands in the United Kingdom. Although DNB outbreaks on Lodgepole pine have not been historically reported in other parts of Europe, it has positively responded to climate change and

continues to expand its' range. In fact, DNB has become the most significant foliar disease on pine trees around the world (Drekhan et al. 2016). Fraser et al. (2016) reported that DNB has also caused severe damage to native Scots pine and exotic Black pine in the United Kingdom. DNB is widely distributed and interactions with Lodgepole should be closely monitored for future outbreaks not just in the United Kingdom, but across Europe.

Northern Sweden and Finland were regions of least concern. Scleroderris canker, a fungal pathogen, is the greatest threat to Lodgepole pine in Sweden. Southern provenances are the most affected; however, northern provenances are stronger performers in Northern Scandinavia and more likely to be used for reforestation purposes, reducing risk to Lodgepole pine. The risk of outbreak will most likely change under climate change: Karlman et al. (1994) found a strong correlation between disease severity and temperature sum at a site. Coastal provenances that were severely damaged by cold winters were the only trees attacked at Moskosel in northern Sweden. Deep snow coverage and long, cold winters that reduce the vitality of Lodgepole pine trees also accelerate the colonisation capacity of Scleroderris canker. Climate projections for northern Sweden predict that average temperatures will increase while the number of days with snow cover is expected to decrease. The risk of future Scleroderris canker in Northern Sweden is expected to be lower under future climate predictions.

The increased risk of pests on native species than exotic species has been reported in literature. Fries (2017) revisited the transcontinental reciprocal transplant experiment with Lodgepole pine and Scots pine in Canada and Sweden mentioned earlier. Lodgepole pine was less impacted by pests in Sweden; Scots pine was less impacted by pests in Canada. Mitchell and Powers (2003) studied a wide range of plants in North America and Europe; they found that 84% fewer fungi and 24% fewer virus species impact each plant species in their introduced habitat than the native range. Cincotta et al. (2009) compared exotic Norway maple trees and the North American sugar maple to compare foliar insect herbivory. This study found that Norway maple had significantly less leaf damage than sugar maple; sugar maple surrounded by Norway maples showed reduced herbivory. This phenomenon can be explained by the enemy release hypothesis: a hypothesis that argues some naturalized species become more successful than native species due to a lack of natural enemies (Mitchell and Powers 2003).

5.2. Implications of the study

Humans have been moving plants for centuries; however the intentional movement of forest stock as an adaptive strategy to climate has only recently become a point of interest. Assisted migration can be used to prevent species extinction, minimize economic loss and sustain ecosystems (Williams and Dumroese 2013). Most importantly, assisted migration could be an excellent climate mitigation and adaptation tool for forests. Climate is changing faster than a trees ability to adapt or migrate to optimal climatic conditions (Gray and Hamann 2013) therefore human intervention can be used to reduce the impact on our forests. However there are several uncertainties and legislative hurdles to overcome when prescribing an assisted migration program. Governments play a role in regulating intentional movement of seeds. Despite established seed transfer guidelines, the forestry community lacks a clear and standard understanding of how, when and where to move commercial forestry species (Williams and Dumroese 2013). Findings from studies such as this one can help establish a stronger understanding in reassessing and determining target migration distance, proper seed selection and deployment strategies. This study also emphasized the high degree of seed variability found within a species. Each genotype should be treated as a single entity and analyzed separate from other origins.

Lodgepole pine is predicted to become maladapted to part of its' native range, while also gaining suitable habitat further north. Moderate assisted migration within predicted suitable habitat has thus far shown favourable results (i.e. Gray et al. 2011). It is important to note that climate change may not follow future projections; a long-range seed transfer outside of predicted suitable habitat may result in severe physiological stress from maladaptation. Long distance seed transfers should be informed and sourced by robust provenance trials with known seed origins and native breeding programs to reduce seed maladaptation or pest outbreak risk. The role of photoperiodic changes and its' impact on different seed origins should also be considered; an unreasonable latitudinal seed transfer results in significant photoperiod changes that may hinder growth performance.

5.3. Limitations of Study

The most important underlying assumption of this project is that the SDM was based on the realized niche, not the fundamental niche of Lodgepole pine in its' native range. As previously discussed, the native range (and therefore the potential suitable habitat in Europe) may be wider but is being limited by competition or other biotic factors. The projections were also based off of the IPCC climate scenarios that are widely accepted, but still maintain a degree of uncertainty that can impact habitat projections. The provenance data was also limited and should have expanded further across Europe for a longer period of time.

An interesting concept that should be explored further is the role of belowground ecosystems in determining the geographic range of a species. Nunez et al. (2009) and Wandrag et al. (2013) find that the absence of key mutualisms from the native range of a plant species can limit the performance in its' introduced habitat.

5.4. Conclusions

The SDM model was able to accurately predict suitable habitat for Lodgepole pine in European regions. The model projection was validated by analyzing interspecific competition and historic pest & pathogen outbreaks. Areas that were considered highly suitable were also areas with lower risk of pest outbreak and lower competition. Consequently, unsuitable regions were also areas that had high interspecific competition and a higher pest outbreak risk. Lodgepole pine is a valuable and adaptive forestry species with a wide tolerance of climatic conditions. It may be worth continuing to invest in provenance trials and breeding programs in northern Europe as a climate mitigation strategy.

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APPENDIX 1.

Table 2. Number of pest outbreak studies retrieved, screened and evaluated from databases Agricultural and Environmental Science Database, Cab eBooks, EBSCO Discover Centre, Google Scholar, Google Search, Open Grey and Web of Science

Database	Query	Number of Articles Retrieved		
		Retrieved	Screened	Evaluated
Agricultural & Environmental Science Database	('lodgepole pine' or 'pinus contorta') AND ('Europe') AND ('disease' or 'pest')	17	17	1
	('lodgepole pine' or 'pinus contorta') AND ('Europe') AND ('pathogen')	3	3	2
	('twisted pine' or 'shore pine') AND ('Europe') AND ('disease' or 'pest')	0	0	0
	('lodgepole pine' or 'pinus contorta') AND ('Sweden') AND ('disease' or 'pest')	48	48	36
	('lodgepole pine' or 'pinus contorta') AND ('United Kingdom') AND ('disease' or 'pest')	6	6	4
	('lodgepole pine' or 'pinus contorta') AND ('Britain') AND ('disease' or 'pest')	18	18	16
	('lodgepole pine' or 'pinus contorta') AND ('Ireland') AND ('disease' or 'pest')	6	6	0
	('lodgepole pine' or 'pinus contorta') AND ('Scotland') AND ('disease' or 'pest')	33	33	21
	('lodgepole pine' or 'pinus contorta') AND ('Finland') AND ('disease' or 'pest')	4	4	1
	('lodgepole pine' or 'pinus contorta') AND ('Norway') AND ('disease' or 'pest')	13	13	0
	('lodgepole pine' or 'pinus contorta') AND ('Latvia') AND ('disease' or 'pest')	0	0	0
	('lodgepole pine' or 'pinus contorta') AND ('Estonia') AND ('disease' or 'pest')	1	1	0
	('lodgepole pine' or 'pinus contorta') AND ('Netherlands') AND ('disease' or 'pest')	2	2	0
	('lodgepole pine' or 'pinus contorta') AND ('Denmark') AND ('disease' or 'pest')	0	0	0
	('lodgepole pine' or 'pinus contorta') AND ('France') AND ('disease' or 'pest')	1	1	0
	('lodgepole pine' or 'pinus contorta') AND ('Poland') AND ('disease' or 'pest')	2	2	0
	('lodgepole pine' or 'pinus contorta') AND ('Belgium') AND ('disease' or 'pest')	0	0	0
	('lodgepole pine' or 'pinus contorta') AND ('Spain') AND ('disease' or 'pest')	2	2	0
	('lodgepole pine' or 'pinus contorta') AND ('Lithuania') AND ('disease' or 'pest')	0	0	0
	('lodgepole pine' or 'pinus contorta') AND ('Croatia') AND ('disease' or 'pest')	1	1	0
('lodgepole pine' or 'pinus contorta') AND ('Central Europe')	2	2	0	

	AND ('disease' or 'pest')			
	('lodgepole pine' or 'pinus contorta') AND ('Northern Europe')	7	7	0
	AND ('disease' or 'pest')			
	('lodgepole pine' or 'pinus contorta') AND ('Mediterranean') AND ('disease' or 'pest')			
CAB eBooks	('lodgepole pine' or 'pinus contorta') AND ('Europe') AND ('disease' or 'pest')	1	1	1
EBSCO Discovery Centre	('IUFRO' and 'contorta')	44	44	44
	('lodgepole pine' or 'pinus contorta') AND ('Europe') AND ('disease' or 'pest')	27	27	2
	('lodgepole pine') AND ('disease' or 'pest') AND ('United Kingdom')	21	20	4
	('lodgepole pine') AND ('disease' or 'pest') AND ('Germany')	24	24	1
	('lodgepole pine') AND ('disease' or 'pest') AND ('Sweden')	95	90	10
	('lodgepole pine' or 'pinus contorta') AND ('provenance') AND ('europe')			
Google Scholar	('lodgepole pine' or 'pinus contorta') AND ('Europe') AND ('disease' or 'pest')	4610	275	4
	('lodgepole pine' or 'pinus contorta') AND ('Europe') AND ('pathogen')	4270	260	6
	('twisted pine' or 'shore pine') AND ('Europe') AND ('disease' or 'pest')	10500	790	0
	('lodgepole pine' or 'pinus contorta') AND ('Sweden') AND ('disease' or 'pest')	1520	950	1
	('lodgepole pine' or 'pinus contorta') AND ('United Kingdom') AND ('disease' or 'pest')	6690	1300	3
	('lodgepole pine' or 'pinus contorta') AND ('Britain') AND ('disease' or 'pest')	5190	3500	2
	('lodgepole pine' or 'pinus contorta') AND ('Ireland') AND ('disease' or 'pest')	561	450	1
	('lodgepole pine' or 'pinus contorta') AND ('Scotland') AND ('disease' or 'pest')	2100	560	6
	('lodgepole pine' or 'pinus contorta') AND ('Finland') AND ('disease' or 'pest')	1090	270	4
	('lodgepole pine' or 'pinus contorta') AND ('Norway') AND ('disease' or 'pest')	2010	700	3
	('lodgepole pine' or 'pinus contorta') AND ('Latvia') AND ('disease' or 'pest')	107	107	2
	('lodgepole pine' or 'pinus contorta') AND ('Estonia') AND ('disease' or 'pest')	172	172	0
	('lodgepole pine' or 'pinus contorta') AND ('Netherlands') AND ('disease' or 'pest')	1760	850	1
	('lodgepole pine' or 'pinus contorta') AND ('Denmark') AND ('disease' or 'pest')	493	400	2
	('lodgepole pine' or 'pinus contorta') AND ('France') AND ('disease' or 'pest')	1880	900	0

	('lodgepole pine' or 'pinus contorta') AND ('Poland') AND ('disease' or 'pest')	666	500	1
	('lodgepole pine' or 'pinus contorta') AND ('Belgium') AND ('disease' or 'pest')	285	285	0
	('lodgepole pine' or 'pinus contorta') AND ('Spain') AND ('disease' or 'pest')	1010	800	0
	('lodgepole pine' or 'pinus contorta') AND ('Lithuania') AND ('disease' or 'pest')	122	122	0
	('lodgepole pine' or 'pinus contorta') AND ('Croatia') AND ('disease' or 'pest')	108	108	0
	('lodgepole pine' or 'pinus contorta') AND ('Central Europe') AND ('disease' or 'pest')	3770	3000	3
	('lodgepole pine' or 'pinus contorta') AND ('Northern Europe') AND ('disease' or 'pest')	3520	3000	8
	('lodgepole pine' or 'pinus contorta') AND ('Mediterranean') AND ('disease' or 'pest')	1180	600	1
Google Search	('lodgepole pine') AND ('provenance') AND ('Europe')	6	6	0
	('lodgepole pine') AND ('government') AND ('germany') AND ('disease' or 'pest')	8	8	0
	('lodgepole pine') AND ('government') AND ('united kingdom') AND ('disease' or 'pest')	5	5	1
	('lodgepole pine') AND ('government') AND ('sweden') AND ('disease' or 'pest')	5	0	0
Open Grey	('lodgepole pine')	4	4	4
	('pinus contorta')	1	1	1
Web of Science	('lodgepole pine' or 'pinus contorta') AND ('Europe') AND ('disease' or 'pest')	19	19	1
	('lodgepole pine' or 'pinus contorta') AND ('Europe') AND ('pathogen')	9	9	0
	('twisted pine' or 'shore pine') AND ('Europe') AND ('disease' or 'pest')	1	1	0
	('lodgepole pine' or 'pinus contorta') AND ('Sweden') AND ('disease' or 'pest')	18	18	12
	('lodgepole pine' or 'pinus contorta') AND ('Britain') AND ('disease' or 'pest')	9	9	3
	('lodgepole pine' or 'pinus contorta') AND ('Ireland') AND ('disease' or 'pest')	3	3	0
	('lodgepole pine' or 'pinus contorta') AND ('Scotland') AND ('disease' or 'pest')	15	15	2
	('lodgepole pine' or 'pinus contorta') AND ('Finland') AND ('disease' or 'pest')	5	5	0
	('lodgepole pine' or 'pinus contorta') AND ('Norway') AND ('disease' or 'pest')	27	27	0
	('lodgepole pine' or 'pinus contorta') AND ('Latvia') AND ('disease' or 'pest')	1	1	0
	('lodgepole pine' or 'pinus contorta') AND ('Estonia') AND ('disease' or 'pest')	0	0	0
	('lodgepole pine' or 'pinus contorta') AND ('Netherlands') AND ('disease' or 'pest')	0	0	0

('lodgepole pine' or 'pinus contorta') AND ('Denmark') AND ('disease' or 'pest')	0	0	0
('lodgepole pine' or 'pinus contorta') AND ('France') AND ('disease' or 'pest')	3	3	0
('lodgepole pine' or 'pinus contorta') AND ('Poland') AND ('disease' or 'pest')	1	1	0
('lodgepole pine' or 'pinus contorta') AND ('Belgium') AND ('disease' or 'pest')	0	0	0
('lodgepole pine' or 'pinus contorta') AND ('Spain') AND ('disease' or 'pest')	5	5	0
('lodgepole pine' or 'pinus contorta') AND ('Lithuania') AND ('disease' or 'pest')	0	0	0
('lodgepole pine' or 'pinus contorta') AND ('Croatia') AND ('disease' or 'pest')	1	1	0
('lodgepole pine' or 'pinus contorta') AND ('Central Europe') AND ('disease' or 'pest')	2	2	1
('lodgepole pine' or 'pinus contorta') AND ('Northern Europe') AND ('disease' or 'pest')	6	6	2
('lodgepole pine' or 'pinus contorta') AND ('Mediterranean') AND ('disease' or 'pest')	1	1	0
Total	54147	20421	243