Predicting decline of threatened species, invasiveness of alien species, and invasibility of semi-natural habitats:

A case study from threatened coastal heathlands and semi-natural grasslands in western Norway

Jan Håkon Vikane

Thesis for the Degree of Philosophiae Doctor (PhD)
University of Bergen, Norway
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2019

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Contents

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List of publications

This thesis is based on four following papers which will be referred by their roman numerical hereafter.

Paper I

Vikane J. H., Rydgren, K., Jongejans, E. & Vetaas, O. R. (2019). Spread of *Picea sitchensis* from plantation into adjacent coastal heathland. Manuscript

Paper II

Vikane, J. H., Rydgren, K., Jongejans, E. & Vandvik, V. (2019). Rainfall and temperature change drive *Arnica montana* population dynamics at the Northern distribution edge. *Oecologia. In press*.

Paper III

Vikane, J. H., Vandvik, V., & Vetaas, O. R. (2013). Invasion of Calluna heath by native and non-native conifers: the role of succession, disturbance and allelopathy. *Plant ecology*, *214* (7), 975-985.

Paper IV

Vetaas, O. R., Vikane, J. H., Saure, H. I., & Vandvik, V. (2014). North Atlantic Islands with native and alien trees: are there differences in diversity and species-area relationships? *Journal of Vegetation Science*, *25* (1), 213-225.

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Declaration

Paper I: Vikane J. H, Rydgren, K., Jongejans, E. & Vetaas, O. R. (2019). Natural regeneration of *Picea sitchensis* from plantation into adjacent coastal heathland.
Vikane, J. H: Study design, collected data, analysed data, wrote the paper.
Rydgren, K: Study design, inputs on analytical design, editing
Jongejans, E: Analysed data, inputs on analytical design, editing
Vetaas, O.R: Project design, study design, editing

Paper II: Vikane, J. H. Rydgren, K., Jongejans, E. & Vandvik, V. (2019). Rainfall and temperature change drive *Arnica montana* population dynamics at the Northern distribution edge.
Vikane, J. H: Study design, collected data, analysed data, wrote the paper
Rydgren, K: Analysed data, inputs on analytical design, editing
Jongejans, E: Analysed data, inputs on analytical design, editing
Vandvik, V: Study design, editing

Paper III: Vikane, J. H., Vandvik, V., & Vetaas, O. R. (2013). Invasion of Calluna heath by native and non-native conifers: the role of succession, disturbance and allelopathy. *Plant ecology*, *214*(7), 975-985.
Vikane, J.H: Study design, collected data, analysed data, wrote the paper
Vandvik, V: Study design, inputs on analytical design, editing
Vetaas, O.R.: Project design, study design, analysed data, editing

Paper IV: Vetaas, O. R., Vikane, J. H., Saure, H. I., & Vandvik, V. (2014). North Atlantic Islands with native and alien trees: are there differences in diversity and species-area relationships?
Vetaas, O. R.: Project design, study design, collecting data, analysed data, wrote the paper
Vikane, J.H: Study design, collecting data, editing
Saure, H.I: Study design, collecting data, editing
Vandvik, V: Study design, input on analytical design, edit

Abstract

Semi-natural habitats are characterised by a large biodiversity, but also associated with a large susceptibility to invasion by non-native species. Coastal heathlands and semi-natural grasslands in Norway, are under pressure from many different drivers, like invasion of non-native species, fragmentation, intensification and currently climate change, leading to concern about the cumulative effects from multiple global change drivers. Success of a non-native species in a new environment and a native species in a changing environment would be dependent on the tolerances to any changes in abiotic and biotic conditions. Thus, to make predictions about potentially invasion or extinction risk of a plant species, information about the whole life cycle of the species, the environmental drivers, and how this translates into any changes in vital rates and population growth rate need to be understood.

This thesis aims to investigate the main drivers behind changes in species abundances over time and space, exemplified by (i) invasion of the non-native conifer *Picea sitchensis* (Sitka spruce, (Bong.) Carr.) and the native species *Pinus sylvestris* (Scots pine, L) in coastal heathlands (Paper I, III) and (ii) the decline of the threatened peripheral species *Arnica montana* (L) in semi-natural grasslands (Paper II). In addition, we zoom out to investigate (iii) the impact of the non-native conifer species *Pinus mugo* coll. (Dwarf mountain pine) on species community and landscape scales (Paper IV). Methods variated from demographic data analysed by means of matrix projection models or integral projections models, field experiments, to data on species composition.

Spread of Sitka spruce was mainly driven by the seed rain from plantations and consequently the naturalisation of Sitka spruce was most abundant near plantations, but with scattered trees at longer distances from plantations. Sitka spruce had a high population growth rate. Both Sitka spruce and Scots pine invade every successional stage of heathland vegetation, but with decreasing recruitment success in later successional stages. Although Sitka spruce seems to invade all vegetation types in adjacent heathlands, our results suggest larger abundance on well-developed and moist soil conditions. The probability of establishment further seems to be

constrained by competition from *Juniperus communis*, another native species which invade the coastal heathlands after land-use abandonment.

Decline of *A. montana* was mainly driven by increasing precipitation. Life-table response experiments revealed that the temporal variability in population growth rate was driven by survival and clonality, whereas the spatial variation was driven by clonality. Our results suggest that *A. montana* has a threshold response to increasing precipitation, likely due to adaptions to local climatic conditions. Surprisingly, the results suggest no effects from habitat quality and population size. The stochastic growth rate was negatively influenced by climate change, indicating an increased extinction risk for marginal populations, possibly leading to range contraction of *A. montana* as climate change proceeds.

Islands with the introduced species *P. mugo* Coll. had more vascular plants than islands with the native species *P. sylvestris*. The latter had forest floor vegetation dominated by bryophytes, reflecting a low light regime and thus lower species richness than the more open *P. mugo* habitats. *P. mugo* islands harboured more species associated with semi-natural habitats compared to the *P. sylvestris* islands which had a more closed late-successional canopy. Thus, habitat and species richness were higher and increased with area on *P. mugo* islands but not on *P. sylvestris* islands.

In conclusion, this thesis highlights the need to include information about the whole life cycle of the species, the main environmental drivers behind the population growth rate and the underlying vital rate to make assessment about the invasion potential of non-native species and threatened species. In addition, it shows that impact of a non-native species on resident vegetation is highly dependent on the specific traits of the species and the resident species community.

Synthesis

Introduction

Semi-natural habitats are hotspots of both biodiversity and invasion by non-native species (Catford et al. 2011, Habel et al. 2013). These habitats, which are characterised by high levels of disturbance, allow for the coexistence of many gap-cued and light demanding plant species (Duflot et al. 2015), but is also associated by a large susceptibility to invasion by non-native species (i.e., high invasibility) (Davis et al. 2000, Catford et al. 2011, Jauni et al. 2015). In Norway, coastal heathlands and semi-natural grasslands, which are key semi-natural habitats (Miljødirektoratet 2016), have been substantially changed during the last 60 years, primarily due to cessation of traditional land-use regimes. These formerly treeless landscapes are currently invaded by native tree species, like *Betula pubescens* and *Pinus sylvestris*, *Picea abies* but also spread of non-native species from commercial forest plantations, like *Pinus mugo* coll. (see under target species for explanation to the coll. acronym) and *Picea sitchensis* which are negatively affecting local species richness and abundance (Saure et al. 2013). Moreover, land conversion (like commercial plantations), intensified management (Uematsu et al. 2010), habitat fragmentations (Lindenmayer and Fischer 2013), atmospheric deposition of nitrogen (Stevens et al. 2010), and increasingly impacts from climate change (Sletvold et al. 2013, Olsen et al. 2016, Töpper et al. 2018) are further deteriorating the prospects for semi-natural habitats and species, leading to concerns over the cumulative and potentially interactive impacts from multiple global change drivers (Hovstad et al. 2018, Hovstad et al. 2018). To make informed management decisions for conservation of semi-natural habitats and their unique biodiversity, we need to disentangle the effects from the many and potentially interacting drivers which are causing either decline (i.e. threatened species) or increase (i.e. invasive species) in abundance of species in this landscape.

Many studies conceptualize invasion as a stage-based process (e.g. conceptual frameworks by Catford et al. 2009, Blackburn et al. 2011), and such approaches can help identify potentially effective management strategies, but may at the same time distort the view of invasion processes as something fundamentally different from basic ecology and evolutionary biology (Gurevitch et al. 2011). In a biogeographic perspective, a non-native species in a new environment would encounter ecological marginality by experience a different ecological context with respect to the species` optimum conditions. Success of a non-native species would depend on the habitat suitability (e.g. abiotic and biotic factors) and the traits of the species allowing it to form self-replacing populations in the new region. In the same way, the abundance and distribution of a marginal and declining native species in a changing environment would be dependent on the tolerance of the species to the (changing) environment, and the availability of habitats with favourable biotic and abiotic conditions, and the species' ability to sustain viable population growth rates in the region given these (changing) external conditions. Although range expansion (e.g. overcoming a major geographic barrier) of a non-native species is mainly driven by human transport (in contrast to natural migration), the dynamic processes that drive any change in local distribution and abundances is similar for a non-native and a native species.

According to Ehrlén and Morris (2015), any changes in a species' abundance and distribution is defined by the i) current abundance of the focal species, ii) the environmental drivers, i.e., relevant abiotic and biotic factors in time and space, iii) how these biotic and abiotic drivers influence vital rates and iv) dispersal, which determines future colonisation (this is scale dependent; e.g. establishment vs. geographical range expansion). Therefore, to make predictions about a potentially invasion or extinction risk of a plant species we need information about the whole life-cycle of the target species (including dispersal and/or establishment), the environmental drivers (abiotic and biotic), and how this is translated into any changes in vital rates and population growth rate. By linking temporal (i.e. among-year) and spatial (i.e. among-site) variation it is possible to identify relationship between vital rates and important environmental drivers, like soil nutrients (Dahlgren and Ehrlén 2009), light availability (Diez et al. 2014) and climate (Toräng et al. 2010, Nicolè et al. 2011). In addition, interactions like competitive ability (stature and growth form), life-history traits (many invasive species are r-strategist ruderals; Van Kleunen et al. 2010), dispersal ability (Jongejans et al. 2008) and interspecific competition (biomass and density) which can either constrain or facilitate abundance need to be included.

These potential drives could be investigated through experiments and/or by means of demographic models (projection matrix models or integral projection models; IPM) where we can gain insight into the relationships between vital rates and environmental drivers and how this influence the population growth rate and in turn the abundance and distribution (Griffith et al. 2016).

When a non-native species has become naturalised and reproduce self-sustainably it can spread into new locations and attain high abundance to influence local biodiversity (Gaertner et al. 2009). Although, many studies on impact from invasive species shows a low consistence in outcomes from invasion, and invasion is highly context dependent (Pyšek et al. 2012), many non-native has a negative impact on species and communities in many different habitats (Powell et al. 2011, Vilà et al. 2011). However, impact is also found to be highly dependent on the specific traits of the invading species, like life-form, stature and performance (Van Kleunen et al. 2010, Pyšek et al. 2012)

This thesis aims to investigate what is the main drivers behind changes in species abundances over time and space, exemplified by invasion by the non-native conifer *P. sitchensis* in coastal heathlands and the decline of the threatened peripheral species *Arnica montana* in semi-natural grasslands (Paper I, II, III). In addition, we zoom out to investigate the impact of the non-native conifer on species community and landscape scales (Paper IV). The methods range from detailed demographic studies of naturally-occurring and introduced populations of long-lived perennial/tree species (Paper I, II), via a seedling recruitment experiment (Paper III), to a space-for-time approach sampling species composition on several coastal islands with and without non-native coniferous species (Paper IV).

Objectives

1. Assess the invasiveness of a coniferous species in coastal heathlands. Paper I
2. Asses how concomitant environmental drivers affects the population dynamics of a threatened peripheral species. Paper II
3. Assess the invasibility of coastal heathlands to native and non-native coniferous species. Paper III
4. Assess the impact of native and non-native coniferous species to species richness. Paper IV

Target species and study systems

Picea sitchensis **(Bong.) Carr. Common name: Sitka spruce, other common names are: Tideland spruce and coast spruce.**

P. sitchensis is a prominent conifer species in certain ecosystems in North America`s northern temperate rain forest. Natural distribution along the western coast is in a narrow strip of 210 km from west to east along its 2900 km extent (Harris 1990). The southernmost *P. sitchensis* trees occur in Mendocino County, California (latitude 39°20‘N) and the species occur north to Prince William Sound (latitude 61°00‘N) and west as far as about longitude 155°00‘W on the Alaskan coast (Figure 1a) (Peterson et al. 1997). *P. sitchensis* is adapted to the wetter hypermaritime biogeoclimatic zone where it is frost tender, but tolerates sodium inputs from brackish water and ocean spray (Taylor 1990, Peterson et al. 1997).

In the wild, *P. sitchensis* sometimes forms pure stands, but it is often associated with *Tsuga heterophylla, Thuja plicata* and *Cupressus nootkatensis* (Peterson et al. 1997). In its natural range, it also hybridizes with *Picea glauca* (white spruce, Moench (Voss)), forming the fertile hybrid *Picea x lutzii* (Lutz spruce, Little). *P. sitchensis* is the earth´s largest spruces, and grows tall (usually 50–70 m) with a diameter at breast height (dbh) around 2 m and with an age of around 200 years, the largest known *P. sitchensis* is 93 metres tall and 5 metres across (Peterson et al. 1997).

P. sitchensis is a prolific seed producer and reaches maturity stage relatively early, normally around 20 years (Stabbetorp and Aarrestad 2012), but cones have been found on individual trees as young as 5 years (Paper I). Stika spruce has a reproductive cycle of almost 2 years, where reproductive buds are initiated late summer the year preceding pollination (may–june) and seed ripening the following winter. Heavy cone crops have been explained in terms of early summer drought the preceding year, and like many other coniferous species *P. sitchensis* has masting year with a periodicity for about 3–5 years (Peterson et al. 1997). Cones hang vertically from a short petiole and falls off after seed releasement, the cones are hygroscopic and release the seeds only in dry weather (Harris 1990, Thorvaldsen 2016). The seeds are small and light (Chaisurisri et al. 1992, Paper III) and attached to a small seed wing. Hence, seed dispersal is restricted, from the edge of a clear cut the majoirty of seeds are dispersed within a distance of 30 m, but when a seed source is high on the ground a dispersal distance of 800 m has been recorded (Harris 1990, and references therein). Natural regeneration of *P. sitchensis* is disturbance and gap demanding (Taylor 1990) and persistence is dependent on a nutrient rich to very nutirent rich moist soil (Klinka et al. 1999).

Plantations of *P. sitchensis* has been established in many coastal regions of Europe, such as Britain, Ireland and parts of Denmark and in the coastal regions of Norway (Stabbetorp and Aarrestad 2012). *P. sitchensis* is adapted to coastal climate and thus it is preferred for afforestation in coastal environments. In Britain, there has been a long tradition for the establishment of *P. sitchensis* plantations (first established in 1830), and today more than 690,000 ha are covered with *P. sitchensis*, and it constitutes 49 % of all coniferous forests in Britain (Moore 2011). In Norway, there was only scattered plantings of *P. sitchensis* until the extensive afforestation scheme in 1950–1990 (Stabbetorp and Aarrestad 2012). *P. sitchensis* is mostly planted along the coast, and today it covers approximately 50,000 ha (Figure 1b).

P. x lutzii which is more adapted to a colder climate (especially early autumn frost; Skúlason et al. 2001) is important for afforestation in the northern part of Norway where approximately 5000 ha of *P. x lutzii* plantations has been established. From later inventories of plantations in Norway it seems that *P. x lutzii* is more common planted than first expected (Elven et al. 2018), this contradict to earlier reports which says that more than 90% of the seed sources used in nurseries came from areas (south eastern part of Alaska; Petersburg, Juneau, Sit. Haines, Ket) outside the hybridization zone (Øyen pers. comm). *P. x lutzii* was first described in Alaska by Little (1953), thus on possible explanation is that seeds for early plantations (around 1950) was collected before the hybrid species was described (Elven et al. 2018). *P. x lutzii* can backcross and together with introgression hybridization second generation trees is difficult to separate from *P. sitchensis* by morphological characteristics, thus many of the naturalized trees could be hybrids and not pure *P. sitchensis* stands (Olsen et al. 2016, Elven et al. 2018). In this thesis I do not separate between *P. sitchensis* and *P x lutzii*

P. sitchensis is invasive in Britain and Ireland (Richardson 2004), and in Norway it is reported to be naturalized in treeless habitats such as heathlands and grazed fields (Elven et al. 2018). Naturalisation is most dominate in areas with regular, irregular or abandon disturbance regimes, like road wedges, heathlands and pastures with reduced grazing pressure or cessation of grazing (Paper III, Malcolm et al. 2001, Page et al. 2001, Page and Cameron 2006).

Naturalization of *P. sitchensis* from plantations into the adjacent heathland (Figure 2) in combination with an increased focus on conserving and restoring cultural landscapes, and an awareness of the negative influence from *P. sitchensis* on species composition in heathland (Saure et al. 2013), has led both local and national authorities recommend removal of *P. sitchensis* plantations and/or naturalised *P. sitchensis* individuals in conservation areas (Klima- og miljødepartementet. 2016).

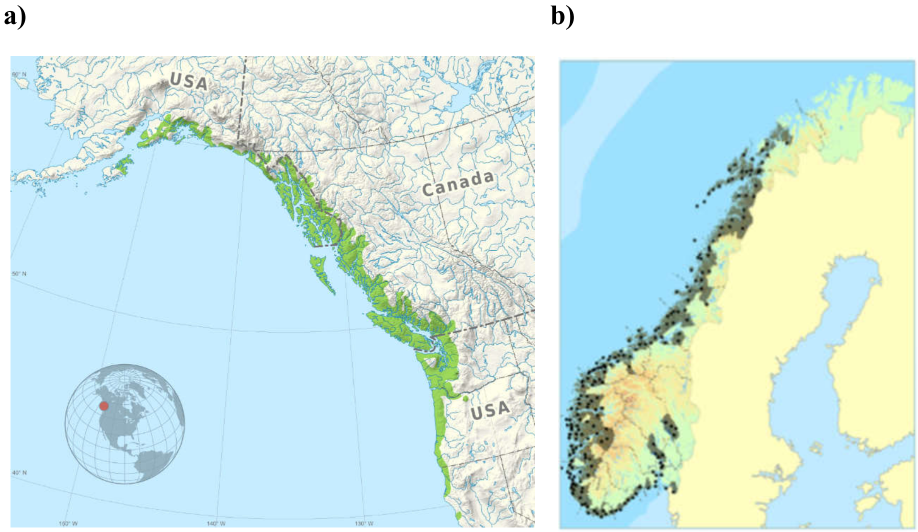
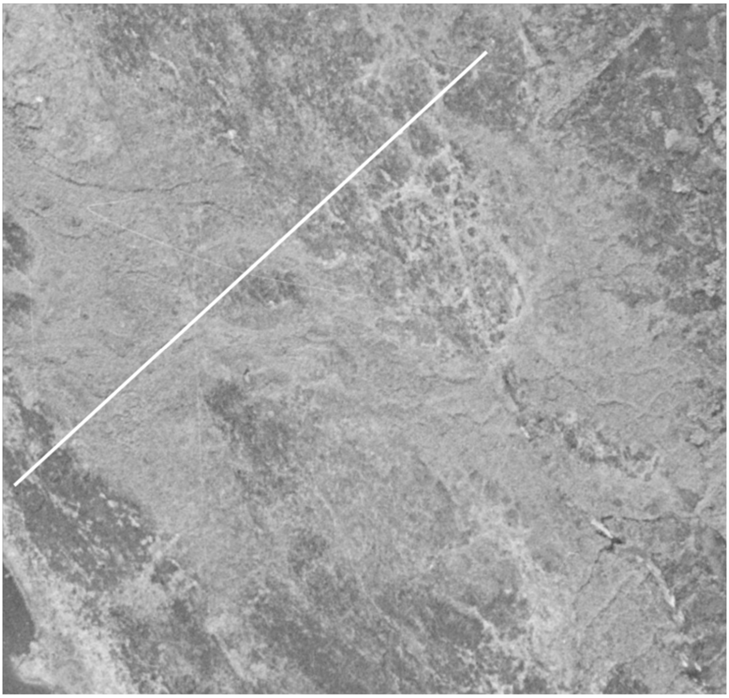
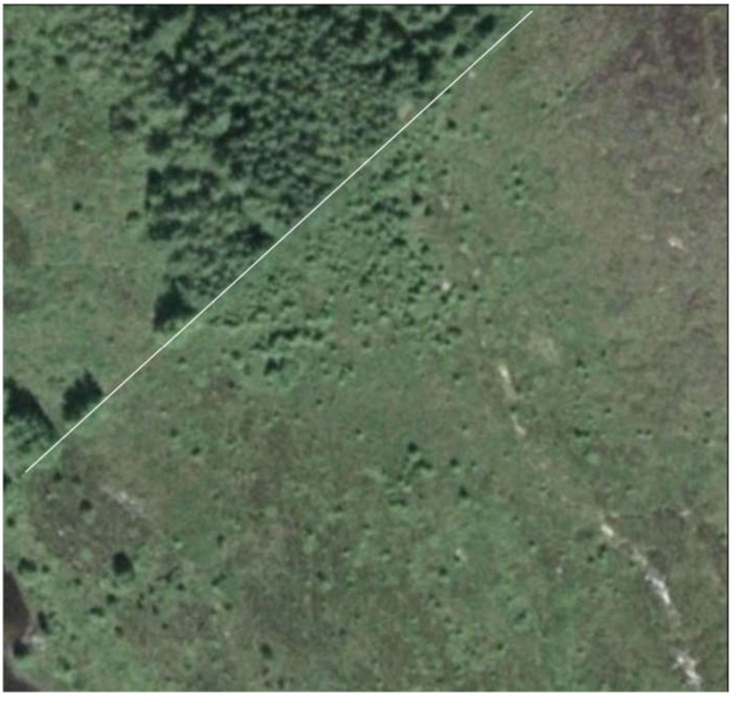


Figure 1. a) Picea sitchensis distribution along the Pacific Northwest coast of North America (Source: Wikipedia 2009). b) Distribution of P. sitchensis and Picea x lutzii plantations in Norway (both dots and fills pattern. Source: Stabbetorp and Aarrestad 2012

a)



b)



c)

Figure 2. Pictures from one of the study populations, H. White line marks property border and edge of plantation. a) Year 1961, before establishment of *Picea sitchensis* plantations. b) Year 2000, around 35 years after establishment of plantations, early stage of naturalisation. c) 2015, around 50 years since establishment of plantations, abundant spread of *P. sitchensis*. Red arrows marks direction of seed trap transects lines.

Arnica montana L. Common name: Mountain arnica, other common names: Wolf's bane, leopard's bane and mountain tobacco.

A. montana (*Asteraceae*) is a long-lived rosette forming herbaceous perennial, endemic to Europe with a distribution reaching from Scandinavia to northern Italy and from Portugal to the Carpathians (Figure 3) (Hultén and Fries 1986). *A. montana* grows in unfertilized, mown or grazed grasslands, and dry heathlands (Lid and Lid 2005).

A. montana reproduces vegetatively by means of short underground rhizomes, sexually by flowering from July until early August. Each plant may have one or several flowering stems which produce 1–5 or up to seven yellow self-incompatible flowerheads. Seeds possess a pappus and is wind dispersed, but dispersal of large seeds (1.3 mg) is very limited (Strykstra et al. 1998). The species has a transient soil seed bank (Thompson et al. 1997).

Land-use changes, deteriorated habitat quality and fragmentation has led to a decline of *A. montana,* especially in the northern part of the distribution range. The species are rated as vulnerable in Norwegian and Swedish red-list (Henriksen and Hilmo 2015, Westling 2015) and critically endangered in part of Europe (Colling 2005), but least concern in European and IUCN lists (Bilz et al. 2011, Falniowski et al. 2013). Although some studies have found some evidence for inbreeding effects (Kahmen and Poschlod 2000, Luijten et al. 2002, Maurice et al. 2012), the species seems to maintain a relatively large genetic variation even in small populations (Luijten et al. 2000, Maurice et al. 2016, Duwe et al. 2017, Van Rossum and Raspé 2018). In our study area, Møre og Romsdal, the species is relatively common, but exists in many isolated populations with a great variability in population size. The species seem to persist in habitat by the ability to produce clonal offspring, even in deteriorated habitat conditions (Maurice et al. 2012, Van Rossum and Raspé 2018, Paper II).

A. montana is a key species in semi-natural grasslands, interacting with insects which are dependent on *A. montana* in part of their life-cycle. The larva of the moth *Digitivalva arnicella* acting as a leaf miner on the leaves of *A. montana* (Elven 2010). The fly *Thephritis arnica* lay eggs in the flowerhead of *A. montana* and the larva is feeding on the undeveloped seeds. In addition, the larva of the parasitic wasp *Pteromalus arnica* parasites the larva of *Thephritis arnica* (Solstad and Bjureke 2011).

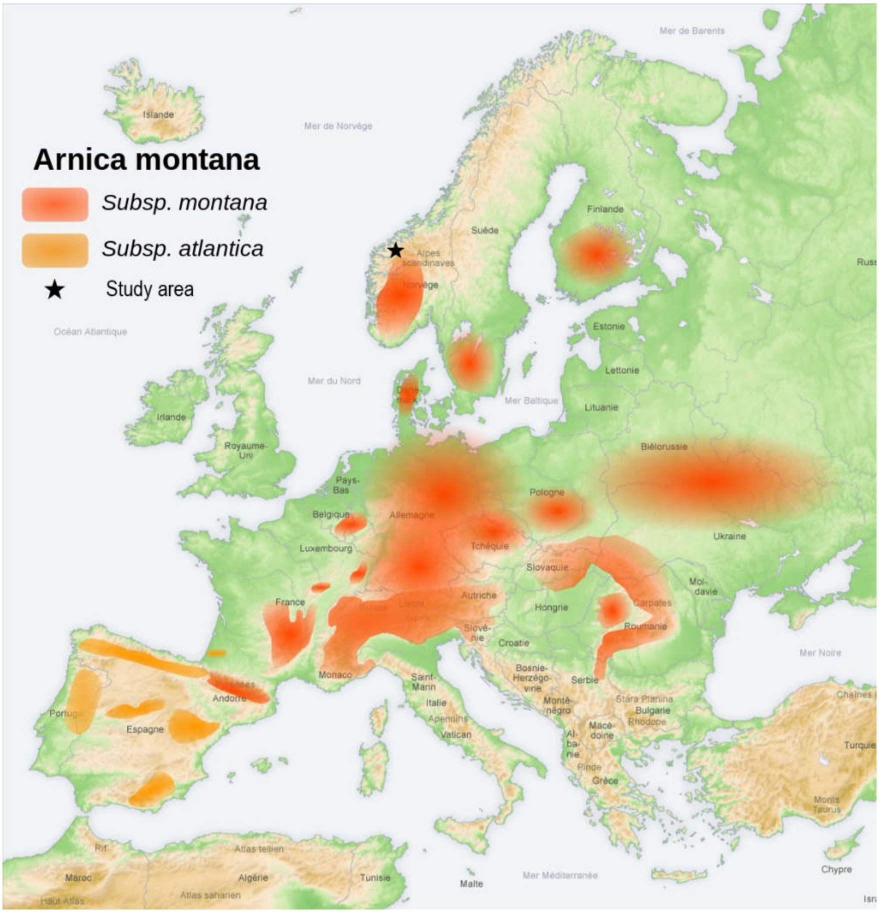


Figure 3. *Arnica montana* (including both subsp.) distribution in Europe. Study area marked with a star. (Source: Wikipedia 2012)

Pinus sylvestris L. Common name: Scots pine

P. sylvestris has a wide geographic range (Figure 4) and is the most widely distributed pine species in the world (Earle and Frankis 1999). It is native throughout the boreal and temperate region of Europe and Asia, and grows across a wide range of elevations, from sea level in the northern parts of its range to 2600 m above sea level in the Caucasus. *P. sylvestris* is a light-demanding pioneer species with a great tolerance to drought, frost, and low nutrient acidic soil conditions, on fertile sites it is often outcompeted by other species (spruce or broadleaved species) (Durrant 2016). However, it has a low tolerance to atmospheric pollution or salty sea winds, except for trees from the extreme west of the range, in NW Scotland, where strong adaptation to oceanic climate is found (Earle and Frankis 1999).

P. sylvestris is a medium sized conifer with a diameter breast height reaching 0.5–1.2 m, and an average height of 23–27 m, but can attain over 40 m. The species could reach an age of 400 years or more. *P. sylvestris* reach sexual maturity as early as 5–8 years, but normally at age between 10–15 years (Sullivan 1993). It is wind-pollinated and is normally monoecious, but mature trees may very occasionally bear only male and female strobilus (Durrant 2016). Cones are 3–6 cm long, conic, mature in November–December, opening in February–April after alternating periods of dry and wet weather and shed the winged (12–20 mm) seeds (black, 4–5 mm), which can be dispersed by wind (Earle and Frankis 1999, Durrant 2016). Seed dispersal distances range from 50–100 m, though the maximum distance is greater than 1 km. Good seed crops are produced every 3–6 years (Earle and Frankis 1999).

P. sylvestris has been widely planted, especially in the United States and Canada (Earle and Frankis 1999), and is found to become invasive in regions outside its natural range (Richardson et al. 1994). In Europe, *P. sylvestris* forests now exceed 28 million hectares, comprising over 20% of the productive area (Mason and Alía 2000). In Norway, *P. sylvestris* have been an economically important species for the production of timber and fire wood, and have been utilised, for example for salt production, tar production and construction timber, with historically export to Britain, the Netherlands and other European countries (Øyen et al. 2006). Consequently, by the first half of the 18th century there was a shortage of mature *P. sylvestris* timber resources. This situation lasts until the beginning of the 19th century, but land-use changes with less use of grazing animals in the outfields, resulted in a natural regenerating of *P. sylvestris* forests, often in combination with *B. pubescens*. In addition, from the beginning of the 19th century there was a reforestation by the establishment of plantations, which lasts until 1945 when planting of *P. abies* and *P. sitchensis* started to dominate. In the beginning of 1990 there was around 305000 ha with *P. sylvestris* forests in the western part of Norway (Øyen 1998).

Figure 4. Distribution of *Pinus sylvestris* in its native range (green color) and introduced and naturalised area (Source: Caudullo 2017).

Pinus mugo Turra. Common name: Dwarf mountain pine, other common names: Mugo pine and scrub mountain pine.

P. mugo has a large morphological variability, including many distinct subspecies and varieties. The taxonomy of *P. mugo* is complicated and some places it refers to the *P. mugo* complex, which consist of a group of closely related taxa of *Pinus* (Christensen 1987). In its natural range, there is intermediate forms between *P. mugo* and the closely related species *Pinus uncinata* (forming *Pinus mugo* subsp. *rotundata*, *Pinus mugo* subsp. *pumilio* and others) which grows together in Central European mountains (Figure 5). These pines are also able to hybridise with *P. sylvestris* where they co-occur (Ballian 2016). In Lid and Lid (2005; Norwegian Flora) *P. mugo* and *P. uncinata* is treated as distinct species (both species is used for forestry purposes), but in Flora Europaea as *P. mugo* ssp. *mugo* and spp. *uncinata* respectively, thus we choose to use *P. mugo* coll.

P. mugo coll is endemic to Southern and Central Europe, where it occurs in mountainous regions from 200 to 2700 m a.s.l, with its most abundant distribution in the subalpine belt of the Eastern Alps and the Carpathians between 1600 to 2200 m a.s.l. Disjunct ranges occur in the mountain regions of the eastern part of Europe and North-East Spain (Figure 5) (Ballian 2016).

P. mugo coll. is a shrub, erect bush or small tree which grows up to 5 m, sometimes with decumbent branches which can spread up to 10 m from the tree. The needles are acuminate and pungent, 2 to 5 cm long and born in fascicles of two. *P. mugo* coll. reach the maturity stage at an age of 10 years, producing 2–5 cm long cones in a group of 1–4, close to shoot tops (Ballian 2016). Seeds ripen during the second year with a size of 3–4 mm width, and a 7–12 mm wing (Earle and Frankis 1999).

P. mugo coll. is light-demanding and adapted to dry stony areas with tolerances to nutrient poor soil, and even anoxic soil peatlands (Ballian 2016). Its adaptive capabilities to varying habitat conditions was the main reason for establishment of *P. mugo* coll. plantations in coastal regions of Norway. It was planted as shelter tree, nurse tree and for timber and wood fire production, mostly on nutrient poor and low developed soil conditions. The first trees were planted in 1836, but more extensive planting started in 1870-ties and decreased in 1950-ties when *P. abies* and *P. sitchensis* plantations were established (Øyen 1999).

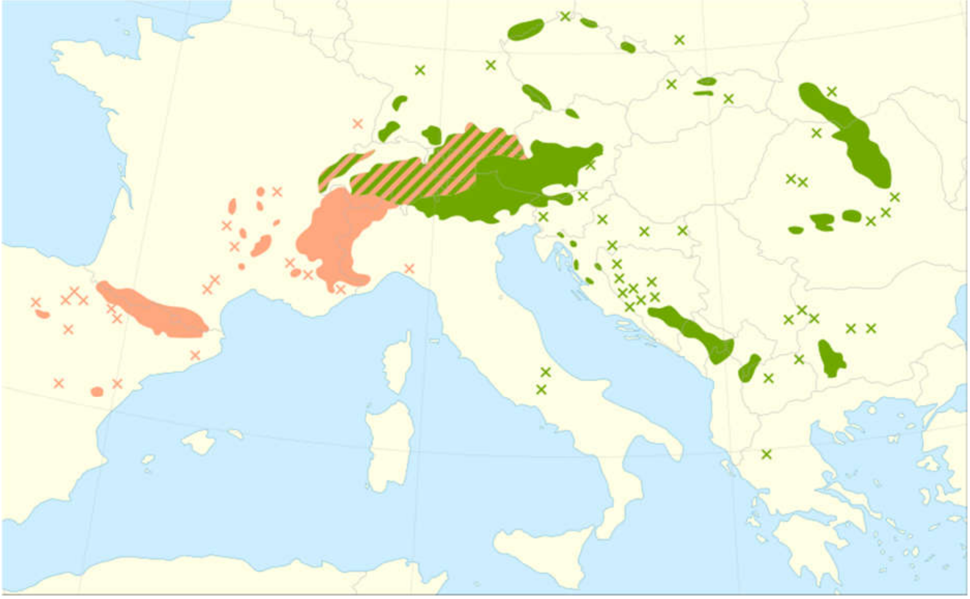


Figure 5. Distribution of *Pinus mugo* (green colour) and *Pinus uncinata* (pink colour) in native ranges (Source: Caudullo 2017)

Study system: Coastal heathlands

Coastal heathlands are semi-natural landscapes along the Atlantic coast of western Europe. It stretches from the Northern part of Portugal to Lofoten in northern Norway – 3600 km, with a narrow strip of 1200 km along the coast of Norway (see maps in Fremstad and Kvenild 1993, Kaland and Kvamme 2013). The open heathland landscape was created by man-induced deforestation started around 5000 years ago. Extensively framing practices which included regular burning, cutting and grazing effectively prevented re-establishment of natural forests (Kaland and Kvamme 2013). Coastal heathlands have conservation values by being an important habitat for many plant and animals, and is assessed as a key cultural landscape in Norway (Miljødirektoratet 2016).

Heathland vegetation is a species-poor vegetation characterised by a mosaic of light-demanding species (dwarf shrubs, sedges, herbs and grasses), mostly dominated by ericaceous species, in particular *Calluna vulgaris,* which is a key species (Nilsen and Moen 2009, Kaland and Kvamme 2013). Although the coastal heathland has a wide south-north distribution in Norway, the vegetation is relatively homogenous. Variability in plant species composition is mostly driven by variation in management regimes, climate, exposition, soil type and height above sea level (Aarrestad et al. 2001, Loidi et al. 2010, Velle 2012, Velle et al. 2014). Variation in a south-north and west-east gradient is defined by the present or absent of hyper-oceanic species (e.g. *Erica cinerea*) and euoceanic species (e.g. *Luzula sylvestris*). In the northern part is *Empetrum nigrum/ hermafroditum* the most dominated species (Kvamme 2004). Most of the bedrock along the coast consists of hard and slowly-eroding bedrock giving rise to nutrient-poor acidic soil (pH between 3–5) (Kaland and Kvamme 2013).

Traditional management of heathland has been a combination of regular grazing, burning and cutting. The oceanic climate with mild winters and low snow cover allowed grazing stock (sheep and goat) to stay out all year. Grasses were the most important fodder in summertime, but throughout the winter, grazing sheep depended upon the evergreen *C. vulgaris*. *C. vulgaris* was also harvested by means of scythe and used as a winter fodder supplement to hay for the cattle kept in byres during winter. Young plants of *C. vulgaris* is most valuable as fodder for grazing animals, therefore *C. vulgaris* was regularly burned (Figure 6), which is also important to maintain the mosaic of graminoids and *C. vulgaris* as a continuous supply of fodder year-round (Kvamme 2004, Kaland and Kvamme 2013). Regular burning is also crucial to maintain the diversity of plant species in coastal heathlands (Måren 2009, Velle 2012), and fire is also found to play an important role as germination cues for *C. vulgaris* (Måren et al. 2010).

After the second world war, the development of new farming practices, artificial fertilisers and changes in domestic breeds, the use of coastal heathlands become uneconomic and the traditional land-use was abandoned. Large areas of coastal heathlands have been lost to commercial afforestation, for example plantation of *P. sitchensis*. Cessation of traditional management practices allow shrubs and trees to re-enter the heathlands, both native species (e.g. *P. sylvestris*, *B. pubescens* and *Juniperus communis*) and non-native shrubs and trees (e.g. plantation species such as *P. sitchensis*) (Webb 1998, Saure et al. 2013). Only a small fraction of the former coastal heathlands remain today, and these has become a threatened semi-natural landscape in Europe and Norway (Sundseth et al. 2008, Hovstad et al. 2018).

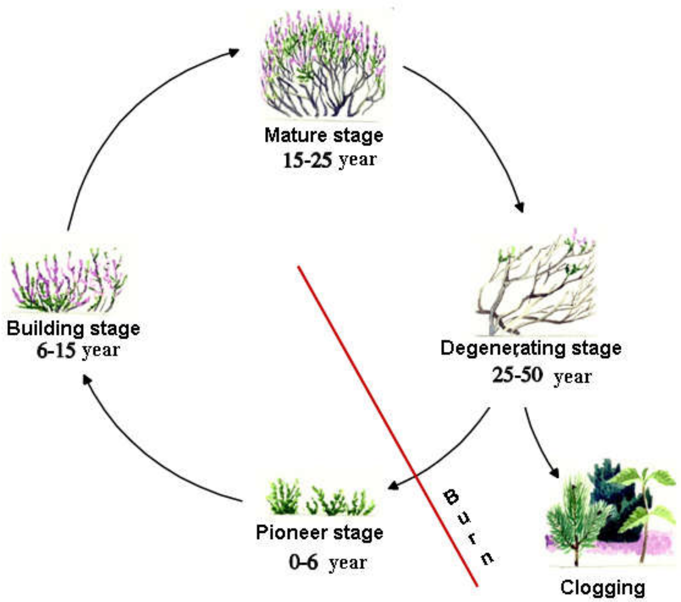


Figure 6. The traditional heathland cycle showing the cyclical management regime of *Calluna vulgaris*. Source: Modified from Kaland and Hazerbroek.

Study system: Semi-natural grasslands

Semi-natural grasslands are human-made landscapes with a high biodiversity of plants, insects and birds (Wilson et al. 2012). Semi-natural grasslands, which in a broad sense includes pastures, wooded pastures, wooded hay meadows and hay meadows, is characterised by open vegetation or only scattered trees, dominated by a mixture of light-demanding grasses, herbs, sedges, rushes, mosses and other low-growing species (Norderhaug 1999). Semi-natural grasslands are habitats created and managed by low-intensity (i.e. unfertilized) traditional land-use regimes. This land-use regime involved creation of a system of infields (arable fields and meadows) near farms, and outlands (outlying land) mainly used for grazing. Thus, large areas were used for utilising resources for food production, creating an open and treeless landscape in a large part of Scandinavia (Eriksson et al. 2002).

From a broad ecological perspective, semi-natural grasslands can be seen as intermediate stages in the development of vegetation over time (Sojneková and

Chytrý 2015). The habitat stays in this intermediate stage due to regular disturbance regimes which involves grazing, trampling (by grazing animals), mowing and raking. This kind of disturbance creates gaps (i.e. regeneration niche according Grubb 1977) in the vegetation turf and allow coexistence of many gap-cueing plant species. Moreover, management involves removal of biomass and the sward is kept low, at least part of the season, allowing for the dominance of grasses, and herbs with ground forming rosettes (Vassilev et al. 2011). In, addition a large proportion of plant species in semi-natural grasslands have the possibility to produce clonal offspring. Clonality act as a second-best solution, in a stressed environment, to increase number and distribution of ramets within a genet (Hamre et al. 2010). This ability is found to be important for the persistence of long-lived species in semi-natural grasslands (Johansson et al. 2011). In contrast, many short-lived species which is dependent on regular regeneration from seeds responds quickly to any decrease in disturbance regimes (Lindborg et al. 2005).

Introduction of artificial fertilizers and the development of forestry from the mid-19th Century and the beginning 20th Century changed the traditional farming system in Scandinavia (Eriksson et al. 2002). Production was increased on infields and use of the outlands was ceased and causing wood encroachment of the former grasslands. In addition, after the second world war, a huge afforestation scheme was started and during the 1950-ties and 1960-ties large areas of former grasslands, especially in Western-Norway, was planted with *P. abies* (fjord areas) and *P. sitchensis* (coastal areas) (Roll-Hansen 2016). Today, only fragments of the former grassland systems is left and consequently many species in semi-natural grasslands have decreased substantially during the last 60-years and constitute a large part of species at the national red list (Henriksen and Hilmo 2015). Although Norway still have a relatively large proportion of semi-natural grasslands, compared to other countries in Scandinavia and Europe, semi-natural grasslands has become a highly threatened cultural landscape (Hovstad et al. 2018).

Methods

This thesis focuses on the invasiveness of *P. sitchensis* in coastal heathlands (Paper I), the decline of the red-listed species *A. montana* in semi-natural grassland (Paper II), the invasibility of coastal heathlands by native *P. sylvestris* and non-native *P. sitchensis* (Paper III) and the impact of *P. mugo* (Paper IV). Details of data collection, analysis of demographic data, experimental design and statistical methods are described in the respective papers. Key aspects of sampling strategies and analytical approaches is briefly presented below

Paper I

Eight study populations were selected in coastal heathlands invaded by the conifer *P. sitchensis*. Four to nine transect-plots were established in each population, each transect-plot had a size 10 m width × 100 m length and 5 m between each transect-plot (Figure 7). Each transect-plot started at the edge of the plantation, oriented in the spread direction of *P. sitchensis* trees. These transect-plots were used for sampling of data on seed dispersal, seedling density, seedling recruitment/survival and demographic data. Every tree in each plot were tagged and the diameter breast height (dbh) were measured. These measurements were repeated in a three-year period.

Seed dispersal was measured in three populations. In each population, 42 seed traps (Figure 8) were placed in three transect-plots (14 in each transect), each transect had a length of 100 m with an inter–distance of seed traps of 5–10 m. Seed traps (total of 126) were cleaned, and number of filled and unfilled seeds were counted.

Seedling density was measured in each population in 1m × 1m plots distributed with a distance of 5m between each plot in three of the transect-plots.

Fecundity were measured as a function of number of seeds to dbh. Seedling recruitment was estimated as number of germinating seedlings in permanent plots (10 plots in each population) used for a seed addition experiment in field conditions. At every new seedling we measured the dbh. Seedling survival was measured as number of seedlings in plots one year after first census.

To get information about the microsite characteristics for recruitment probability, we recorded (i) soil dept, (ii) soil humidity, (iii) functional group covers, and (iii) vegetation height. Soil depth was measured by using a metal stick, we categorized soil humidity into three different classes: wet, intermediate and dry as a combination of soil depth and vegetation type. We measured the percent cover (0–100%) of the following functional groups in each plot: Bryophytes, graminoids, herbaceous, ericoid and deciduous species, in addition, the cover of *C. vulgaris* and *J. communis* was separately measured.

To get information about the characteristics of invaded and uninvaded sites of *P. sitchensis* we used 10 (5 invaded, 5 uninvaded) 4 m × 4 m plots divided into 4 subplots in each population. In each subplot we recorded the same abiotic and biotic variables as in plots used for seed addition experiment (see above).

Integral projection models (IPM) were used for calculation of population growth rate. Biotic and abiotic data was analysed by use of linear mixed-effects models with site as random effect.

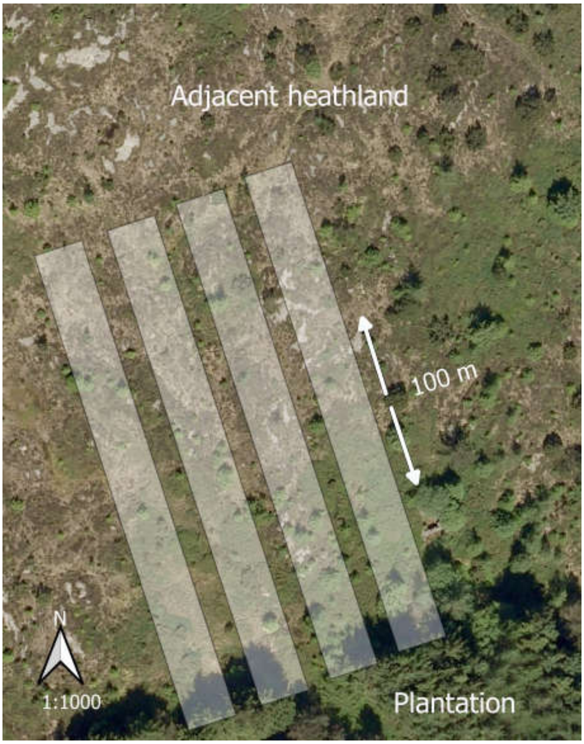


Figure 7. Transect-plot design (100 m × 10 m, 5 m between transect-plots) used for sampling of data on dispersal, seedling density, seedling recruitment and demographic data.

Figure 8. Picture of one of the seed traps (40 cm × 40 cm) placed in transects which stretched from plantations and into the adjacent heathland, with a total length of 110 m and 42 seed traps in each population (D, E, H).

Paper II

In July 2005, eight populations of *Arnica montana* were selected in semi-natural grasslands, make sure to represent a range of population size, semi-natural grassland management regimes and bioclimatic conditions. At each population 3 – 12 demography plots (0.5 m × 0.5 m) were established, each individual rosette was tagged until we got around 200 rosettes in each population. For each tagged rosette we measured the following demographic data: rosette size, survival, dormancy, clonal offspring, and sexual fecundity. These data were measured annually for six years (2005–2010). Sexual fecundity was calculated for each population as the product of mean number of ripe seeds per flowering plant and recruitment probability of a seed on bare soil in a seed addition experiment (Figure 9 b, c, d).

Following abiotic and biotic variables was collected: Population size was determined annually as the number of flowering rosettes during peak flowering. To obtain a proxy of the underlying habitat quality we recorded the species composition.

Aboveground biomass was assessed by cutting all aboveground organic material in five randomly placed 25 cm × 25 cm plots and drying these samples at 60°C for 48 h before weighing. Four different weather variables: (i) the mean daily (24 h) surface (2 m) temperature, (ii) the 24 h daily accumulated precipitation, (iii) the monthly precipitation normal (1961–90) and (iv) the monthly temperature normal (1961–90) was downloaded from Arctic Data Centre (2017). Precipitation data was used to calculate rainfall anomaly index (RAI).

7 × 7 projection matrices were constructed by the seven life-stage classes: two vegetative classes (small and large), two classes of newly-formed clonal offspring (small and large), flowering rosettes, seedlings and dormant rhizome. We also analysed the vital rates underlying the matrix elements (Jongejans et al. 2010). Specific for each stage class we calculated the survival rates (σ) in a size class, growth (γ_{ij}) to a larger size class (conditional to survival and not becoming dormant or flowering), retrogression (ρ) to a smaller size class (also conditional to survival and not becoming dormant or flowering), the number of clonal offspring (κ) produced by an individual, flowering (ϕ, conditional to survival and not become dormant), becoming dormant (ε, conditional to survival), and the number of new seedlings per flowering rosette (π),

We calculated the deterministic population growth rate (λ) for each of the 39 population × year matrices. The 95% confidence interval for each λ was constructed by bootstrapping using the percentile method. The stochastic population growth rate was calculated for each population. Stochastic elasticity was calculated for each of the seven types of vital rates.

Information about dominating gradients (habitat quality and soil moisture) was included by a vegetation-environmental relationship. The gradient structure was extracted from the species composition in the set of 60 plots by means of detrended correspondence analysis, DCA. Ellenberg indicator values (Ellenberg et al. 1992) was used as surrogates for the environmental variables for each plot with four environmental variables: nitrogen, soil reaction (pH), soil moisture and light. The effects of the abiotic and biotic variables: rainfall anomaly index (RAI; sum of June – August), temperature (mean June –August), population size (log-transformed), habitat quality (mean plot values from DCA axis 1) and soil moisture gradient (mean plot values from DCA axis 2), were tested using linear mixed-effects models (using R package *lme4*, (Bates et al. 2015), with site as a random effect. A two-way fixed-design life-table response experiment (LTRE) was used to quantify the contribution of different vital rates to the observed spatial and temporal variability of

Figure 9. a) Picture of the study species *Arnica montana*. b) Treatment with bare soil in seed addition experiment used for testing seedling establishment. c) One of four blocks in seed addition experiment with treatment bare soil and not bare soil. d) Seedlings in bare soil gaps.

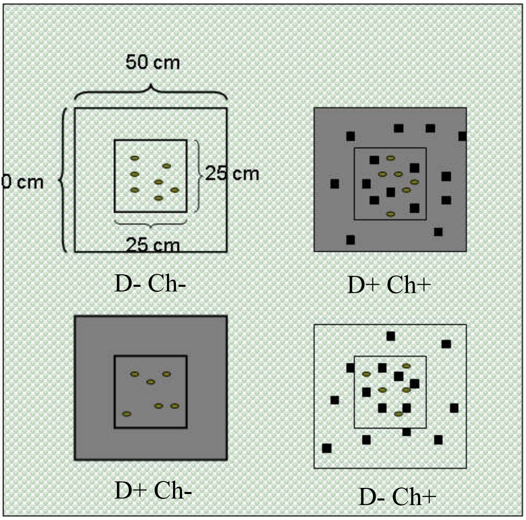
Paper III

This study was conducted as a seedling recruitment experiment (native species: *P. sylvestris* and non-native species: *P. sitchensis*) in three different successional stages- pioneer, mature and degenerated (sensu Gimingham 1972)- in heathland vegetation. We used a randomized factorial block design with four crossed treatments (tree species × successional stages × disturbance × charcoal). Thirty *C. vulgaris* patches were selected. Within each block, four 0.5 m × 0.5 m treatments plot were marked and organized in a 2 m × 2 m quadrate. Two treatments, disturbance (D+, D-) and charcoal (Ch+, Ch-) in each bloc (Figure 10 a). Disturbance treatment involved cutting off all aboveground vegetation, and removal of moss and litter layer. We used, an amount of charcoal, which was similar to what is found to neutralize phytotoxins from *Vaccinium myrtillus* in boreal forests (Zackrisson et al. 1996). 51 seeds of *P. sitchensis* and 40 seeds of *P. sylvestris* were sown in each plot. Seeds were sown on June 2010 and seedling emergence was recorded in September 2010, and seedling establishment recorded in June 2012. The resulting data consisted of two datasets (emergence and establishment) with number of tree seedling as response variable.

To get information about the structure and underlying environmental variability in heathland landscape we measured vegetation height in all plots, stem diameter of 10 randomly selected individuals of *C. vulgaris*, composition of vascular plants (presence/absence) in every treatment plot and explored compositional patterns and environmental variability based on Ellenberg indicator values (Ellenberg et al. 1992) in an indirect ordination analysis.

Effects of the four crossed treatments (tree species × successional stages × disturbance × charcoal) on the main response variables (number of seedling emergence and establishment) were analysed with separate linear mixed effects models with Poisson distribution, using model simplification by backward elimination. To assess the significance of one-way difference in mean we used the Welch *t*-test and Tukey`s HSD for post-hoc comparisons of treatment levels. Principal component analysis (PCA, ter Braak and Šmilauer 2002, Lepš and Šmilauer 2003) was used to analyse the vegetation-environment relations.

a)



b)

Figure 10. a) Experimental design of seed sowing experiment with four treatments, disturbance (D +/-), charcoal (Ch +/-). Seeds of *Pinus sylvestris* and *Picea sitchensis* were sown in centre quadrate. b) Each block consisted of four plots which was covered by a wire cage to protect against grazing animals

Paper IV

The study took place on an archipelago with island size range from 0.1–4.6 ha in the south-western part of Norway. Small islands were selected based on their forest cover of either native *P. sylvestris* or introduced *P. mugo* coll., with mean size of 9811 m^2 and 9679 m^2 respectively. Sampling area were restricted to the vegetated (forested) areas, excluding the littoral zone. Species were recorded during a clock-wise coil-shaped walk form sea levels towards the top and a counter-clock wise from the top towards the littoral zone. Intensive investigation of species composition was done in two 100 m^2 plots, located at the middle of each island and in forest close to seashore.

The principal response variable was the number of native species, excluding coniferous trees and species restricted to the littoral zone. The species-area relationship between islands was compared by means of linear regression, i.e. log species against log area. The species-area relationship was used to correct for island size (taking account the two-dimensional species ordination space) before the difference in species number between *P. mugo* coll. and *P. sylvestris* was analysed using univariate statistics (t-test). Detrended correspondence analysis (DCA) on binary data was used to extract the species composition in species ordination space. To account for spatial autocorrelation, we calculated Moran`s *I* by means of geographical coordinates and ordination scores on first and second ordination axes, both for the response variable, and for the residuals after multiple regressions (GLM), where explanatory variables was area and native vs. introduced trees. To increase variability between islands we added an explanatory variable in form of grazing indicators. Moving average (MA) was used as a spatial regression approach to include the spatial structure of geographical space and species space.

Results and discussion

The investigated species in this thesis show how distribution and abundance are affected by different biotic and abiotic drivers through the effects on vital rates and in turn the population growth rate. Although the different species are affected in different ways depending on traits of the species and the habitat conditions, all species show the importance to include information about the whole life-cycle. In addition, the impact from an increase in abundance of a non-native species is dependent on the specific traits and the persistence of species community composition, thus a non-native species is not always negatively affecting the resident community. In the following chapters, I first discuss how dispersal contribute to changes in distribution and abundance of *P. sitchensis* in coastal heathlands (Paper I), then I discuss the role of disturbance, as a major driver to changes in distribution and abundance in semi-natural habitats, (Paper I, II, III), followed by making a link between environmental drivers and population growth rate to the changes in abundance and distribution (Paper I,II), at least I discuss the impact of increasing abundance of the non-native species *P. mugo* coll (Paper IV).

Dispersal as a driver to changes in distribution and abundance

In our study populations, *P. sitchensis* has spread from established plantations into the adjacent heathlands. Even though *P. sitchensis* is a prolific seed producer most of the seeds are dispersed within 20-40 m from the seed source (Paper I). This is in accordance with other studies on wind-dispersed conifers where almost all seeds were dispersed typically less than 25 m from seed trees source (Nathan and Muller-Landau 2000) and with even shorter distances from trees in closed canopy forests (Nuttle and Haefner 2005). One likely explanation for this relatively short dispersal distance is that *P. sitchensis* has a small seed wing and intermediate terminal velocity (0.9 m s^{-1}, Vikane unpubl.). Wind dispersed trees with seed terminal velocity of 1 m s^{-1}, which is typical for North-American wind-dispersed tree species, is predicted spread rates of only 4–8m year $^{-1}$ (Kuparinen et al. 2009). In contrast, a study of Fastie (1995) at the glacier forelands at Glacier Bay, Alaska, *P. sitchensis* trees were estimated to advance at rates of 300–400 m year $^{-1}$. However, spread rates on the order of 300–400 m year^{-1} require high survival coupled with seed abscission only in strong winds (Caplat et al. 2012). At glacier fronts (primary succession) seed germination of *P. sitchensis* is found to be 9–12% and seedling survival to the second year 50–85%, but were considerably lower in advanced succession stages (Chapin et al. 1994). Such exceptionally high survival corresponds to the high survival probabilities required for a rapid spread (Clark et al. 2001). In our study we found mean seedling survival rate at 3.7% in coastal heathland vegetation (Paper I), thus it is unlikely with a spread rate on the order of 300–500 m year $^{-1}$ in coastal heathlands, although this is not unrealistic in highly disturbed habitats, like roadsides.

Although seed dispersal distances are relatively short under normal conditions, heavy windspeed under the right conditions is found to increase the spread rate of wind-dispersed seed significantly (Nathan et al. 2011). Dry winds from east or south (cones of *P. sitchensis* only opens in dry weather) in combination with heavy seed load (masting years) and seed release period (Nov–April) could increase the dispersal distance and spread rate of *P. stichensis* in semi-natural habitats (Thorvaldsen 2016).

Secondary generation mature trees are observed in our study populations, although our results suggest that plantations are the main seed source, these freestanding trees could play an important role for the future spread rate of *P. sitchensis* (Paper I). However, seedling recruitment of *P. stichensis* in heathland vegetation is quite low and seed rain decreases in distance from plantations (Paper I, III), consequently, seedling establishment and tree density are largest close to the plantations where seed rain is most abundant (Figure 2). A similar pattern is also reported from inventories in different semi-natural landscapes in Norway, where *P. sitchensis* is found to invade adjacent semi-natural habitats (Appelgren and Torvik 2017, Kyrkjeeidet et al. 2017, Nygaard and Øyen 2017).

Disturbance as a driver to changes in distribution and abundance

Seedling emergence and establishment of the non-native species *P. sitchensis* and the native species *P. sylvestris* and *A. montana* is positively affected by the removal of vegetation and litter/turf layer (Figure 9), seed addition experiment paper II, and paper III). Although invasibility of heathland vegetation decline with time after managed fire as a continuous vegetation cover is established, both *P. sitchensis* and *P. sylvestris* invaded every successional stage after fire. In contrast, *A. montana* had no seedling emergence and establishment in untreated vegetation (Paper II), thus *A. montana* seems to be more constrained by vegetation cover than the investigated native and non-native tree species. This contrasting response could be related to the traits of the species and how it interacts with the species community. Many invasive species (*P. sylvestris* is here treated as a potentially invasive species in heathland sensu Bullock 2009) are characterised by having ruderal traits and act as early successional species with a rapid life cycle, high reproductive output (i.e. r-strategists) and plasticity (Van Kleunen et al. 2010, Davidson et al. 2011, Lamarque et al. 2011). Hence, invasive plant species have the potential to invade many different habitats and invasibility is especially found to be enhanced by disturbance (Catford et al. 2012, Jauni et al. 2015). In contrast, *A. montana* seems to be more dependent on a specific management practice which creates gaps in the vegetation turf; a characteristic of many gap-cued and light demanding species in semi-natural grasslands (Bullock 2000).

The species´ responses to disturbance as discussed above have direct consequences for the population growth rate achievable. The ability of *P. sitchensis* to invade every successional stage in combination with heavy seed rain would lead to an increase in abundance of the species (Paper I). Although coastal heathlands are characterised by disturbance (with magnitude dependent on management regimes) and thus a relatively high invasibility, the spatial distribution of available microsites is not homogenous (Bullock 2009, Velle et al. 2014). Seedling emergence and establishment of *P. sitchensis* (and *P. sylvestris*) is enhanced by soils moisture, open space and no competition for light (Paper I, II). Thus, the spatial distribution and abundance of *P. sitchensis* would reflect the distribution of available microsites with right habitat conditions for successful establishment. In *A. montana* populations we observed a very low number of seedlings which is likely because of a low proportion of bare soil present in habitat and consequently a very low fecundity rate (i.e. number of new seedling per flowering rosettes). Increasing fecundity rate has a positive influence on the population growth rate (like population A: 2005–06 and F: 2005–06 and 2007–08, which is above unity). Thus, in an environment which is under pressure from increasing climatic factors an active management regime is even more important for the viability of *A. montana*, which is in accordance to similar trends found for other species in semi-natural grasslands (Bucharová et al. 2012, Bütof et al. 2012).

Linking environmental drivers and population growth rate to changes in distribution and abundance

Species in semi-natural habitats are under pressure from many different drivers, both indirect drivers like increased biotic interactions (e.g. invasion by native or non-native species, Paper I, II, Saure et al. 2013), decreased habitat quality (e.g. abandonment, Hamre et al. 2010) or direct drivers like light availability (Diez et al. 2014). Currently, climate change is causing further pressure on species in semi-natural habitats (Töpper et al. 2018, Paper II).

Our results from the study of *A. montana* shows a long-lived species which forms persistence populations in deteriorated habitats. Temporal variability in precipitation and temperature was negatively affecting the population growth rate through effects on survival, growth and flowering rate. A life table response experiment (LTRE analysis) showed that temporal variability in survival mattered most at the population level, indicating a key role for precipitation in driving temporal variability in local population dynamics (Paper III). This is in accordance with other studies on species in semi-natural grasslands, where climatic drivers, like increasing or decreasing precipitation, is negatively affecting population growth rate through effects on vital rates (Toräng et al. 2010, Töpper et al. 2018).

Indirect drivers like habitat quality and soil moisture gradients extracted from the vegetation-environment relationship or population size did not have any effects on population growth rate. These results were unexpected but could be explained by narrow variability in habitat quality, plasticity to habitat conditions and persistence due to the ability of producing clonal offspring`s (Paper III). It is likely that decreasing habitat quality with increasing biotic interactions has played an important role in the general decline of the species. Such time lags in responses to changing habitat conditions are common for many perennial species in semi-natural habitats (Johansson et al. 2011), where species persists for a long time after abandonment before changes in vital rates leads to extinction or decrease in population size (Lehtilä et al. 2016).

Study populations of *A. montana* were located at the peripheral part of the species range (see Figure 4). According to the overall “centre-periphery hypothesis” (and many underlying hypothesis e.g centre-abundance hypothesis), there is an assumed concordance between geographical “peripherality” and ecological marginality (e.g. harsher environmental conditions at range margins), and species is supposed to perform less at the range margin. However, there is no consensus about this assumption, and more work is needed to elucidate the interplay between range-wide patterns of abundance, demography and environmental suitability (Sagarin and Gaines 2002, Pironon et al. 2016). In our study area, *A. montana* exists in refugia of former semi-natural grasslands which indicate a strong adaptation to specific habitat conditions. Narrow tolerances to specific environmental conditions could explain the steep decline of the species due to increasing precipitation which exceeds the historical climate envelopes of these populations (Peterson et al. 2018). Although the ability to produce clonal offspring could locally compensate the negative contribution from decreasing survival, the stochastic growth rates indicate a species which is slowly declining. In, addition due to increased fragmentation from land-use changes the species exists in small patches distributed within a landscape matrix. Consequently, the connectivity between populations decreases and the populations cannot be “rescued” by dispersal from neighbouring populations (source-sink dynamics). Thus, the decline of *A. montana* is driven by a complexity of interacting drivers which is revealed by getting insight into population growth rate and the underlying vital rates. Therefore, “peripherality” or ecological marginality cannot explain the decline of *A. montana* alone, but it is likely an interplay with the niche breath–range size in determining the future expansion of the species (Slatyer et al. 2013).

Invading *P. sitchensis* in coastal heathlands exists as randomly distributed trees with different size and in different life-cycle stages, from small seedlings to larger cone-bearing trees. Even though seedling recruitment and survival rate are relatively low, *P. sitchensis* can form self-sustaining populations in heathland vegetation (Paper I). *P. sitchensis* appears to be enhanced by a developed humid soil layer but constrained by increasing cover of *J. communis* (Paper I). Moreover, seedling emergence and establishment is largest in pioneer vegetation and enhanced by disturbance, which is also found to account for the native coniferous species *P. sylvestris* (Paper III). Thus, a current and immediate situation is that unmanaged adjacent coastal heathlands would be characterised by abundant, but scattered groups of *P. sitchensis*, mixed with characteristic heathland flora, including the key species *C. vulgaris* and native tree species like *B. pubescens, P. sylvestris*, and *J. communis*, the latter two on dry and undeveloped soil conditions. This situation could change as the invading *P. sitchensis* trees grow taller, and with potential canopy closure, and according to our findings this is a likely future situation in adjacent heathlands close to the plantations (Paper I).

Impact from increasing abundance of non-native species

Conifer species is found to have a negative impact on plant species richness in coastal heathlands (Saure et al. 2013, Saure et al. 2014). In our study where we compared species composition and species richness between islands reforested by the native *P. sylvestris* or the non-native *P. mugo* coll., we found more vascular plants on the islands with the introduced non-native species (Paper IV). Our results suggest that *P. sylvestris* forest represent an older successional stage compared with *P. mugo* coll. forests. Extensive carpets of *Sphagnum* spp. and other bryophytes have developed on these islands and cover most of the forest floor. Thus, our results suggest the cover of bryophytes suppress establishment of vascular plant species, which is in accordance with our finding about the establishment of conifer species in later succession stages (Paper III). In, addition *P. sylvestris* forests represent a stable stage community with lack of disturbance, compared to the *P. mugo* coll. islands which are regularly disturbed by tree-fall of *P. mugo* coll. Regular disturbance work as a reset mechanism on succession and facilitate the establishment of gap-cued and light-demanding species (Bullock 2000), which explains the difference in species richness between island forested by native *P. sylvestris* and non-native *P. mugo*.

Our findings contrast to the assessment of *P. mugo* in The Alien species list of Norway, where *P. mugo* is categorised as a species with high ecological impact (Elven 2018). In our study, we are collectively treating *P. mugo* and *P. uncinata* as the same species despite a very different growth habit. *P. mugo* have a decumbent growth, especially as juvenile, and thus it could act as an effective competitor and suppress other vegetation in early stages after establishment. When it becomes older the growth habit changes and it forms erect stems with an open tree crown. In contrast, *P uncinata* has an erect growth in juvenile stages and would not suppress resident vegetation in the same way as *P. mugo*. Although our study is performed in relatively old forests (70 years) and thus both represent late life-history stages and similar growth form, the difference between species could have contributed to the contrasting results.

Our study shows that impact from a non-native species is strongly context dependent and influenced by the traits of the invading species. This is in accordance with many other studies which find contrasting effects from invasive plant species (Pyšek et al. 2012 and references therein). In a global perspective, conifer species is found to invade many different geographical regions and habitats (Richardson 2004, Richardson and Rejmanek 2011). In coastal heathland of Norway, the combination of many plantations, life history traits of the conifer species and an open landscape have caused an abundant spread of *P. mugo* and *P. sitchensis*, which has consequences to the conservation of this key cultural landscape. Level of management will have to be a balance between economic interests in commercial plantations and the need to preserve a selection of key cultural landscapes.

Conclusions and perspectives

In this thesis, the aims were to investigate what are the important drivers behind the changes in abundances over time and space, exemplified by invasion by the non-native conifer *Picea sitchensis* in coastal heathlands (Paper I, III) and the decline of the threatened peripheral species *Arnica montana* in semi-natural grasslands (Paper II). In addition, we zoom out to investigate the impact of a non-native conifer on species community and landscape scales (Paper IV).

Our results show that *P. sitchensis* can produce self-sustaining populations in coastal heathlands (Paper I). Although seedling recruitment and establishment is partly constrained by the heathland vegetation, leading to a patchy distribution, high seed dispersal rate in combination with high population growth rate is causing a spread of *P. sitchensis*. According to these findings the non-native *P. sitchensis* is an invasive species (sensu Richardson et al. 2000, Pyšek et al. 2004) in coastal heathlands of western Norway. Further research is recommended with respect to record long-distance seed dispersal ability of *P. sitchensis* by means of analytical models on seed dispersal by wind. Further invasion potential of *P. sitchensis* in other habitats than coastal heathlands need to be investigated, which would provide knowledge on the potential impact of *P. sitchensis* in a variability of species communities.

Decline of the peripheral species *A. montana* in semi-natural grasslands is mainly driven by decreasing survival due to increasing precipitation (Paper II). results give important implications on the importance of disentangle the effects from multiple drivers. Further prospect of this species should involve investigation of population dynamics on a larger scale and involve the whole species range which could give insight into interesting centre-peripheral dynamics.

Impact from invasive plant species is dependent on the context of invasion and the traits of the invading species (Pyšek et al. 2012). Our results in the study on the impact from the coniferous species *P. mugo* coll. shows that due to the open decumbent growth form this species is in a state of perpetual gap dynamics causing no effects on species richness. Further research on the effects from non-native coniferous species should combine information on different levels like population dynamics, spread and community to assess the invasion potential and to get insight into invasion as an ecological phenomenon.

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Papers

Paper IV:

North Atlantic Islands with native and alien trees: are there differences in diversity and species-area relationships?

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North Atlantic Islands with native and alien trees: are there differences in diversity and species-area relationships?

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Keywords
Autocorrelation; Diversity; Introduced species; Island biogeography; Pine; Richness; Spatial Autoregression; Species space

Abbreviations
DCA = detrended correspondence analysis; GLM = generalized linear models; ISAR = Island species–area relationship; MA = moving average

Nomenclature
Lid & Lid 2005

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Abstract

Questions: Are there differences in species composition and richness between islands that were reforested more than 70 yr ago with the introduced *Pinus mugo* compared with islands supporting the native *Pinus sylvestris*? Do the results depend on autocorrelation in geographical space and species ordination space? Species richness is expected to increase as a function of the size of an island; are the responses to island size different between *P. mugo* and *P. sylvestris* islands. Does the land-use history have an impact on the current species composition and richness pattern?

Location: The archipelago is in the oceanic section of the Atlantic bioclimatic zone, west Norway. This archipelago was part of the ancient and widespread treeless heathland found along the European west coast.

Methods: Data on vascular plants were compiled from the forested islands, and their differences in species composition were analysed by ordination. The hypotheses were tested by means of *t*-tests and generalized linear models, the spatial component was accounted for by means of Moran's *I* and spatial autoregression with the moving average approach. This was done both in geographical space and species ordination space.

Results: There are more vascular plants on the islands with introduced *P. mugo* than on the islands with native *P. sylvestris*. The latter have rather homogenous undergrowth dominated by bryophytes. This may explain lower richness on islands with native forest and why island size is not correlated with species richness on these islands. In contrast, *P. mugo* is easily wind-felled in autumn storms, which keeps rocky microhabitats exposed to air and new forest habitats are created. Species that are associated with the previous land-use system (grazing) prevail on islands with introduced pine, and thus contribute to higher plant richness.

Conclusions: The difference in species richness and island species–area relationship (ISAR) between *P. mugo* and *P. sylvestris* islands may relate to the same underpinning causes. Species from the old land-use system have survived on *P. mugo* islands, but not in the late-successional forest with a more closed canopy that has developed on *P. sylvestris* islands. Thus habitat and species richness is higher and increases with area on *P. mugo* islands but not on *P. sylvestris* islands.

Introduction

The Millennium Ecosystem Assessment (MEA 2005) identifies the transport of species across biogeographic boundaries as a major threat to biodiversity worldwide. This has been widely accepted by conservationists (cf. Lodge & Shrader-Frechette 2003; Perrings et al. 2005). However, while some studies find that invasive species have strong negative impacts on native biodiversity, comparable to the effects of habitat destruction (Wilcove & Chen 1998; Pimentel et al. 2001; Pauchard & Shea 2006), others fail to document any negative impacts and conclude that plant invasions do not cause species extinctions, at least not on regional or broader scales (Sax et al. 2002; Gurevitch &

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Padilla 2004; Maskell et al. 2006; Stohlgren et al. 2006). It has thus been argued that direct effects of alien species on the species richness component of biodiversity is not very well documented (Gurevitch & Padilla 2004; but see Powell et al. 2011), and the overall global impact is still rather enigmatic (Rosenzweig 2001; Slobodkin 2001; Barney & Whitlow 2008).

There are several reasons for these ambiguous reports (Davis 2003). First, there is a lack of coherent scaling across studies, which makes direct comparisons of ecological impacts questionable (Shea & Chesson 2002; Gooden et al. 2009). Second, it is often difficult to make clear causal links between the spread of alien plants and the demonstrated negative impact. Third, the concepts and terminology in the emerging field of invasive biology are often ambiguous (Colautti & MacIsaac 2004), for instance, it is important to distinguish between infrequent introduced species that have minimal ecological impacts and species that are invasive due to high rates of population growth, rapid spread and strong negative impacts on native species richness and ecosystem function (Young & Larson 2011).

The potential impact of introduced species will also depend on biogeographic conditions. Alien species may represent a threat to young terrestrial ecosystems, such as forest ecosystems on small islands along biogeographically isolated coasts (Pretto et al. 2010). A number of small islands along the North Atlantic coast of Norway have emerged since 7000 BP due to sea level fluctuations in postglacial times (Kaland 1984; Bondevik et al. 1998). This relatively young archipelago has a very peripheral location at the north-western fringe of the Palaearctic flora region, and it is not certain if these areas are saturated with species from the Eurasian species pool (cf. Svenning & Skov 2007). The flora of Norway, which covers this study area, consists of a high proportion of introduced species, partly because of an almost complete glacial cover during the last glacial period. Between 22% and 50%, depending on the temporal criteria applied (Fremstad & Elven 1997), of the vascular plants in Norway have been introduced. Only a subset (ca. 4%) of these has spread, and only a small proportion of these species has had a potentially significant negative ecological impact (Gederaas et al. 2008). The biogeographical conditions along the North Atlantic coast indicate that this area might be vulnerable to the potential effects of introduced species.

Scots pine (*Pinus sylevstris* L.) is a potentially dominant canopy tree in large fractions of the boreo-nemoral and North Atlantic parts of the Palaearctic, both on the mainland and the islands. The natural pine forests along the North Atlantic coast of Europe were, however, transformed by humans 1–5 kyr BP. Fire was used to create open heathlands suitable for year-round grazing by domestic animals (Kaland 1986; Loidi et al. 2010). During the last 130 yr, a decreasing farming population, changes in farming practices and public reforestation schemes have resulted in pine forest on many of the islands. Some islands have native Scots pine (*P. sylvestris*) and others have a mix of mountain dwarf pines (*Pinus mugo* Torra complex, mainly subsp. *mugo* and subsp. *uncinata*). Alongside this reforestation, the traditional land-use regime and open heathlands have persisted. The rugged coast and many islands of western Norway have allowed different forest types to persist alongside each other within the same landscapes. This study is carried out within an archipelago of coastal islands, and compares islands that have been reforested for at least 70 yr with native Scots pine (*P. sylvestris*) with islands that were planted at least 70 yr ago with introduced mountain dwarf pines from the sub-alpine zone in the Pyrenees, i.e. *P. mugo* subsp. *mugo* and *P. mugo* subsp. *uncinata* (hereafter *P. mugo* coll.).

The first step in the study is to analyse the relationship between the size of the islands and their number of species, i.e. the well-documented island species–area relationship (ISAR; Rosenzweig 1993; Whittaker & Fernandez-Palacios 2007; Tjorve & Tjorve 2011). Larger islands have a higher probability of harbouring more species than smaller islands, which is often explained by an increased number of habitats as a function of island size (Whittaker & Fernandez-Palacios 2007). However, some studies have tried to disentangle the 'size effect' from the 'habitat effect' (Westman 1983; Kallimanis et al. 2008). The number of habitats or 'entities' within a landscape is not easy to delimit, and therefore the relative importance of area vs habitat effects is elusive. In this study, we explore these phenomena by contrasting the ISAR of islands reforested with native Scots pine vs islands of the same size range that are planted with introduced pine. We assume that the size of the island correlates with the number of topographically and edaphically defined habitats, but the two tree species have different effects on habitat heterogeneity, as the old-growth Scots pine forests can tolerate the severe wind conditions at the coast and are therefore relatively undisturbed. Within these forests, light conditions appear more uniform due to a closed tree canopy, and on the ground there are extensive moss carpets that cover the microtopographic variation. Thus, we hypothesize that Scots pine forests, which are in a moss-dominated late-successional phase, may counteract the positive effect of island area. Due to proportionally fewer plant habitats on islands with old-growth Scots pine forest, we predict a relatively shallow regression slope of ISAR (i.e. lower z-value) on islands reforested with native Scots pine.

The direct effect of *P. mugo* coll. on species richness is the overall research question. It is either a passenger species that does not influence the local environment (Chabrerie et al. 2008), or it is more of an ecosystem engineer that directly influences species composition and richness

(Jones et al. 1994). The potential biological life span of the introduced pine is much shorter than that of *P. sylvestris,* and it is easily wind-felled during storms, resulting in higher disturbance and more variable light and temperature conditions on islands reforested with the introduced pine. The higher disturbance frequency may also result in higher colonization success on islands with *P. mugo* (hereafter *P. mugo* islands) than islands with *P. sylvestris* forest (hereafter *P. sylvestris* islands). These ecological differences predict higher species richness per unit area on *P. mugo* islands compared with *P. sylvestris* islands. At the same time, however, many coniferous species are invasive and particularly within the genus *Pinus* (Richardson & Rejmanek 2004; Richardson 2006), which predicts negative impacts on native diversity. Hence, we test the null hypothesis of no difference in species richness between *P. mugo* and *P. sylvestris* islands, and interpret any deviations from this null hypothesis (positive or negative) in light of the invasive species effect and habitat heterogeneity hypotheses outlined above. The clear spatial nature of studies on oceanic islands requires that we take autocorrelation into account (Selmi & Boulinier 2001), and we have explicitly considered both the geographical space and species ordination space in the analyses. The primary aims are to test the following hypotheses

1. The increase in number of species as a function of the size of an island is steeper on *P. mugo* than *P. sylvestris* islands
2. There is no difference in species richness between islands reforested with *P. sylvestris* and those that are reforested with *P. mugo* coll.
3. The significance of the differences in species richness is independent of the positions of islands in geographical space and species ordination space.

If the two last hypotheses are rejected, we aim to use differences in species composition and ecological attributes among the species unique to one type of island to aid the causal interpretation of the differences. The land-use argument will be reinforced if shade-tolerant forest core species prefer islands with old-growth Scots pine forest, whilst anthropogenic grazing-tolerant species are more frequent on islands that have been reforested by *P. mugo* coll.

Methods

Area

The study took place on an archipelago in the south-western part of the Scandinavian Peninsula, bordering the North Atlantic Ocean (59°42′–60°44′ N, 05°02′–05°35′ E; Fig. 1). The islands range from 0.1 to 4.6 ha (mean = 1.0 ± 0.12 ha). The bedrock consists mainly of

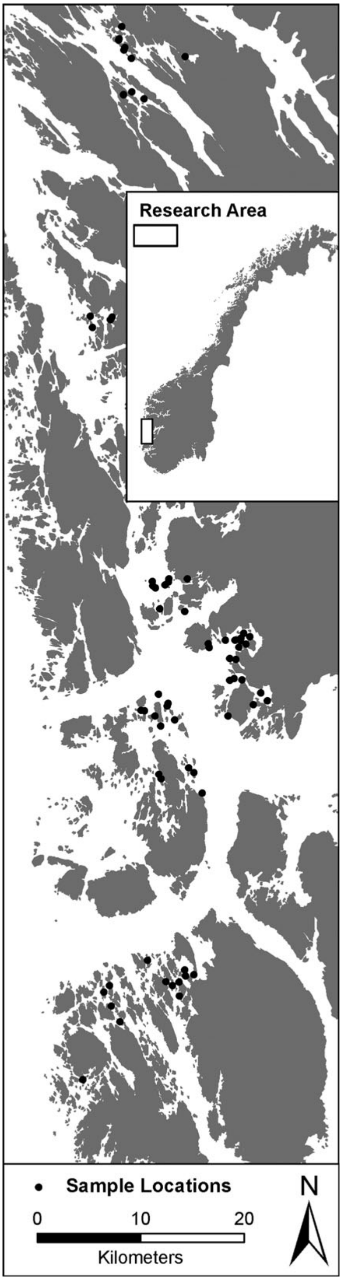

Fig. 1. Map showing the study area in Norway and a crude indication of the area where the 70 islands were sampled.

gneiss and granite, mostly with an acidic and thin soil layer, although there are large areas that consist of humus directly on bedrock. Typical podsol profiles develop in favourable microtopographic locations. The islands are uninhabited and are not actively used for agricultural or forestry purposes.

The climate is oceanic with mild winters with high precipitation and cool and moist summers. The mean annual temperature is 6.7 °C, mean summer temperature (June–July) is 13.3 °C, and mean winter temperature (February) is 0.7 °C. Mean annual precipitation is 1815 mm, and winds are strong, with an October average of 5.5 $m \cdot s^{-1}$, but events with wind speeds above 20 $m \cdot s^{-1}$ are common every year (Flesland airport climate station). The archipelago is located in the euoceanic section of the Atlantic bioclimatic zone (Moen 1998). *Pinus sylvestris* is the only coniferous forest tree native to this region, and forest cover is typically not dense, with several deciduous trees contributing to the lower canopy, including *Betula pubescens, Sorbus aucuparia*, *Prunus padus* and *Alnus glutinosa,* with *Juniperus communis* common in the shrub layer. Dwarf shrubs (chamaephytes) such as *Empetrum hermaphroditum* and *Calluna vulgaris* dominate, together with species belonging to the genera *Vaccinium* and *Erica*. Herb and graminoid richness and cover are relatively low, but a few ferns are very common, e.g. *Polypodium vulgare* and *Dryopteris dilatata*. The ground layer is well developed and dominated by bryophytes, such as *Hylocomium splendens* (H edw.) B.S.G., *Pleurozium schreberi* (Brid.) Mitt. and *Sphagnum* spp. Nomenclature for all vascular plants follows Lid & Lid (2005), except *Pinus mugo* Torra complex (Christensen 1987) and *Picea sitchensis* (Bong) Carr.

Land use

The original deforestation of the pine forest on these islands was not synchronized, which suggests that it was driven by land use (Kaland 1986; Hjelle et al. 2010). This is marginal agricultural land, but rich fishing resources contributed to livelihoods and supported a relatively high coastal population. In the late 1800s these islands were very heavily utilized due to steep human population growth, combined with a largely agricultural economy with more than 85% of the population in western Norway engaged in smallholder farming and animal husbandry (Oyen et al. 2006). The reforestation started in the late 19th century as a result of emigration, urbanization and government schemes to promote *P. mugo* subsp. *mugo*, aiming to provide the poor farmers with fuelwood. Later, in the 20th century, *P. mugo* subsp. *uncinata* was also planted. The islands with native *P. sylvestris* were also deforested during the most intensive farming period due to high demand for timber and fuel (Oyen et al. 2006). As judged from the age of the oldest trees on the studied islands, the forests are at least 70 yr old.

Field methods

Small islands were selected based on their forest cover of either native pine ($n = 36$) or introduced pine ($n = 34$) forest of at least 70 yr old. Other native trees are present in the forests (see above), and some individuals of *Picea abies* and *P. sitchensis* (Bong.) Carr had also been planted on the *Pinus mugo* islands. The size class distributions of the two island types are similar, with a mean size of 9811 ± 1789 m^2 (native) and 9679 ± 1507 m^2 (introduced). The island size and area sampled were restricted to the vegetated (forested) areas, excluding the littoral zone. Consequently, species with habitats restricted to the littoral zone were not included in the species list for each island, but species that occurred on outcrops within the forested area (e.g. *Arctostaphylos uva-ursi, Sedum anglicum*) were included. We only included native species, which means species such as *Cotoneaster* spp. and *Acer pseudoplatanus* were excluded. There were never more than one or two species of this type on each island and they normally amounted to a few individuals. Species were recorded during a clockwise coil-shaped walk from sea level towards the top. We then made a similar walk (counter-clockwise) from the top towards the littoral zone. To improve the species search we did an intensive investigation of two 100-m^2 plots, one of which was located in the middle of the island (normally the top), and the other in the forest near sea level in a somewhat flat area. Approximately 90–180 min were spent sampling each island, depending partly on the size of the island, but variable topography and accessibility made it impossible to set a fixed time proportional to the size of the islands for sampling. The islands have relatively few vascular plants (mean 20.8 ± 0.7); thus it is not unreasonable to assume that the number of recorded species approximate the total number of vascular plants on each island.

Numerical analyses

The analytical path

The principal response variable is the number of native species excluding coniferous trees and species restricted to the littoral zone. First, we compared the species–area relationship between islands by means of linear regression, i.e. log species against log area, a model derived from the classical Arrhenius (1921) formula (Tjorve & Turner 2009). There is no significant correlation between species richness and the distance from the mainland (isolation effect). Richness is negatively correlated with the estimated terrestrial area within a 500-m radius around the island centre. The

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species–area relationship was used to correct for island size before the difference in species number between *P. mugo* and *P. sylvestris* islands was analysed using univariate statistics. If the difference was significantly different from zero, we continued the significance test with multivariate regressions, including spatial models in combination with ordination. This enabled a test that takes account of both the location of islands in geographical space and the location of islands in species space (two-dimensional species ordination space; Diniz-Filho et al. 2003). The rationale is that, on average, species richness on nearby islands has a higher probability of being similar compared with distant islands, i.e. standard spatial autocorrelation or distance decay. Spatial autocorrelation violates the standard statistical assumption that observations are independent of one another, and is problematic because it will inflate the degrees of freedom and hence the chance of making a type-I error, i.e. rejecting a correct null hypothesis (Dormann et al. 2007). There are three main approaches to this challenge: (1) the partial approach is to partial out the deviance that correlates with geographical coordinates and then analyse with respect to the target explanatory variable (Borcard et al. 1992); (2) the residual approach aims to test the residuals for remaining spatial structure posterior to testing of the predictor (Hawkins et al. 2007); and (3) the simultaneous approach includes the spatial structure in a spatial regression (Bini et al. 2009). In species richness analyses, however, the similarity in species composition should also be taken into account, i.e. location in species ordination space (Diniz-Filho et al. 2003). To obtain this, we used detrended correspondence analysis (DCA) on a binary data set based on presence of all species in the forest in each of the 70 islands, excluding species only found on two islands (69 species in total). The rationale is that if two neighbouring islands have the same number of species, but a totally different flora, the number of species is actually statistically independent (no effect of the proximity in space). Although this extreme example is unlikely in nature, it illustrates how the degree of shared species will also determine the degree of statistical independence between the islands. Many shared species yield high statistical dependence and vice versa, i.e. species ordination space autocorrelation. The location of sampling points in species ordination space will be almost as important as the geographical distance because this determines the statistical independence of species richness observations. We therefore used both geographical coordinates and ordination scores on first and second ordination axes (see below) and calculated Moran's *I* as a measure of autocorrelation. This was done both for the response variable (species richness) and for the residuals after multiple regressions, where the explanatory variables are area and native vs introduced trees. If there is significant autocorrelation in several distance classes in the residuals it may indicate that an important variable is missing (Hawkins et al. 2007). In our case, we added an explanatory variable that indicates how well the grazing indicators have survived after the gazing practice ceased, i.e. number of grazing indicator species based on Norderhaug et al. (1999) and Fremstad (1997). This is merely a variable that may aid interpretation of the results. Finally, we used moving average (MA) as a spatial regression approach to include the spatial structure of geographical space and species space in the regressions, where area was entered before the target predictor of native vs non-native forest, and the grazing indicator.

Numerical tests and software

We used a simple *t*-test to check if the there are significant differences in species richness between *P. mugo* and *P. sylvestris* islands. We used generalized linear models (GLM) with a log-link function (assuming a Poisson distribution of errors) to test if species richness is explained by the forest type on the islands, and included island size as a covariable. The residuals from this regression were then checked with Moran's *I* for significant positive spatial autocorrelation, both in geographical space as well as in species ordination space (applying the DCA axes score for ordination above). We used Moran's *I* to test for positive spatial autocorrelation of the response variable before and after the GLM regressions. As a third alternative, we used moving average (MA) as a simultaneous spatial regression approach because it has the ability to minimize spatial autocorrelation in residuals, although we are not able to quantify all biological and ecological processes generating the spatial structure in the data (Bini et al. 2009). We used default DCA in CANOCO (v. 4.5 for Windows, Microcomputer power, Ithaca, NY, USA) to display graphically the islands on the basis of species present in the forest of the islands, and relate the axes to spatial coordinates, size of islands, type of forest and browsing/grazing indicator species. R software was used for the *t*-test and GLM regressions (R Foundation for Statistical Computing, Vienna, AT). Spatial analysis in macroecology (SAM, v. 4.1; Rangel et al. 2010) was used for Moran's *I* and spatial autoregression with the MA approach.

Results

Island species–area relationships

There is a statistically significant relationship between island size and total number of species found on the islands (Fig. 2a). The *z*-value (regression slope) is 0.1 for the total data, but the slopes vary between island types: whereas the increase in species number as a function of island size is steep and highly significant on

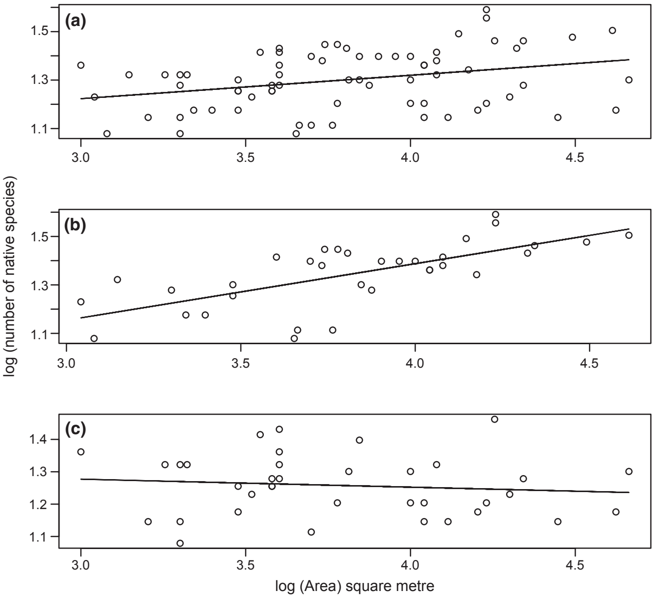

Fig. 2. Island species–area relationship (ISAR): (**a**) for all islands together: log(spp) = 0.93 + 0.1 × log(area) ($P < 0.01$), (**b**) *Pinus mugo* islands: log(spp) = 0.48 + 0.23 × (log)area ($P < 0.001$). (**c**) *Pinus sylvestris* islands (not significant).

P. mugo islands (z-values = 0.23; Fig. 2b), no statistically significant ISAR relationship is found on *P. sylvestris* islands (Fig. 2c).

Species richness

A total of 77 native vascular plant species were recorded on *P. sylvestris* islands, whereas 75 species were recorded on *P. mugo* islands. The mean number of species is 18.5 ± 0.69 on *P. sylvestris* islands and 23.2 ± 1.14 on *P. mugo* islands, which is a statistically significant difference ($P < 0.001$, $t = 3.5$). When the species numbers are corrected for island size, mean number of species on *P. mugo* islands decreases somewhat, but is still significantly different ($P < 0.001$, $t = 3.1$; Fig. 3) from the mean species richness on *P. sylvestris* islands. The null hypothesis of no difference in species number between *P. mugo* islands and *P. sylvestris* islands is therefore rejected, but see below for how the outcome varies depending on the approach used in multivariate analyses to tackle the autocorrelation challenge.

Islands in species space and species turnover

The difference in species composition between *P. mugo* and *P. sylvestris* islands is significant, although not very

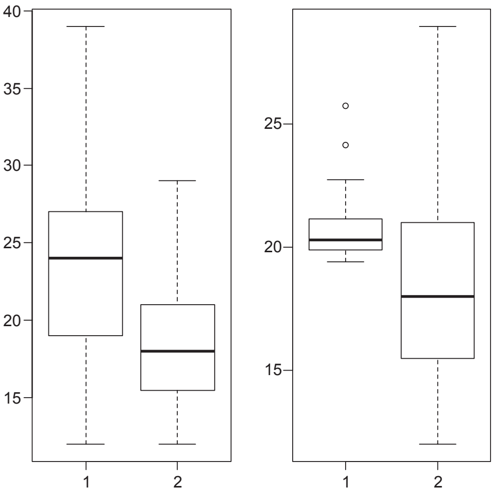

Fig. 3. Box plots showing significant differences in mean species number on *Pinus mugo* islands (1) and *Pinus sylvestris* islands (2). The panel to the left depicts uncorrected values (1 = 23.2 ± 1.4; 2 = 18.5 ± 0.7), and the panel to the right depicts corrected values for *P. mugo* islands (1 = 20.7 ± 0.7). The overall uncorrected mean is 20.8 ± 0.7.

strong (Fig. 4). The variation along the first ordination axis in Fig. 4 correlates with geographical position (east–west): *P. sylvestris* islands are more common in the eastern part of the study area, towards the mainland, whereas *P. mugo* islands are more commonly found in the west. The latter islands are characterized by *Erica cinerea, Phegopteris connectilis, Carex rostrata* and species that indicate light and/or disturbance, including *Digitalis purpurea, Juncus conglomeratus* and *Rubus idaeus,* which are almost exclusively on *P. mugo* islands. Forest species such as *Myrica gale*, *Linnaea borealis* and *Melampyrum pratense* are almost exclusively in the native pine forest (Fig. 4, Appendix S1). Species turnover (SD units) within each island type differs only slightly between the two types of island (*P. mugo*: 1.65 SD; *P. sylvestris*: 1.73 SD). The covariation between species composition and geographic location represents an analytical challenge (see below).

Table 1. Summary statistics of detrended correspondence analyses (DCA) on a binary species by island matrix (69 × 70; cf. Fig. 4, Appendix S1). The first and second axes are used in the autocorrelation and regression analyses. Total inertia = 1.548. Significant correlation coefficients are shown for the covariables (area, east, north) as well as explanatory variable (grazing indicators), and the direction of maximum richness (natspp) and number of alien tree species on the islands (alien).

DCA axes	1	2
Eigenvalue	0.137	0.10
Gradient length	1.86	1.45
Species–env. correlation	0.85	0.73
North	ns	0.47
East	0.23	ns
Natspp	−0.70	ns
Log(area)	ns	0.58
Alien	−0.45	ns
Grazing	−0.75	0.22

Autocorrelation

Species richness on the islands is affected by the location of the island, both in geographical and species ordination space (Fig. 4, Table 1). This is captured by Moran's *I* where species richness (uncorrected) is significantly autocorrelated in geographical space, particularly over short distances (<0.1–0.5 km; Fig. 5a). The three alternative approaches used to deal with this autocorrelation yield different results. The first approach was to partial out the spatial or compositional structure in the data by including either of these structural variables as covariates in the GLM regression models. Using this approach, the difference in richness between *P. mugo* and *P. sylvestris* islands is statistically significant if geographical space is a covariable (Table 2B), but not if species ordination space is used (Table 2C).

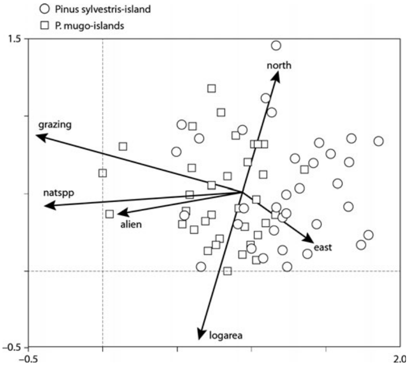

Fig. 4. DCA ordination diagrams of binary data showing the difference between *Pinus sylvestris* islands and *P. mugo* islands. Geographical and biological variables are correlated with DCA axes and superimposed on the diagram. natspp = number of native vascular plants on each island; grazing = number of indicator species that are associated with grazing activity (see Appendix S1); east = eastern coordinates; north = northern coordinates, log-area = log size of the islands; alien = number of alien tree species found on the islands.

The second approach was to first regress and then examine the residuals for autocorrelation. The two forest types differ significantly in the GLM regression model with species richness as the response variable and (log)area as a covariable (Table 2A). The residuals from this GLM model show only marginally significant autocorrelation over the

Table 2. Generalized linear model (GLM) where native vs non-native pine forest is the explanatory variable and null deviance is 114.1 with 69 df. (A) Residual analyses approach where (log)area is the only covariable, and explanatory variables are first native vs alien pine (native) and then grazing indicator (grazing). The residuals are checked for autocorrelation by means of Moran's *I* with respect to geographical space (cf. Fig. 5b) and species ordination space (cf. Fig. 5c), and here we also added grazing as an explanatory variable (cf. Fig 5d). (B) Partial regression approach: covariables are island size log(area) and geographical position (north and east), and (C) log (area) and locations in species ordination space (DCA axes 1 and 2). Native is not significant when ordination space is added first (C), cf. analyses of residuals (Fig 5c).

	Variables	*df*	Deviance	Resid. df	Resid. Dev	Pr(Chi)
A	Log(area)	1	13.90	68	100.18	<0.001
	Native	1	17.04	67	83.14	<0.001
	Grazing	1	41.28	66	41.86	<0.001
B	Log(area)	1	13.90	68	100.18	<0.001
	North	1	2.04	67	80.93	>0.15
	East	1	7.02	66	91.55	<0.01
	Native	1	7.08	65	84.04	<0.01
C	Log(area)	1	13.90	68	100.18	<0.001
	DCA-1 score	1	46.70	67	53.48	<0.001
	DCA-2 score	1	3.33	46	50.15	>0.06
	Native	1	0.11	65	50.05	>0.74

df, degrees of freedom; Resid., residuals; Dev., deviance; Pr(Chi), *P*-value of Chi-test.

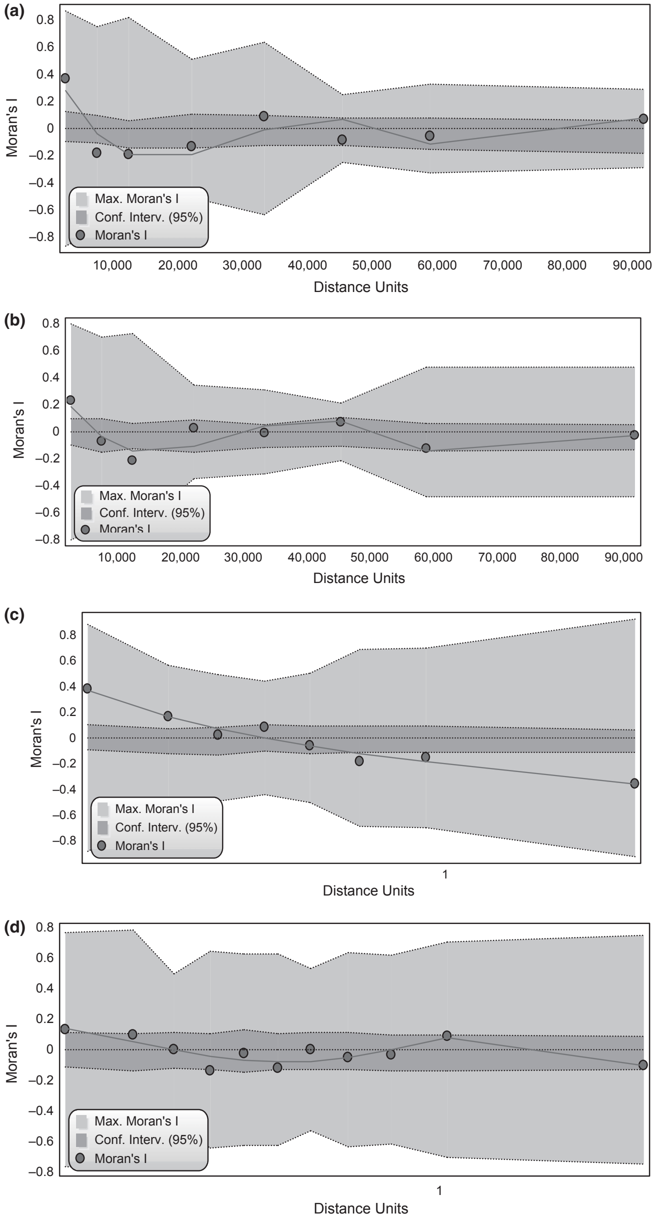

Fig. 5. (**a**) Moran's I of uncorrected species richness values as a function of geographical distance indicates significant spatial autocorrelation in species richness. The shortest distance class of the residuals is significantly autocorrelated ($P = 0.03$), i.e. residuals from GLM regression (cf. Table 2A; island size = covariable; native/alien forest = predictor). (**b**) Moran's I of residuals after a GLM (model: species richness ~ log(Area)) plotted against geographical distance. (**c**) The same residuals as in (**b**) plotted against species ordination space distance. (**d**) When grazing indicator variable is added to the above GLM model; only marginal positive autocorrelation in the shortest distance class of the residuals remains (cf. Table 2A). Negative autocorrelations, i.e.more different than random expectation are not interpreted. The distance units in (**a**) and (**b**) are geographical distances based on UTM coordinates, (c) and (d) are arbitrary based on species ordination space (DCA axes 1 and 2). Conf. Interv., confidence interval.

Table 3. Spatial regression with moving average (MA) approach. Log-area, native vs non-native pine forest, and number of grazing indicator species (grazing) are explanatory variables. The spatial structure is entered as (A) geographic coordinates with $F = 20.97$; $R^2 = 0.65$; spatial autoregressive parameter rho = 0.916; and (B) species ordination space with $F = 40.97$; $R^2 = 0.81$ and rho = 0.982 (alpha = 1.0 in both cases).

Variables	OLS coeff.	MA coeff.	Std. coeff.	SE	*t*-value	*P*-value
(A) Constant	−0.311	−10.719	0	5.481	1.984	>0.051
Log-area	4.793	7.070	0.483	1.389	5.088	<0.001
Native	1.928	−1.489	0.211	0.943	2.638	<0.001
Grazing	2.049	1.956	0.632	0.299	6.535	<0.001
(B) Constant	−0.311	1.719	0	4.244	0.405	>0.687
Log-area	4.793	5.224	0.357	1.090	4.792	<0.001
Native	1.928	−1.860	0.157	0.884	2.105	<0.039
Grazing	2.049	1.856	0.600	0.257	7.233	<0.001

OLS, ordinary least square regression; MA, moving average; Coeff., coefficient; Std, standard.

shortest distance (Fig. 5b), but the residuals in species composition space show very clear and significant autocorrelation (Fig. 5c). When we added the grazing indicator variable (Table 2A), the residuals from this GLM model show no significant autocorrelation (Fig. 5d).

The third approach was to apply simultaneous spatial regression with moving average, with geographical space implicitly taken into account and island size included as a covariable and the grazing indicator variable added. These yield significant differences between *P. mugo* and *P. sylvestris* islands, but the significance is strongest in geographical space and rather weak in species ordination space ($P < 0.03$; Table 3B).

Discussion

The number of species found in the entire forest on each island is higher on *P. mugo* islands than *P. sylvestris* islands, except when using the partial regression approach with DCA axes as covariables. There are also clear differences in the species–area relationships between *P. sylvestris* islands (*z*-value ~0) and *P. mugo* islands (*z*-value = 0.23). We will discuss how the differences in ISAR and species richness composition may be related to similar underpinning causal factors, and how the demonstrated autocorrelation, particularly in species ordination space, may aid the interpretation and the plausible causal links (cf. Diniz-Filho et al. 2003).

Island species–area relationships

We confirmed the hypothesis that the increase in species as a function of island size is steeper on islands with non-native rather than native pine. The *z*-value on *P. mugo* islands is in the expected range (Lomolino & Weiser 2001 and references therein) and very close to the theoretical suggested value of 0.26 (MacArthur & Wilson 1963), whereas for *P. sylvestris* islands the relationships is not significant. The latter result may relate to the 'small island effect' (SIE; Niering 1963): the studied islands are within the size range for which several authors have claimed that there is no systematic trend in species richness (Lomolino & Weiser 2001; Triantis et al. 2006). However, it is unlikely that SIE is only apparent on islands with native pine forest that are very similar environmentally. We therefore hypothesize that the independence between species number and the size of the *P. sylvestris* islands is caused by the ecological conditions in the forest on these islands. Although we did not quantify the number of habitats in the forests on these islands, we did observe reduced microtopographic relief on *P. sylvestris* islands. This is due to extensive carpets of *Sphagnum* mosses that have developed on these islands, which cover most small depressions and form minor blanket bogs on steeper slopes. Dominant forest floor bryophytes (e.g. *Sphagnum, Polytrichum,* feather mosses) are able to suppress establishment and growth of vascular plants by reducing access to light, water, nutrients and space (Grime et al. 1990; Okland et al. 2004), and this effect may be more pronounced in oceanic climates with long, moist growing seasons (Okland et al. 2004). This is in contrast to *P. mugo* islands, where disturbance from wind-felled trees creates a variety of microhabitats, including openings in the forest, exposed rock outcrops and small open ponds not overgrown by *Sphagnum* mosses (these ponds must have been vital waterholes for the animals that used to browse on these islands). Extensive *Sphagnum* mats are more common on the largest islands that are well protected against the heavy sea storms, whereas on the small islands the wind pressure is not so effectively reduced, and *Sphagnum* mats cannot expand without interruption. This lack of disturbance causing differences in richness is in line with other studies that have shown that islands not affected by disturbance (e.g. fire, grazing, wind tree-felling) for a long time period may undergo 'ecosystem retrogression' (Peltzer et al. 2010), which means a reduction in decomposition rates, microbial biomass, light interception and increase in humus depth. This will not facilitate species richness of vascular plants, but may enhance the bryophyte diversity. Data from pine forests on lake islands in Scotland show that two-thirds of the total species number are bryophytes, whereas the number of vascular plants is in the same range as our plot data (not shown; Kerslake 1982). This indicates that the above rationale is valid for vascular plants, but not for bryophytes.

In conclusion, the number of potential habitats may be significantly reduced on the larger *P. sylvestris* islands relative to the *P. mugo* islands, and hence the number of vascular plant species did not increase as a function of island size. This reasoning assumes that the main cause of enhanced number of species on larger islands is mainly related to a positive correlation between habitat diversity and island area (Westman 1983; Whittaker & Fernandez-Palacios 2007; Kallimanis et al. 2008; Hortal et al. 2009).

Species composition, richness and autocorrelation

We found a geographical east–west gradient in species composition that co-varies with the variation in species richness (Fig. 4). This is a typical autocorrelation problem that inflates the degrees of freedom (Legendre 1993; Dormann et al. 2007). If we crudely partial out all deviance correlated to geographical space or species ordination space, the number of species between the two sets of islands is significantly different in the former approach but not in the latter. However, the GLM residual approach indicates that species richness is significantly higher on islands with introduced pine than native pine. The autocorrelation over short distances depicted by Moran's *I* for species richness is significant (Fig. 5a), but for the residuals after regression this disappears, except for the shortest distance class (Fig. 5b). The autocorrelation remains over several distances in species ordination space (Fig. 5c), but if we add the grazing indicator variable to the model the residuals show no significant autocorrelation (Fig. 5d). This result is followed up by the simultaneous approach where MA in spatial regression indicates that native vs non-native pine forest is a significant predictor together with the grazing indicator variable when geographical space or species ordination space are used in the MA model. The latter is a rather novel approach for autocorrelated species richness analyses (cf. Diniz-Filho et al. 2003). The rationale is outlined in Diniz-Filho et al. (2003), who emphasized the fact that neighbouring sampling locations (islands) may lack statistical independence if they have similar species composition. However, if they, in theory, had totally different species compositions they will actually appear as statistically independent. Thus it is equally important to take account of the location in species space as well as in geographical space, but one should be aware of the fact that the theoretical peak in richness can be anywhere in the geographical space, whereas in species ordination space it is only possible at one single spot were all species are present. This is because species composition and richness are intrinsically dependent on each other because both are an emergent property of species distributions. The location of this richness peak is most probably (but not necessarily) in the centre of a given species ordination space. However, in our case the maximum richness vector is pointing to the border of the species space and correlates with the first ordination axis. This illustrates that the grazing indicator species that have survived on the *P. mugo* islands are additional to the very common generalist type of species that cover many of the islands. The crucial point here is whether species composition and richness are driven by the same factors (Wagner & Fortin 2005). All the autocorrelation-related analyses clearly indicate that this is the case here, providing both an analytical challenge and an aid for interpretation.

Plausible causes of differences and management implications

In our case, species richness is enhanced on *P. mugo* islands, but this introduced species is more a passenger than an ecosystem engineer (Didham et al. 2005; MacDougall & Turkington 2005). The islands with higher species number have a set of grazing-tolerant species present that are rare on *P. sylvestris* islands. It is mainly these species that make the significant differences in species composition and richness. These species are associated with the past land-use regime, i.e. small stock grazing and fire, and have survived after grazing declined and *P. mugo* coll. was introduced (Fig. 4, Appendix S1). Although both types of islands have been irregularly burned and used for grazing in the first decades of the 20th century, the number of grazing-adapted species is higher on *P. mugo* islands. We hypothesize that this is related to the inherent properties of the two types of pine tree. The native *P. sylvestris* has been able to develop a closed canopy and represents an older successional stage compared with *P. mugo* forest. These conditions have facilitated extensive moss carpets, whereas the light-demanding herbs and grasses have disappeared. *Pinus mugo* on the other hand, is a sub-alpine species in its natural habitat, and in these extreme oceanic environments the trees are easily wind-felled in the autumn storms. Tree-fall caused by autumn storms is much more common on *P. mugo* islands than on *P. sylvestris* islands. This creates open habitats for herbs, grasses and ferns that were more common during the old land-use regime. This is, in part, in line with Lindborg & Eriksson (2004), who found time lags of 50–100 yr in the response of plant species diversity to a change in habitat in the landscape. In conclusion, one may argue that after the anthropogenic pressure was released and forest succession started, the successional phase on the *P. mugo* islands has been slower because of wind disturbance. It is not uncommon to find more vascular plant species in mid-successional phases than in old-growth forest (Vetaas 1997 and references therein), which explains the difference in species richness.

The initial rationale underpinning the introduction of *P. mugo* coll. was to conserve the soil, prevent erosion and provide fuelwood (Oyen et al. 2006). It has definitely contributed to the build-up of carbon stocks on these islands and has facilitated a succession towards forest. In this respect one has to re-evaluate *P. mugo* coll. from a potential invasive species threatening biodiversity to a species that contributes to restoration of the forest cover (cf. Schlaepfer et al. 2011). Although pine, at a global scale, is a genus that consists of many invasive species, particularly in the southern hemisphere (Richardson & Rejmanek 2004), we will argue, along with Schlaepfer et al. (2011), that in some exceptional cases the introduced species may actually contribute to ecological restoration and do not represent a threat to the local flora. Most of the islands do have a few native Scots pine individuals, and there were very few seedlings and saplings of *P. mugo* on these islands, therefore it is not unlikely that these islands will be forested with Scots pine in the future.

Conclusions

The difference in species richness and ISAR between *P. mugo* islands and *P. sylvestris* islands may relate to the same underpinning causes. The natural disturbance regimes are the same, but the native *P. sylvestris* is adapted to autumn storms, whereas the introduced *P. mugo* forests are in a state of perpetual gap dynamics. This may explain why *P. mugo* islands have a mixture of forest species and light-demanding species that are associated with grazing. Lower species richness in the mature old-growth *P. sylvestris* forest is due to an extensive moss carpet that reduces habitat diversity, and all the grazing indicator species have been shaded out. This may also explain why large size does not correspond to more species or a positive species–area relationship on the *P. sylvestris* islands.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. List of species that occur on more than two islands.

Errata

After submission of thesis, a few technical and formatting errors were found. Most of these affects visual quality and/or readability of the thesis, but not the scientific content of the work. These errors are therefore corrected as follows:

General

- Text is block adjusted throughout the thesis
- Reference to figures are consistently formatted (some figures were referenced in bold text and Fig. instead of Figure.)
- Text is corrected for wrong use of is/are, was/were

Results and discussion

- P. 31, line 29: Type error is corrected in the word “native”
- P. 32, line 14: “Depend” is changed to “dependent”
- P. 35, line 9: “Currently” is changed to “current”
- P. 35, line 29: “Regular” is changed to “regularly”
- P. 36, line 2: Type error is corrected in the word “and”

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