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The effect of vegetation reclamation on birds and invertebrates in Iceland

A comparative study of barren land, restored heathland and land revegetated by Nootka lupin

Brynja Davíðsdóttir

Landbúnaðarháskóli Íslands
Agricultural University of Iceland

Faculty of Environmental Sciences

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Brynja Davíðsdóttir

90 ECTS thesis submitted in partial fulfilment of a Magister Scientiarum degree in Environmental Sciences

Supervisors: Tómas Grétar Gunnarsson,
Guðmundur Halldórsson and Bjarni Diðrik Sigurðsson

Agricultural University of Iceland
Faculty of Environmental Sciences

Declaration of author

I hereby declare that the collection of data, statistical analysis and writing of this thesis is my work under the supervision and assistance of my advisors Tómas Grétar Gunnarsson, Guðmundur Halldórsson and Bjarni Diðrik Sigurðsson.

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Brynja Davíðsdóttir

Abstract

Degradaton of ecosystems and introduction of invasive species are two major threats to global biodiversity. Restoration and revegetation actions of degraded, barren areas are important counteractions for amending habitat loss and ecosystem processes and to protect species of plants and animals. Iceland has lost a large proportion of its vegetation cover since its settlement. Actions against erosion and revegetation of barren areas have taken place for over a hundred years and result mostly in the restoration of heathland vegetation. However, the introduced Nootka lupin, which has also been used for revegetating eroded areas, forms long lasting ecosystems dominated by the lupin. Its use is controversial as the plant can disperse over existing vegetation, mostly heathland. Successful habitat restoration often results in colonisation of animals in the new restored habitats and their abundance and diversity can be a useful measure of restoration success.

A survey was conducted on 26 sites, across Iceland, to evaluate the effect of two different methods of revegetating barren land on the density and species composition of birds and density and group assembly of invertebrates. These methods were: a) Restoration of native heathland on barren land, usually by protection from grazing and/or seeding with grass species and fertilisition and b) revegetation of barren land by sowing of Nootka lupin. Barren land served as a control. Birds were counted on transects and invertebrates were sampled by sweepnet in each habitat on the 26 sites. Further, sweepnet catches were compared to catches in pitfall traps on 5 sites.

Highest total numbers of invertebrates and birds were recorded on land revegetated with Nootka lupin, followed by land restored to heathland and then barren land. The average invertebrate numbers per sweepnet were 2 on barren land, 22 on heathland and 58 in Nootka lupin. The average numbers of invertebrates per pitfall trap per day were 0.8, 1.6 and 3.3 individuals on barren land, heathland and Nootka lupin, respectively. On average 31 birds were recorded on km^2 of barren land, 337 on heathland and 627 in Nootka lupin. Group and species compositions were found to differ between the three habitat types. Restored heathland provided habitat for waders of internationally decreasing populations while Nootka lupin stands harboured more common bird species. Golden Plover and Dunlin, generally common on mature heathland, were most common on restored heathland but Snipe and Meadow Pipit which characterise taller swards were most common in Nootka lupin. The most common invertebrate groups in Nootka lupin stands were beetles, spiders and slugs, whereas in the restored heathland mites, spiders and beetles were dominating. Successional stages within habitats were related to bird density and diversity. A comparison of methodologies showed that sweepnet catches were positively correlated with the total invertebrate abundance caught by pitfall traps. Sampling invertebrates by sweepnet can, therefore, give a rapid index of the total abundancy of invertebrates, many of wihch are important food for birds. Also, there was a positive correlation between invertebrate numbers caught by sweepnet and the total density of birds on the same sites.

Ágrip

Hnignun vistkerfa og framandi ágengar tegundir ógna líffræðilegum fjölbreytileika á heimsvísu. Endurheimt og landgræðsla eru mikilvægar aðgerðir til að bæta upp búsvæðatap og líffræðilega ferla innan vistkerfa og til viðhalds á stofnum og fjölbreytileika plantna og dýra. Mikill hluti gróðurhulu Íslands hefur tapast síðan um landnám. Aðgerðir til að hefta jarðvegseyðingu hafa staðið yfir í rúm hundrað ár á Íslandi og leiða flestar til endurheimtar mólendis. Alaskalúpína (*Lupinus nootkatensis*) hefur einnig verið mikið notuð við landgræðslu hérlendis og myndar hún vistkerfi þar sem lúpína er ráðandi um tíma. Notkun alaskalúpínu er umdeild því erfitt er að hefta útbreiðslu plöntunnar sem getur dreift sér yfir gróið land, einkum mólendi. Í kjölfar landrgæðslu taka dýr sér bólfestu í nýju gróðurlendi og getur fjöldi þeirra og fjölbreytileiki gefið árangurs mat á endurheimt viskterfisins.

Rannsókn var gerð á 26 stöðum á Íslandi, til að meta áhrif tveggja mismunandi aðferða við till að græða upp örfoka land, á þéttleika og tegundasamsetningu fugla og þéttleika og hópasamsetningu smádýra. Uppgræðsluaðferðirnar voru: a) Endurheimt mólendis á ógrónu landi, oftast með beitarfriðun og/eða grassáningu og áburðardreifingu og b) landgræðslu ógróins lands með sáningu alaskalúpínu. Ógróið land var haft til viðmiðunar. Fuglar voru taldir á sniðum og smádýr veidd í háf í öllum gróðurlendum á öllum 26 stöðunum. Einnig voru niðurstöður háfunar smádýra á fimm stöðum bornar saman við veiði smádýra í fallgildrur.

Hæstur þéttleiki smádýra og fugla var í lúpínubreiðum, svo í endurheimtu mólendi en lægstur á ógrónu landi. Meðalveiði smádýra í háf var 2 dýr á ógrónu landi, 22 í mólendi og 58 í alaskalúpínu. Meðalveiði í fallgidru á dag var 0.8, 1.6 og 3.3 smádýr á ógrónu landi, á mólendi og í alaskalúpínu. Að meðaltali komu fyrir 31 fugl á km^2 ógróins lands, 337 á mólendi og 627 í alaskalúpínu. Samsetning fuglategunda og smádýrahópa var breytileg eftir gróðurlendi. Uppgrætt mólendi stóð undir fuglategundum sem hafa hnignandi heimsstofna en algengari tegundir á heimsvísu sóttu í alaskalúpínu. Heiðlóa og lóuþræll, algengir fuglar í mólendi, voru algengastir fugla á endurheimtu mólendi en hrossagaukur og þúfutittlingur sem einkenna hærri gróður voru algengastir í lúpínu. Algengustu hópar smádýra í lúpínu voru bjöllur, köngulær og sniglar en í endurheimtu mólendi voru mítlar, köngulær og bjöllur ráðandi. Mismunandi framvindustig innan gróðurlenda tengdust þéttleika og tegundasamsetningu fugla. Samanburður á veiðiaðferðum smádýra sýndi að fjöldi smádýra sem veiddist í háf hafði jákvæða fylgni við smádýrafjölda sem veiddist í fallgildrur. Smádýrasýni sem tekið er með háfi getur því gefið gott mat á heildarframleiðni smádýra, sem mörg hver eru mikilvæg fæða fyrir fugla. Einnig var jákvæð fylgni milli fjölda smádýra sem veiddust í háf og þéttleika fugla á sömu svæðum.

Lykilorð: Endurheimt, fuglar, hryggleysingjar, landgræðsla, lúpína, ógróið land, mólendi, samanburður, smádýr.

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Table of contents

Original papers included in the thesis

The following thesis is based on two manuscripts, which are referred to by roman numerals.

I. Davidsdottir B., Gunnarsson T.G., Halldorsson G. & Sigurdsson B.D. (2013). Avian abundance and communities in areas revegetated with exotic versus native plant species. To be submitted to Restoration Ecology.

II. Davidsdottir, B., Halldórsson G., Gunnarsson T.G. & Sigurdsson B.D. (2013). Effect of revegetation with exotic versus native plant species on invertebrate fauna. To be submitted to Icelandic Agricultural Sciences.

List of Tables

List of Figures

1. Introduction

1.1. The importance of restoration and revegetation

In the past fifty years degradation of land and ecosystems and consequent loss of biodiversity has occurred faster than in any other era in the history of mankind (Millenium Ecosystem Assessment 2005). Diminishing biodiversity is primarily caused by habitat loss due to unsustainable use of natural resources, for instance through over use of pastoral rangeland (Pearce et al. 2010), deforestation (Reynolds & Stafford Smith, 2002; Millennium Ecosystem Assessment 2005; Jha & Bawa 2006; FAO 2009) and also as a result of climate change and the outspread of invasive species (Schmitz & Simberloff 1997; Donald 2004; Waltert et al. 2005; Mainka & Howard 2010; Pysek & Richardson 2010). Strategic plans have been announced by The Convention of Biological Diversity (CBD) for slowing down biodiversity loss by half, and to restore 15% of the degraded ecosystems before the year 2020, as well as taking action against the continuing distribution of invasive species (CBD 2013).

Ecosystem restoration and ecological conservation aim to conserve biological diversity but also to reclaim and protect important ecosystem processes and functions, such as carbon sequestration and balance, the seepage and retension of water and the cycling and retension of nutrients, primary productivity and trophic levels which add up to habitat integrity and are the basis for the maintainance of biodiversity (c.f. Cabello et al. 2012). When ecosystem functioning, food webs and the interactions among species are taken into consideration during restoration and revegetation efforts, they have been shown to become more successful (Richardson et al. 2000; Memmot, J. 2009; Aradóttir 2011).

1.2. The function and importance of invertebrates

Invertebrates can be divided into many functional groups which have important roles in ecosystem functioning. They contribute to nutrient cycling through detrivory; influence vegetation growth, composition and distribution, through herbivory, pollination and distribution of seed; and function as ecosystem engineers (Forlup et al. 2008; Losey & Vaughan, 2006; Weisser & Siemann 2004). Furthermore, invertebrates play an important role in primary succession of barren land (Ingimarsdottir et al. 2012.) Invertebrates are also critical food resource for many birds (Robel & Xiong 2001).

Habitat degradation can change the composition and trophic structure of invertebrate communities (Dupont & Nielsen 2006), especially those at higher trophic levels (Gibb & Hochuli 2002). Such changes can have drastic consequences at the ecosystem level (Weisser & Siemann 2004), not solely with a negative effect on plant pollination and fruit set (Mustajarvi et al. 2001), but also in diminished ecosystem functions resulting in lowered productivity and retention of soil nutrients (Weisser & Siemann 2004).

A reintroduction of all taxa and species of invertebrates is not likely to be practically possible during restoration. It is therefore important to aim for a restoration of functional characteristics of faunal responses (Gibb and Hochuli 2002). Although restoration can have a positive effect on invertebrates, a total recolonization of all key functional groups can take time as the assemblage and diversity of plant communities has a large effect on invertebrate diversity (Davis & Ustrup 2010). Knowing this, invertebrates and their function within an ecosystem can be used to monitor restoration success (Davis & Ustrup 2010).

1.3. The function and importance of birds

Birds are important mobile links in the dynamics of ecosystems (Sekercioglu 2006). They serve roles as various functional groups, for instance as dispersers of seed (Sanchez et al. 2006; Garcia et al. 2010), passive transporters of less mobile invertebrates and plants (Green & Sanchez 2006; Sekercioglu 2006; Magnusson et al. 2009) and nutrients (Sigurdsson & Magnusson 2010). Avian transport and dispersal of seeds, invertebrates and nutrients enables colonisation and regeneration of fauna and flora, enhances and shapes plant diversity and contributes to soil formation in damaged ecosystems, remote areas (Sigurdsson & Magnusson 2010) and on barren land (Sekercioglu 2006; Kaiser-Bunbury et al. 2010). By their passive transport, birds contribute to the restoration of plant-animal mutualisms (Kaiser-Bunbury et al. 2010) and enhance genetic variation of plants on local and regional scales (Farwig & Berens 2012). Therefore seed dispersal by birds and animals has been shown to be a key process in the natural restoration of damaged ecosystems (Farwig & Berens 2012), benefiting restoration projects directly by reducing management costs and facilitating ecosystem productivity and increased carbon storage in the long run (Farwig & Berens 2012). In addition birds can take part in controlling invertebrate pests (Sekercioglu 2006). As birds are near the top of the food chain and reflect productivity patterns at lower levels (Klvanova et al. 2009; Doxa et al. 2010), they are commonly used as biodiversity indicators in various national environmental schemes (Gregory et al. 2005; Klvanova et al. 2009; Gregory & Strien 2010).

1.4. Invasive plant species

Alien, invasive plants have become a threat to natural ecosystems by affecting native plant communities, often out-competing native plants in competition for resources; light, space or nutrients (Enquist et al. 1999; Feng et al. 2007), and by this they can also disrupt animal species assemblages (Henson et al. 2009).

1.4.1 The effect of invasive plant species on bird and invertebrate life

Invasive plants affect animal life in different ways throughtout the world, altering abundance and diversity of animals (Henson et al. 2009, Ceia et al 2011; Crooks 2002). Invasive plants can disrupt native plant-animal relationships, for instance between native plants and their pollinators or seed dispersers, through highly competitive attraction of unspecialized mutualists (Traveset & Richardson 2006**)**. This can increase their negative effect on native ecosystems (Czarnecka et al. 2012). They can also affect different animal species within each existing habitat (Braithwaite et al. 1989; D´Antonio & Vitousek 1992; Knapp 1996; Kinvig & Samways 2000), and with time they can facilitate invasions of other excotics with cascading effects (Crooks 2002). While some invaders have a positive effect on ground nesting birds such as waders (Pampush & Anthony 1993) other invasions have been shown to alter the population sizes of terrestrial invertebrate groups without affecting the existing bird community (Kennedy et al. 2009). Other studies of invasive species in low growing vegetation show a negative effect on bird community composition through changes in vegetation structure and subsequent decline in habitat quality (Scheiman et al. 2003; Fleishman et al. 2003), affecting specialist birds in particular (Ma et al. 2011) and those foraging on or near the ground (Flanders et al. 2006). Such cascading effects can result in loss of diversity with time and even in erosion problems **(**Knapp 1996).

1.4.2 Nitrogen fixing plants

Some plants fix nitrogen through symbiosis between plant roots and microbiota. Certain plants have a wide range of symbiosis while others are obligately mutualistic with specific mycorrhizal fungi (Richardson et al. 2000). Some N- fixing plant species when translocated from their native environment have become invasive (Forseth & Innis 2004; Yelenik et al

2004) often becoming dominant following major disturbances or erosion (Körner et al. 2012). The introduction of symbiota to a new environment can facilitate growth (Einarsson et al. 1993) and subsequent invasion of an introduced N-fixing plant (Richardson et al. 2000). Also invasive floras have been known to contain a higher proportion of N-fixing species than the corresponding native floras (Kurokawa et al. 2010).

1.4.3. Lupinus

Lupinus, a genus of the pea family contains 165 Species and 355 accepted taxa overall (USDA 2013). Because of their N-fixing abilities and good performance on disturbed ground (Körner et al 2012), N-American lupins (*L. polyphyllus, L. arboreus, L. nootkatensis*), have been successfully used for revegetation purposes in Iceland, Scandinavia, New Zealand and Northern Eurasia, only later to become invasive (Magnusson 2010; Fremstad 2010; Körner 2012).

1.4.4 Invasive plant species as tools in revegetation projects

The use of invasive plant species in revegetation actions is questionable as invasive plants can disrupt and change established ecosystems resulting in a cascading negative effect on population growth of native plants and their pollinators (Traveset & Richardson 2006). However invasive plant species can have a boosting effect on productivity and biodiversity where little is left of native vegetation (Kaiser-Bunbury et al. 2010). The introduced and now invasive Nootka lupin in Iceland is a good example of this, as it has been used successfully to revegetate vast barren and eroded areas, forming large stands which provide habitat for numerous birds and invertebrates (Sigurdardottir 2002; Oddsdottir et al. 2008, Gunnarsson & Indridadottir 2009).

1.5. The current state of Iceland

Iceland (63-66°N) is a volcanic island of about 100.000 km^2 in the North-Atlantic Ocean. The climate is oceanic with a variable annual precipitation of 900-1100mm (Vedurstofa Islands 2013a) and mean annual temperature in the lowland (<400 m a.s.l.) of 0-4 °C (Vedurstofa Islands 2013b). The soil consists mainly of Histic, Gleyic and Brown Andosols (>50% of total area) and Virtisols (30% of total area) (Arnalds 2004).

1.5.1 Vegetation cover

Since its settlement in the late 9th century, Iceland has been subject to unsustainable land use and in combination with harsh weather, a short growing period, delicate volcanic soils and volcanic activity; this resulted in vast areas of habitat loss and desertification (Arnalds et al. 1997; Arnalds 2008; Gisladottir et al. 2010; Aradottir & Halldorsson 2011).

To date Iceland has the highest rate of soil erosion in Northern-Europe, with 40.000 km^2 of limited plant cover, including volcanic areas and natural deserts (Arnalds 2011). This has resulted in 40% of the country's surface consisting of deserts as opposed to an estimate of 5 – 15% at the time of settlement (Arnalds 2011). As a result, Iceland must have suffered great loss of biodiversity during the degradation of vegetation, loss of natural habitats and soil cover (Gisladottir et al. 2010). Unaided repair of heavily eroded areas through natural succession can take decades to centuries to reach a plant cover of 1-5% in Iceland (Gretarsdottir et al. 2004).

1.5.2 Invertebrate life in Iceland

The number of known soil-living invertebrate species is relatively low in Iceland compared with neighbouring countries (Jeffery et al. 2010). A total of 1245 species of invertebrates have been found and described in Iceland and new species are frequently found in the country (Ólafsson 1991). On Icelandic heathland mite, spiders and beetles are the most common macro invertebrate groups (Ingimarsdottir et al. 2007).

1.5.3 Terrestrial birdlife in Iceland

In comparison with many neighbouring European countries relatively few bird species nest in Iceland, but often in high densities (Gunnarsson 2010). Heathland and rangelands provide important feeding and nesting grounds for common heathland birds and waders (Charidrii) (Gunnarsson 2008) and an estimate of five million individual waders leave the country at the end of a nesting season (Gudmundsson 1998). Many wader populations around the world are declining in numbers, mainly as a result of habitat loss and degradation (International Wader Study Group 2003).

Most of the ten wader species found nesting in Iceland (Gunnarsson, 2010) are of internationally important proportions (Gunnarsson et al. 2006; Magnusson S.H. et al 2009), including over half of the global estimated population of Golden Plover (*Pluvialis apricaria*), 40% of all Whimbrels (*Numenius phaeopus*), 32% of the Ringed Plover (*Charadrius* *hiaticula*) population, 19% of Redshank (*Tringa totanus*) and 16% of Dunlin (*Calidris alpina*) (Gunnarsson et al. 2006).

Icelandic heathland bird species are generally attracted to low-growing vegetation (Gunnarsson et al. 2006) and many of them, adults and their young, rely on invertebrates and berries (Van de Kam et al. 2004; Green et al. 2006; Gunnarsson 2010) as an important foodsource throughout the summer season. Consequently these birds are important mobile links in ecosystems of Iceland, as distributors of nutrients, seeds and invertebrates between and within wetlands and other preferred inland habitats, such as heathlands (Gunnarsson et al. 2006; Green & Sanchez 2006; Sanchez et al. 2006).

1.6. Revegetation efforts in Iceland

A law on combatting erosion was inacted in Iceland in 1907 and concurrently The Soil Conservation Service of Iceland, the first agency of its kind, was founded (UOA 3013). To date a total of around 5 700 km^2 of eroded land is in the process of being revegetated (Crofts 2011) in addition to vast areas that have been restored through natural succession, following initial stabilization or enhancing measures, such as livestock exclusion, grazing management or river regulation (SCS 2013, Guðjónsson et al. 2007).

The most common method for revegetating barren land in Iceland is protection from grazing, either without other actions or combined with top dressing of fertilizers and sometimes sowing of mixed grass seeds (Halldorsson et al. 2011b). With time this usually results in the formation of biological soilcrust and the restoration of vegetation cover of local native heathland species such as *Agrostis vinealis, Empetrum nigrum, Festuca vivipara, Thymus praecox* ssp. *arc., Salix lanata, Salix phylicifolia* and *Caluna vulgaris* (Gretarsdottir et al. 2004; Aradottir et al. 2008). A minimum of 1 500 km^2 have been restored with these methods (Halldorsson et al 2011a) and in total, heathland is estimated to cover around 30.000 km^2 of Iceland or ca. 30% of its area (Arnalds 2011).

Sowing of the introduced Nootka lupin has been successfully used in Iceland for land reclamation (Halldorsson et al. 2011b). This is an economical and effective method (Einarsson et al. 1993; IINH & SCS 2010), as the plant accelerates soil development directly through nitrogen fixation, high litter production and fast litter decomposion and effective trapping of windblown particles. Biomass production of lupin fields varies from 3 to 5 t/he DM depending on substrate (Björnsson et al 2004) Although this method is the fourth most common revegetation method currently used in Iceland (Halldorsson et al. 2011b), the use of

Nootka lupin has been controversial and increasingly questioned by the public and environmental authorities in recent years (IINH & SCS 2010; Petursdottir et al. 2013).

It is known that lupins can influence successional rates and directions for instance through their fixation of nitrogen (Bishop 2002). In Iceland the Nootka lupin forms vast fields resulting in a novice ecosystem dominated by lupin with few coexisting plant species for at least some decades and possibly longer (Magnusson et al. 2001, 2002) showing different growth performance depending on annual precipitation and temperature (Magnusson et al. 2003). The plant is recognized as an invasive species in Iceland (Magnusson 2010; Nobanis), as it has in some occasions dispersed over existing native heathland reducing plant species richness (Magnusson et al. 2001, 2002). A secondary succession, where the Nootka lupin is generally replaced with fertile grasslands after some decades has been shown to occur, but again, the successional rate is highly dependent on annual precipitation and location in Iceland (Magnusson et al. 2001; 2002; 2003). Another known trajectory of secondary succession of Nootka lupin stands is where another introduced invasive plant species, cow parsley (*Anthriscus sylvestris* Hoffm.), forms tall stands (Magnusson 2010; Thoroddsen et al. 2009). The total distribution of Nootka lupin is unknown in Iceland, but it can be found and is common in all parts of the country (IINH & SCS 2010).

1.6.1 The effect of revegetation actions on animal life in Iceland

Surveys on the effects of revegetation in Iceland, where a variety of animal functional groups have been considered, show a noteworthy increase in animal numbers compared with unvegetated land (Friðriksson et al. 1976; Sigurdardottir 2002; Halldorsson et al. 2004; Oddsdottir et al. 2008, Gunnarsson & Indridadottir 2009). An increase in invertebrate numbers has been noted in various grass sowings on eroded barren land (Friðriksson et al. 1976; Halldorsson et al. 2004) and where barren land has been revegetated with Nootka lupin (Sigurdardottir 2002; Oddsdottir et al. 2008, Gunnarsson & Indridadottir 2009). Nootka lupin stands in Iceland have been shown to attract and sustain a high abundance of birds, invertebrates and soil arthropod life compared to barren land (Sigurdardottir 2002; Oddsdottir et al. 2008, Gunnarsson & Indridadottir 2009). Invertebrate numbers have been shown to be lowest on scarce heathland in comparrison with other native vegetation in Iceland (Jóhannesdóttir 2013).

2. Aims of study

The main aims of this study were

a) to compare bird numbers and species composition on/in: a) barren land, b) barren land restored to heathland and c) barren land actively revegetated by the introduced invasive N-fixing Nootka lupin.
b) to compare the effect of different successional stages of heathland restorations and lupin stands on individual bird species.
c) to evaluate the relationship between bird density and numbers of invertebrates caught by sweepnet on the same sites.
d) to asseess the validity of using one occasion sweepnet sampling as an indicator of invertebrate abundance per site.
e) to compare invertebrate abundance between the three habitat types.
f) to compare invertebrate group composition between the three habitat types.

In **Manuscript I** results regarding the effects of different revegetation methods on birdlife and invertebrates caught by sweepnet across Iceland are reported.

In **Manuscript II** comparison of different revegetation methods on invertebrate numbers and group composition are reported and two different invertebrate sampling methods are compared.

3. Materials and methods

Bird and invertebrate surveys were carried out in 26 areas in Iceland (Figure 1). Each survey site consisted of three habitat types: i) Barren land that had been eroded during the past few centuries and where secondary succession was still in its early stages due to physical or biological pressures. ii) Heathland restored on formerly barren land sometime during the past 50 years. iii) Areas, where barren land had been revegetated by the introduced N-fixing Nootka lupin in the past 40 years (see list in Appendix 1).

The three habitat types within a survey site were most often in the vincinity of each other, at similar height above sea level, climate and other physical conditions, apart from the difference in vegetation and soil properties (Manuscript I). Habitats were visited once during the main bird study (Manuscript I) but a subset of survey sites more often during the invertebrate sampling method assessment and emptying of pitfall traps (Manuscript II)(Figure I). Temperature varied between regions in Iceland before and during the study period in 2011. In late May and June the temperature was around average in South and West Iceland, but in North Iceland it was unusually cold with snowfall in late May and the mean monthly temperature was 2.4 °C under the 30-year average in June (Vedurstofa Islands 2013c).

3.1. Bird study

Bird surveys were carried out from 29 May to 25 June 2011 on 26 survey sites (Figure 1), each including three habitats. Birds were recorded on transects (Bibby et al. 2000) with 50 m inner belt and 100 m outer belt, in more-or-less homogenous vegetatation. The transect length varied with size of homogenous vegetation patches, but was on average 0.74 km (SE 0.12 km). All birds were recorded at the distance from where they were first seen to the transect line and their behavior noted. Birds further than 100 m from the transect line and those overflying were recorded but excluded from further analysis. The unit calculated was individual birds, of each species, per km^2. For further information, data and statistical analyses see Manuscript I.

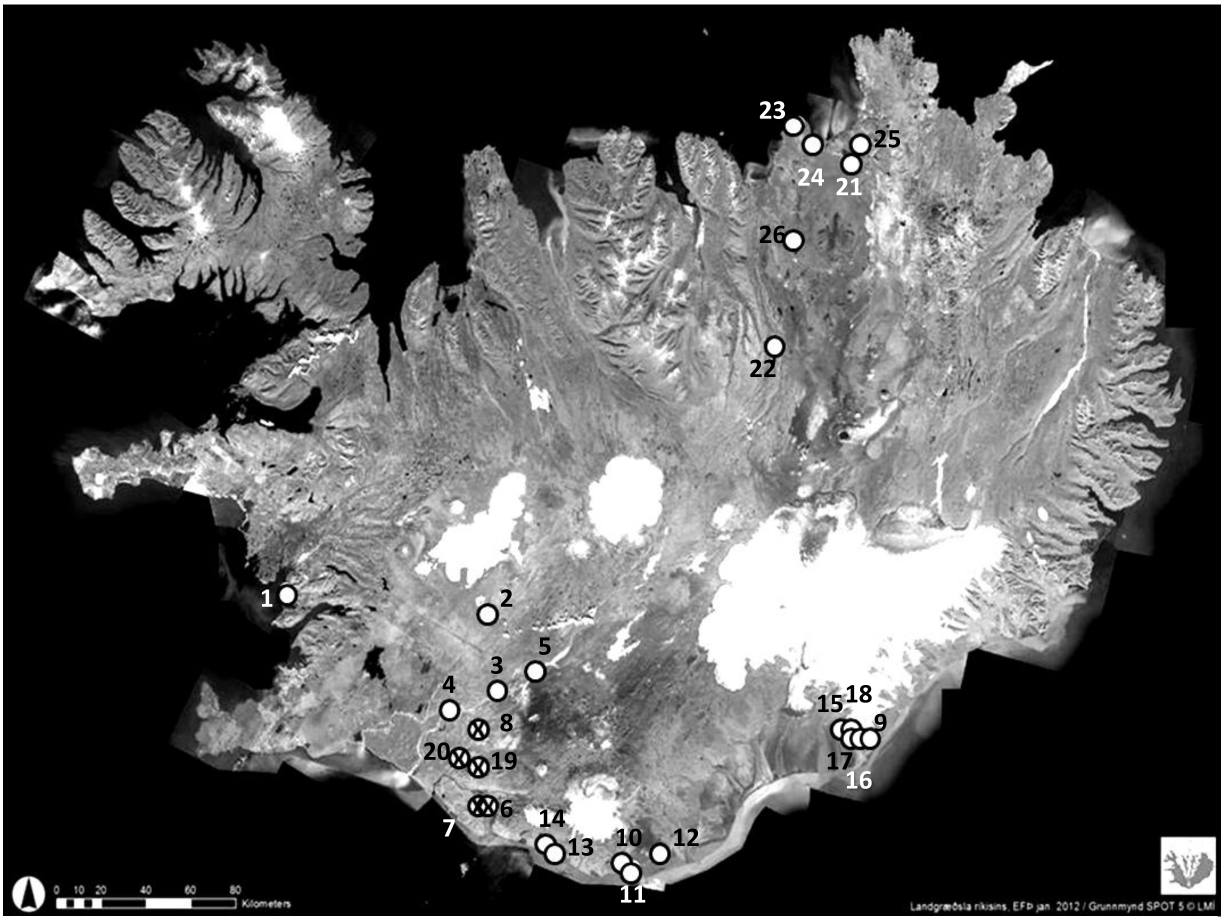

Figure 1. Distribution of survey sites where birds and invertebrates were recorded/sampled. Each dot stands for three habitat types studied as a cluster. White dots: Invertebrate sampling only by sweepnet. White dots marked with X: Invertebrate sampling by sweepnet and pitfall traps. Numbers refer to locations listed in Appendix 1.

3.2. Invertebrate study

3.2.1 Sweep-netting

Invertebrates were sampled concurrent with bird studies in 2011 on each survey site (26 x 3 habitat types) with a handheld insect net which was swept over the surface of each habitat type with ten, non overlapping 2 m long strokes. The number of caught flies (Diptera), moths (Lepidoptera) and spiders (Arachnea) (>3 mm) were recorded and the animals then released. This was repeated three times in every habitat. I used the total sum of the three catches per area for each invertebrate group for calculations, giving the total invertebrate catch for each habitat type.

3.2.2 Pitfall traps

Sampling was conducted on five different survey sites (Figure 1) in South Iceland, each consisted of three habitat types, barren land, lupin and heathland. The traps were active from 14 June until 14 August and emptied three times during that period (Table 1). Two traps were laid out in each lupin and heathland site but four on barren sites, because of higher likelihood of disturbance due to wind and blowing sand. Two randomly selected traps from each plot in the barren land were used for analysis of invertebrate catch.

The total catch from each study site was summed up and divided by the number of days each trap had been active, to obtain the average catch per trap-day per habitat. Invertebrates were divided in to seven groups: beetles (Coleoptera), spiders (Arachnea), mites (Acari), slugs (Gastropoda), moths (Lepidoptera), earthworms (Lombricus) and a group consisting of all other invertebrates. The average pitfall catch per day was estimated for each habitat type, as well as the average catch per invertebrate group per habitat. For further information, data and statistical analyses see Manuscript II. Because of a small sample size and that invertebrates smaller than 3 mm were excluded from analysis, a significance limit of $P<0.10$ was used in the study presented in Manuscript II.

Table 1. Sites and habitats within sites where pitfall traps were laid out. With dates of setting and emptying of traps and the accumulitive days of trapping between emptying of traps. No of sites correspond to numberings on Figure 1 and Appendix 1.

No	Sites	Habitat	Pitfall traps set	1st emptying	Days	2nd emptying	Days	3rd emptying	Days
8	**Boholt**		14.6.11						
		Barren land		29.6.2011	15	19.7.2011	20	14.8.2011	26
		Heathland		29.6.2011	15	19.7.2011	20	14.8.2011	26
		Lupin		29.6.2011	15	19.7.2011	20	14.8.2011	26
6	**Dímon**		15.6.11						
		Barren land		29.6.2011	14	20.7.2011	21	14.8.2011	25
		Heathland		29.6.2011	14	20.7.2011	21 one**	14.8.2011	25
		Lupin		29.6.2011	14	20.7.2011	21	14.8.2011	25
20	**Geitasandur**		14.6.11						
		Barren land		-->*	-->*	19.7.2011	35	14.8.2011	26
		Heathland		29.6.2011	15	19.7.2011	No data**	14.8.2011	No data**
		Lupin		29.6.2011	15	19.7.2011	20	14.8.2011	26
21	**Gilsbakki**		14.6.11						
		Barren land		29.6.2011	15	22.7.2011	23	14.8.2011	23
		Heathland		29.6.2011	15	22.7.2011	23	14.8.2011	23
		Lupin		29.6.2011	15	22.7.2011	23	14.8.2011	23
7	**Markarfljótsaurar**		15.6.11						
		Barren land		29.6.2011	14	20.7.2011	21	14.8.2011	25
		Heathland		29.6.2011	14	20.7.2011	No data**	14.8.2011	No data**
		Lupin		29.6.2011	14	20.7.2011	21	14.8.2011	25

* The traps were set on 19 June and not emptied until in 2nd emptying. ** Loss of traps. Most often due to lifestock disturbing.

3.2.3 Comparison of two invertebrate sampling methods

Concurrent with each emptying of the pitfall traps shown in Table 1, invertebrates were sampled with a sweep-net (Table 2). A comparison was made of the mean sweep-net numbers and calculated daily catch by pitfall trap (for more information refer to Manuscript II).

Table 2. Sites and habitats within sites where invertebrates were caught by sweepnet on three dates during the study period. No. of site is corresponding to numberings on Figure 1.

No	Site	Habitat	Date	Date	Date
8	**Bolholt**	Barren land	14.6.2011	29.6.2011	19.7.2011
		Heathland	14.6.2011	29.6.2011	19.7.2011
		Lupin	14.6.2011	29.6.2011	19.7.2011
6	**Dímon**	Barren land	15.6.2011	29.6.2011	20.7.2011
		Heathland	15.6.2011	29.6.2011	20.7.2011
		Lupin	15.6.2011	29.6.2011	20.7.2011
20	**Geitasandur**	Barren land	14.6.2011	29.6.2011	19.7.2011
		Heathland	14.6.2011	29.6.2011	19.7.2011
		Lupin	14.6.2011	29.6.2011	19.7.2011
21	**Gilsbaki**	Barren land	14.6.2011	29.6.2011	20.7.2011
		Heathland	14.6.2011	29.6.2011	20.7.2011
		Lupin	14.6.2011	29.6.2011	19.7.2011
7	**Markarfljótsaurar**	Barren land	15.6.2011	29.6.2011	20.7.2011
		Heathland	15.6.2011	29.6.2011	20.7.2011
		Lupin	15.6.2011	29.6.2011	20.7.2011

4. Results

In this chapter the main results from both appending manuscripts will be presented. Results are viewed in more detail in manuscripts I and II. Manuscript I covers results from bird surveys and invertebrate sweepnet catch from across the country (Figure 1). Manuscript II covers results from seasonal comparative invertebrate studies in the three habitat types in five sites in the south of Iceland (Table 1 and 2), as well as results on a sampling method asessment.

4.1. Birds

Overall a total length of 59 km of transects was walked during the fieldwork in May to June 2011 and 1511 birds of 19 species were detected. On average 31 birds/km^2 were found on barren land and both revegetation methods greatly increased bird density from the barren state with a mean number of 337 birds/km^2 on heathland and 627 birds/km^2 in lupin fields. In total 12 species of birds occurred on barren land, 16 on restored heathland and 15 in revegetated Nootka lupin stands.

Of the nine most commonly occurring species within study sites, none were most abundant on barren land and there were significantly fewer bird species on average on barren land than in heathland or in Nootka lupin stands (ANOVA: $F_{2.77}$=37.25; P<0.001). The average number of bird species did, however, not differ significantly between the two revegetation methods (ANOVA - $F_{4.03}$ = 1.7616; P = 0.1904).

Species composition differed between habitats and detected presence varied within and between habitat types (Manuscript I). On heathland Golden Plover and Dunlin were most common, with a mean density of 74.2 (± 34.1) and 72.4 (± 23.1) individuals per km^2, respectively, but in Nootka lupin Snipe and Meadow Pipit were most common with a mean density of 96.6 (± 22.2) and 337.2 (± 43.5) individuals per km^2, respectively. Successional stage, within habitat type, had some effect on bird abundancy and species composition (Manuscript I). Species that generally favour taller vegetation were more common in dense Nootka lupin whereas species more common on heathland avoided the denser lupin (Manuscript I).

4.2. Invertebrates

4.2.1 The difference in invertebrate density and diversity between survey sites

In sweepnet catches from all 26 survey sites from around the country there was no significant difference between sweepnet catch in young heathland and barren land (t-test: $t_{26} = 2.06$, P = 0.180) but significantly more invertebrates were caught in Nootka lupin than on young heathland (t-test: $t_{26} = 2.055$, P = 0.002) or 73% of the total catch (Table 3, Figure 2).

Table 3. Total sum of individual invertebrates in groups caught in sweep-nets on each habitat type

Habitat	Diptera	Spiders	Moths
Barren land	75	0	0
Heathland	131	10	0
Nootka upin	550	19	25
Grand Total	756	29	25

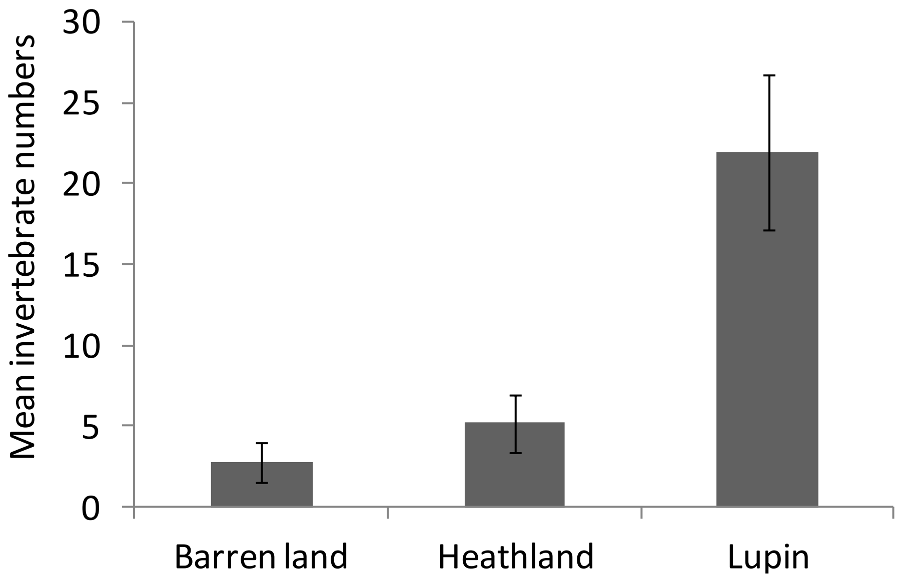

Figure 2. The mean invertebrate catch per sweepnet (with standard error bars) from 26 survey sites in each habitat.

Sweepnet and pitfall traps were used in five study sites in South Iceland (Figure 1), each with three habitat types. There the abundance of invertebrates, as determined by sweepnet, increased significantly by revegetation, both by the restoration of heathlands (Mann-Withney U-test; P<0.07) and by the sowing of Nootka lupin (P<0.001). Same occurred when invertebrate abundance was determined by pitfall traps (Manuscript II). Both methods yielded more than double the invertebrate numbers in Nootka lupin stands compared with restored heathlands (Manuscript II).

Invertebrate group composition differed between the three habitats (Manuscript II). On barren land beetles and spiders were the most abundant invertebrates, but on heathland mites, spiders and beetles were the most common invertebrates. In the Nootka lupin stands beetles, spiders and snails were the three most common invertebrate groups, in addition to the abundant diptera (Manuscript II).

4.2.2 Sampling method assessment

There was a strong positive correlation ($r = 0.850$, $P < 0.001$) between the mean invertebrate catch per day per pitfall trap and the total number of invertebrates caught by sweepnet in the same sites in all three habitat types (Manuscript II).

4.2.3 Connection between birds and invertebrates

There was a significant positive relationship between the total abundance of birds and the total abundance of invertebrates caught by sweep-net on all transects, when compared across all habitat types, indicating that bird density and invertebrate abundance were both higher on the same sites (Spearman rank correlation with untransformed data: Rho = 0.592, $P < 0.001$) (Manuscript I). Bird numbers (Manuscript I) and the number of invertebrates from the regional study (Manuscript II) were significantly lowest in barren land, higher in heathland and highest in Nootka lupin stands.

5. Discussion

This study assessed and compared the effects of two revegetation methods of barren land on birds and invertebrates in Iceland, the restoration of native heathlands and revegetation with the introduced invasive Nootka lupin (Manuscript I and II). Density and diversity of birds was acessed as well as the density of invertebrates and invertebrate group composition. Both revegetation methods had a substantial positive effect on the avifauna, increasing both the density and diversity of birds, as well as increasing invertebrate abundance. These results confirm prior findings on restored habitats and other revegetation efforts in Iceland, which provide valuable habitat for birds (Williams et al. 2012) and invertebrates (Friðriksson et al. 1976). Also the results gave new information on the importance of heathland restorations for bird species of internationally decreasing populations (International Wader Study Group 2003; MacKinnon et al. 2012).

When the two revegetation methods were compared, a difference in the density of birds and foliar invertebrates was revealed (Manuscripts I and II). The total numbers of birds and invertebrates were lowest on barren land, higher on heathland and highest in Nootka lupin stands. When caught by sweepnet the average invertebrate numbers were 1.93 individuals on barren land, 22.27 on heathland and 58.20 in Nootka lupin. When sampled by pitfall traps the average invertebrate numbers per pitfall trap per day were 0.76, 1.60 and 3.27 individuals on barren land, heathland and Nootka lupin, respectively. The low numbers of invertebrates in heathland compared with Nootka lupin reflected Jóhannesdóttirs (2013) results ofinvertebrate numbers on poor heathland compared wiht richer native vegetation in Iceland. The observed increase in invertebrate abundance between barren land and lupin stands was in accordance to earlier results on invertebrate abundance (Sigurdardottir 2002; Oddsdottir et al. 2008; Halldórsson et al. 2004). The invertebrate group assembly differed between the two habitats. In heathlands, mites and spiders were the most common invertebrates accompanied by beetles, resembling the invertebrate composition of mature heathland (Friðriksson 1976; Ingimarsdottir et al. 2012). In Nootka lupin stands, however, diptera were very abundant and the most common terrestrial invertebrates were beetles, spiders and snails.

Many of Iceland’s heathland birds and waders feed on berries and seeds as well as various invertebrates (Van de Kam et al. 2004; Green et al. 2006). Birds are known to participate in the dispersal of less mobile invertebrates and seeds with their passive distribution. This is considered of central importance in vegetation recovery during restoration

(Garcia et al. 2010) and is worth taking into consideration (Kaiser-Bunbury et al. 2010) in decision making on restoration methods.

On average 31 birds/km^2 were recorded on barren land, 337 on heathland and 627 in Nootka lupin. Bird densities on heathland and grassland in lowland Iceland have been shown to vary between 109 and 270 paris/km^2 (Magnússon et al. 2006) and 274 birds/km^2 on poor heathland but 500 birds/km^2 on rich heathland and grassland (Jóhannesdóttir 2013). In native habitats in Iceland bird densities are higherst in wetlands and semi-wetlands with up to 640 birds/km^2 (Jóhannesdóttir 2013) wich is similar to here detected bird densities in Nootka lupin. Golden Plover, Dunlin and Ringed Plover, all of which show a preference to open low growing vegetation (Gunnarsson et al. 2006), and characterize the bird fauna of heathland vegetation (Jóhannesdóttir 2013), were common in the revegetated heathlands, but avoided Nootka lupin stands. As early successional areas have become scarce in Europe and in North America (Dettmers 2003; Oehler 2003) and avian early successional specialists are subsequently rarer than generalists and woodland birds (Šálek 2012), the results of this study indicate that heathland restoration of barren lands in Iceland is of great value for the maintenance of biodiversity of such early successional specialists. Also it is valuable for avian conservation, because many of the key heathland birds found on excisting or restored heathlands in Iceland have internationally decreasing populations (International Wader Study Group 2003; MacKinnon et al. 2012; Jóhannesdóttir 2013). Barren lands revegetated with the introduced Nootka lupin had positive effects on Medow Pipit, Snipe, Redwing and Redshank (Manuscript I). All these species showed a preference for lupin stands and have all been associated with taller wet swards, shrubland or woodlands in Iceland (Nielsen 2003; Jónsson et al. 2005; Gunnarsson et al. 2006; Magnusson et al 2006; Nielsen et al. 2007; Jóhannesdóttir 2013).

Bird species responded differently to various successional stages within vegetation types (Manuscript I). In the very early stages of heathland succession, early successional specialists (Gunnarsson et al. 2006), such as Ringed Plover and Golden Plover, were most abundant. Woody plants, dwarf bushes and shrubs became more noticeable in the latest stage of heathland succession, where Whimbrel, Snipe and Meadow pipit were increasingly abundant. This is in accordance with other studies on birds in poor and rich heatland in Iceland (Jóhannesdóttir 2013). Nootka lupin stands, on the contrary, tended to form mosaics of tall lupin patches with gravel or low vegetation in between plants in early and late successional stages, respectively, but stands dominated by tall dense lupin in the intermediate stages. There were indications that this middle successional stage of dense lupin had a less positive effect on bird diversity than the other two successional stages and attracted mostly Snipe and Meadow Pipit.

The sampling method assessment showed a positive connection between invertebrate numbers caught by sweepnet and the mean invertebrate numbers caught by pitfall trap per day (Manuscript II). This shows that only sampling with sweepnet, where more detailed invertebrate studies are not feasable, can indicate invertebrate population density of a site more generally. When compared across all habitat types the total abundance of birds and invertebrates, caught by sweepnet, showed a significant positive relationship, indicating that bird density and invertebrate abundance were both higher on the same sites (Manuscript I) However ther was not a significant difference between invertebrate numbers on barren land and heathland in the larger survey (Manuscript I). This has been shown in other studies of poor heathland in Iceland (Jóhannesdóttir 2013) but was possibly also influenced by varying successional stages within habitats and foremost, the differences in weather conditions within the country at the time of sampling. Temperatures were around average in South Iceland during surveys, but unusually cold in North Iceland, with snow in late May and temperatures well below average during the time of data collection (Vedurstofa Islands 2013c).

6. Conclusions

The results of this study indicated that revegetation action on barren land in Iceland, resulting in native heathlands or Nootka lupin stands, created valuable habitat for invertebrates and birds.

The effect of the revegetation actions varied both with successional stages of revegetated areas and revegetation methods. Overall, bird density and invertebrate numbers were lowest on barren land, higher on heathland and highest in lupin stands.

Restoration of heathland vegetation on barren land resulted in a successfull restoration of common invertebrate groups found in mature heathland and provided habitat for common heathland birds, supporting internationally decreasing populations of some species. As many heathland birds in Iceland feed on berries and invertebrates, the bird species detected in this study are likely to participate in the restoration process by their passive dispersal of seeds and invertebrates.

Revegetation with Nootka lupin provided a novel habitat in Iceland, rich in bird and invertebrates, but with a different group assembly to that of heathland, more resembling woodland or forest vegetation during middle stages of succession. Because of the different effects Nootka lupin has on bird life, depending on successional stages and the unpredictable successional trajectories of mature Nootka lupin stands, the future effects of such revegetated areas on animal life are difficult to predict.

The one-off sampling method of using a sweepnet, which catches mostly dipteral flies, was positively correlated to the abundance of surface active and foliar invertebrates caught by pitfall traps in the same locations and positively correlated to the density of birds. Sweepnet catches can therefore be used as indicators of the over all invertebrate abundance per site and as an indicator for the abundance of food for birds on site, and is an important finding for future invertebrate and bird studies in Iceland.

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1. Appendix

Appendix 1. Table of studyplots, their location, part of country, Habitat type, GPS location of bird transects and year of known revegetation action. Abreviations: S = South Iceland, SA = South East Iceland, N = North Iceland. Habitat: L = Nootka lupin, H = Heathland, B = Barren land.

No	Name of studyplot	Farm/name of area	Part of country	Habitat	Succession	N	W	Start of action (year)
1	Hafnarmelar	Engjalækur/Fiskilækjarmelar	S	B	0	N64°27,080'	V21°58,090'	NA
1	Hafnarmelar	Selhóll/Geldingaá	S	H	1	N64°25,663'	V21°54,100'	2005
1	Hafnarmelar	Fiskilækjarmelar	S	L	2	N64°26,577'	V21°57,035'	2002
2	Haukadalsheiði	Háalda	S	B	0	N64°22,200'	V20°06,830'	NA
2	Haukadalsheiði	Djúphólar	S	H	1	N64°23,550'	V20°04,240'	2000
2	Haukadalsheiði	Selhagar	S	L	2	N64°22,130'	V20°06,350'	1998
3	Þjórsárdalur	Sandártunga	S	B	0			NA
3	Þjórsárdalur	Vikrar Þjórsárdal	S	H	1	N64°07,196'	V19°53,551'	2007
3	Þjórsárdalur	Ásólfsstaðir	S	L	3	N64°05,710'	V19°58,600'	1960
4	Laugarás	Læmi v/Þjórsá	S	B	0	N64°01,355'	V20°27,037'	NA
4	Laugarás	Mjóanes/Reykjasandur	S	H	3	N64°03,476'	V20°26,900'	2003/1907
4	Laugarás	V/Höfða	S	L	3	N64°07,948'	V20°29,226'	1994
5	Hólask. Þjórsárdal	Hólaskógur	S	B	0	N64°09,798'	V19°39,722'	NA
5	Hólask. Þjórsárdal	Hólaskógur	S	H	1	N64°09,540'	V19°40,162'	1980
5	Hólask. Þjórsárdal	Rjúpnavellir/Þjófafoss	S	L	1	N64°02,437'	V19°49,880'	1998
6	Dímon	Ljósárdíll/Langhólmi	S	B	0	N63°39,260'	V20°01,240'	NA
6	Dímon	Ljósárdíll	S	H	1	N63°40,541'	V19°00,839'	Data missing
6	Dímon	Brú Griðungamelar	S	L	4	N63°50,290'	V20°21,850'	2000
7	Markarfljótsaurar	Réttarsandur/Leifsstaðir	S	B	0	N63°39,742'	V20°06,260'	NA
7	Markarfljótsaurar	V.Höttukíl/Gunnarshólmal.	S	H	3	N63°39,225'	V20°05,505'	Data missing
7	Markarfljótsaurar	Réttarsandur	S	L	4	N63°39,708'	V20°06,503'	2000
8	Bolholt	Örlygsstaðamelar	S	B	0	N63°56,443'	V20°08,422'	NA
8	Bolholt	Grashraun	S	H	2	N63°56,020'	V20°05,140'	2010
8	Bolholt	Víkingslækjahraun	S	L	2	N63°55,040'	V20°05,331'	2005
9	Hnappavellir	Hnappavellir, Stígá	SA	B	0	N63°54,569'	V16°33,352'	NA
9	Hnappavellir	Hnappavellir, Stígáraur	SA	H	2	N63°54,769'	V16°34,028'	2000
9	Hnappavellir	Hnappavellir, Lágusker/Vík	SA	L	2	N63°54,113'	V16°36,539'	2005
10	Mýrdalssandur1	Mýrdalssandur	SA	B	0	N63°29,894'	V18°30,633'	NA
10	Mýrdalssandur1	Hólmsá/Kjalnatóarkvísla	SA	H	2	N63°37,108'	V18°27,130'	1995
10	Mýrdalssandur1	Mýrdalssandur	SA	L	2	N63°27,690'	V18°36,854'	1996
11	"Mýrdalssandur"2	Morsárdalur	SA	B	0	N64°03,140'	V17°00,867'	NA
11	"Mýrdalssandur"2	Kerlingadalsá	SA	H	2	N63°25,146'	V18°57,817'	2003
11	"Mýrdalssandur"2	Drangar	SA	L	2	N63°26,454'	V18°45,248'	1992
12	Vík/Mýrdalss	Múlakvísl	SA	B	0	N63°26,589'	V18°49,452'	NA

12	Vík/Mýrdalss	Við Vík	SA	H	1	N63°25,329'	V18°54,807'	2003
12	Vík/Mýrdalss	Múlakvísl	SA	L	4	N63°26,291'	V18°50,182'	2000
13	Skógar	Með Skógará	SA	B	0	N63°30,662'	V19°32,434'	NA
13	Skógar	Með Skógará	SA	H	2	N63°31,252'	V19°31,935'	2010
13	Skógar	Vestan Jökulsár	SA	L	3	N63°30,154'	V19°24,922'	1992
14	Drangshlíð	Skógasandur	SA	B	0	N63°30,025'	V19°31,127'	NA
14	Drangshlíð	Við Kleifarhelli	SA	H	2	N63°31,886'	V19°34,577'	2002
14	Drangshlíð	Skógasandur	SA	L	3	N63°30,321'	V19°31,627'	2002
15	Svínafell	Við Virkisá landi Svínafells	SA	B	0	N63°57,213'	V16°50,948'	NA
15	Svínafell	Með Svínafellsá landi Svínafells	SA	H	2	N63°58,777'	V16°52,119'	Data missing
15	Svínafell	Með Svínafellsá landi Freysness	SA	L	3	N63°59,124'	V16°52,490'	Data missing
16	Rauðhóll	ofan vegar NA við Rauðhól	SA	B	0	N63°53,370'	V16°37,549'	NA
16	Rauðhóll	NA Blesakletts	SA	H	2	N63°52,847'	V16°38,069'	1994
16	Rauðhóll	ofan vegar V við Rauðhól	SA	L	2	N63°53,322'	V16°37,610'	1994
17	Fagurhólsmýri	við flugvöll	SA	B	0	N63°54,300'	V16°43,038'	NA
17	Fagurhólsmýri	við flugvöll	SA	H	1	N63°52,330'	V16°39,249'	Data missing
17	Fagurhólsmýri	Hofsnes ofan vegar	SA	L	4	N63°53,029'	V16°38,365'	1996
18	"Hofsnes"	Hof, neðan Kotárjökuls	SA	B	0	N63°56,247'	V16°47,683'	NA
18	"Hofsnes"	Hof, neðan Kotárjökuls	SA	H	2	N63°56,953'	V16°49,613'	Data missing
18	"Hofsnes"	Fátækramannahóll, Hofsnesi	SA	L	2	N63°52,895'	V16°40,847'	2002
19	Geitasandur	Hella	S	B	0	N63°49,218'	V20°08,087'	NA
19	Geitasandur	Hella	S	H	2	N63°48,268'	V20°10,089'	2001
19	Geitasandur	Hella	S	L	2	N63°49,736'	V20°10,100'	1992
20	Gilsbakki	Við Hellu	S	B	0	N63°50,983'	V20°20,440'	NA
20	Gilsbakki	Við Hellu	S	H	2	N63°50,973'	V20°20,354'	1960
20	Gilsbakki	Við Hellu	S	L	4	N63°50,356'	V20°21,409'	2000
21	Ássandur	Við Ásbyrgi	NA	B	0	N66°03,271'	V16°33,212'	NA
21	Ássandur	Við Ásbyrgi	NA	H	1	N66°01,987'	V16°29,311'	2009
21	Ássandur	Við Ásbyrgi	NA	L	2	N66°03,370'	V16°33,137'	2001
22	Mýri	Bárðardal, við Mjóadalsá	NA	B	0	N65°21,940'	V17°21,237'	NA
22	Mýri	Bárðardal, við Mjóadalsá	NA	H	2	N65°21,698'	V17°22,160'	1996
22	Mýri	Bárðardal, við Mjóadalsá	NA	L	1	N65°22,161'	V17°21,808'	1996
23	Húsavík	Bratti	NA	B	0	N66°11,666'	V17°05,551'	NA
23	Húsavík	Bratti	NA	H	1	N66°11,980'	V17°05,463'	2000
23	Húsavík	Við raflínur nálægt Búðará	NA	L	4	N66°02,145'	V17°19,453'	2000
24	Vatnsbæjargirðing	Við Lónsós	NA	B	0	N66°07,331'	V16°55,868'	NA
24	Vatnsbæjargirðing	Flæðar við Lónslón	NA	H	2	N66°07,015'	V16°54,968'	1940
24	Vatnsbæjargirðing	Flæðar við Lónslón	NA	L	2	N66°06,771'	V16°54,308'	1999
25	Ærlækjarsel	Ærlækjarsel I	NA	B	0	N66°05,705'	V16°29,562'	NA
25	Ærlækjarsel	Ærlækjarsel I	NA	H	3	N66°07,503'	V16°32,708'	1940
25	Ærlækjarsel	Ærlækjarsel I	NA	L	2	N66°05,836'	V16°29,467'	2000
26	Hólasandur	Hólasandur	NA	B	0	N65°44,707'	V17°07,701'	NA
26	Hólasandur	Hólasandur	NA	H	0	N56°42,594'	V17°02,907'	2000
26	Hólasandur	Hólasandur	NA	L	1	N65°45,123'	V17°07,556'	2002

Avian abundance and communities in areas revegetated with exotic versus native plant species

BRYNJA DAVIDSDOTTIR[1], TOMAS GRETAR GUNNARSSON[2], GUDMUNDUR HALLDORSSON[3] AND BJARNI D. SIGURDSSON[1]

[1] *Agricultural University of Iceland, Hvanneyri, IS-311 Borgarnes, Iceland (brynjad@live.com)*
[2] *University of Iceland, South Iceland Research Centre. Tryggvagata 36, IS-800 Selfoss and Gunnarsholt, IS-851 Hella, Iceland (tomas@hi.is)*
[3] *Soil Conservation Service of Iceland. Gunnarsholt, IS-381, Hella Iceland (gudmundur.halldorsson@land.is)*

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Corresponding author: Brynja Davidsdottir, Seljavegur 19, 101 Reykjavik, Iceland. brynjad@live.com

Abstract
Degradaton of ecosystems and introductions of invasive species pose a threat to global biodiversity. Ecosystem restoration and revegetation actions are important for ammending habitat loss and for the protection of species of plants and animals. Iceland has the highest rate of soil erosion and desertification in Northern-Europe and counteractions to erosion and revegetation measures have taken place for over a century. We surveyed the effect of revegetation on the density and composition of birds and invertebrate numbers in 26 survey areas comparing: a) unvegetated eroded areas, b) native heathlands restored on eroded land and c) revegetation by the introduced and invasive Nootka lupin (*Lupinus nootkatensis*) established on eroded land. Birds were counted on transects and invertebrates sampled with sweepnet. Both revegetation methods affected bird density positively. Highest total numbers of invertebrates and birds were recorded on land revegetated with Nootka lupin. On average 31 birds were recorded on km^2 of barren land, 337 on heathland and 627 in Nootka lupin. Bird species composition differed between the two revegetation methods. Restored heathland provided habitat for waders of internationally decreasing populations while Nootka lupin stands harboured more common bird species. Golden Plover and Dunlin, generally common on mature heathland, were most common on restored heathland but Snipe and Meadow Pipit which characterise taller swards were most common in Nootka lupin. Different successional stages of revegetation methods affected bird species composition. Invertebrate numbers increased with revegetation and were most abundant in Nootka lupin stands. There was a positive correlation between invertebrate numbers and bird density in the same sites.

Keywords: birds, barren land, ecological restoration, invasive species, heathland, invertebrates, Nootka lupin, revegetation, waders.

INTRODUCTION

Habitat loss is the greatest cause of diminishing global biodiversity followed by the distribution of invasive species (Schmitz et al.1997). The Convention of Biological Diversity (CBD) has announced a Strategic Plan for Biodiversity 2011-2020 aiming to slow down the rate of natural habitat loss by fifty percent and restore at least 15 percent of degraded ecosystems by 2020 as well as controling or eradicating invasive species, preventing their introduction and establishment (CBD 2013).

To obtain the CDB goals as efficiently as possible it is important to combine knowledge from the many branches of ecology, habitat management and ecological restoration and to obtain new knowledge on ecosystem response to rapidly changing environmental factors. The study of interactions within ecosystems also adds to more comprehensive understanding of the effects of invasive alien species (Memmot 2009). Invasive plants become a threat when affecting excising plant communities through greater compatibility for resources; light, space or nutrients (Enquist et al. 1999; Feng et al. 2007). Alien plant invaders can also disrupt vital mutualist relationships between native plants and their pollinators or seed dispersers, by highly competitive attraction of unspecialized mutualists **(**Traveset & Richardson 2006). This can further increase their effect on native ecosystems (Czarnecka et al. 2012)**.**

Excotic plant species invading low growing vegetation have various effects on excisting bird communities. While invasions of grass species in established grassland communities have been shown to alter the relative sizes of terrestrial invertebrate groups without affecting the excisting passerine bird community (Kennedy et al. 2009) other studies of invasive species in low growing vegetation show a negative effect on bird community composition through changes in vegetation structure and subsequent decline in habitat quality (Scheiman et al. 2003; Fleishman et al. 2003), affecting specialist species in particular (Ma et al. 2012) and those foraging on or near the ground (Flanders et al 2006).

However, where invasive species are established they can provide valuable habitat for birds (McCusker 2010; Fisher et al. 2012) and where little is left of native vegetation, invasive plant species can have a boosting effect on productivity and biodiversity (Kaiser-Bunbury et al. 2010). So studying highly degraded ecosystems revegetated with introduced species gives important information on the effect of alternative revegetation actions on native plant and animal communities (Kaiser-Bunbury et al. 2010).

Birds have been shown to play an important role in ecosystem engineering, transporting seeds (Bruun & Poschlod, 2006; Whelan 2008; Garcia et al. 2010) and invertebrates, with limited dispersal abilities (Green & Sanchez 2006; Sanchez et al. 2007), into newly established habitats contributing to the restoration of plant-animal mutualisms (Kaiser-Bunbury et al. 2010). For judging environmental health, birds and bird groups can be good indicators (Doxa et al. 2010; Defra 2013) as they are near the top of the food chain and reflect productivity patterns at lower levels (Klvanova et al. 2009; Doxa et al. 2010) and at large spatial scales. Therefore birds are one of the best animal groups for evaluating the success of ecological restoration (Da Silva & Vickery 2002) and are used as biodiversity indicators in various environmental schemes by some national governments and by the European Union (Gregory et al. 2005; Klvanova et al. 2009; Gregory & Strien 2010).

Iceland has undergone severe loss of vegetation cover since its settlement in the late 9th century (Arnalds et al. 1997). Currently it has the highest rate of erosion and desertification of countries in Northern Europe, with over 40.000 km^2 (ca. 40% of its total surface area) of barren land with limited plant production as opposed to an estimated 5.000-15.000 km^2 at the time of settlement (Arnalds 2011). This loss was primarily due to unsustainable land use on highly erodable volcanic soils, combined with harsh weather conditions, volcanic eruptions and sand driving winds (Arnalds et al. 1997, Arnalds 2008, Crofts 2011). Significant efforts to restore eroded land in Iceland started in 1907 (Crofts 2011). The most common method is protection from livestock grazing, without other actions or combined with other methods; the most common being top dressing with fertilizers, which again is often combined with spreading of a mixture of grass seeds (Halldorsson et al. 2011a). All these methods lead in the long run to the restoration of local vegetation, mostly native heathland (Gretarsdottir et al. 2004, Aradottir et al. 2008). In addition the introduced nitrogen (N) fixing Nootka lupin (*Lupinus nootkatensis* Donn ex Sims, here after referred to as lupin) has been extensively used for revegetation, being the fourth most common revegatation method in Iceland (Halldorsson et al. 2011a).

The lupin is an economic and effective tool for revegetating barren land where other methods are unfeasible (IINH & SCS 2010), even if its use has increasingly been questioned in recent years (IINH & SCS 2010; Petursdottir et al. 2012). It has been shown to disperse over native heathland (Magnusson et al. 2001; 2002) and has been recognized as an invasive species in Iceland (Magnusson 2010) and potentially invasive in Finland (NOBANIS 2013). Its total area coverage in Iceland to date is unknown but it is now found in all parts of the country (IINH & SCS 2010). The lupin has been widely used by the Soil Conservation Service of Iceland (SCS) and presently, the total area of lupin stands established by this institute is estimated to be ca 100 km^2 or 0.1% of Iceland's surface (Thorsson, in prep.). Other parties have also distributed the lupin and it has also expanded extensively in some places where livestock grazing is limited (Thoroddsen et al 2009; IINH & SCS, 2010; Björgvinsdóttir 2012).

In Iceland the lupin forms large patches with few coexisting plant species during its first successional stages (Magnusson et al. 2002), showing different growth performance depending on annual preticipation and temperature. In inland North and East Iceland, where annual precipitation is 500-800 mm, lupins mostly grow tall along the edge of the establishing patches, but within the patches the plants are low and not so competitive to other plant species (Magnusson et al. 2001). In South and West Iceland, where annual precipitation is higher or 900-3400 mm, lupin plants tend to be relatively tall and form dense uniform fields (Magnusson et al. 2003). A secondary succession, where the lupin is generally replaced with fertile grasslands after some decades, has been shown to occur, but again, the successional rate is highly dependent on annual precipitation and location in Iceland (Magnusson et al. 2001; 2002; 2003). Another known trajectory of secondary succession of lupin stands is where another introduced invasive plant species, cow parsley (*Anthriscus sylvestris* Hoffm.), forms tall stands (Magnusson 2011; Thoroddsen et al. 2009).

The variation in growth form and successional trajectories may have a different effect on invertebrate fauna, bird abundance and species composition. Icelandic studies on soil fauna and birds (Sigurdardottir 2002; Oddsdottir et al. 2008, Gunnarsson & Indridadottir 2009) have revealed an increase in animal abundance in lupin compared to eroded land and an increasing animal density with increasing time from the establishment of a lupin stand. This is also true for soil invertebrate fauna after grass seeding (Friðriksson et al. 1976). However, few systematic surveys have compared the potential differences in bird species composition and density between eroded areas restored with native plant species or areas that have undergone natural secondary succession (passive restoration) in contrast to those that have been revegetated with the introduced lupin.

The avifauna of Iceland is characterized by relatively large populations of few species, which in some cases represent large proportions (10-40%) of world populations, as is the case with most of the ten wader (Charidrii) species found nesting in Iceland (Gunnarsson et al. 2006). Populations of waders in the world are proportionately small compared to many other groups and in addition nearly half of them are currently in decline, mainly due to habitat loss and degradation (International Wader Study Group, 2003; IPCC 2007; MacKinnon et al. 2012). Heathland is an important breeding ground for waders in Iceland (Gunnarsson et al. 2006, Magnusson et al 2009). The present coverage of heathland in Iceland is estimated to be ca.

30,000 km^2 (Arnalds 2011). In total ca. 5,700 km^2 of eroded areas are in the process of being restored in Iceland (Crofts 2011), whereof a minimum of 1,500 km^2 is restored heathland (Halldorsson et al 2011b), primarily in lowland areas.

Here we assessed wether different revegetation methods have different effects on the abundance and composition of bird species in Iceland. We compared bird numbers and species composition on: a) barren land, b) barren land in the restoration process to heathland and c) barren land actively revegetated by the exotic N-fixing lupin. As restored and revegetated areas were inevitably in different stages of succession we accessed the effect of different successional stages within the two revegetated habitat types on the most common bird species.

METHODS

Study sites

Iceland (63-66°N) is a volcanic island of about 103.000 km^2 in the North-Atlantic Ocean. The climate is oceanic with a variable annual precipitation of 500-3400 mm. The soil consists mainly of Histic-, Gleyic- and Brown Andosols (>50%) and Virtisols (30%) (Arnalds 2004). Bird and invertebrate surveys were carried out in different regions of Iceland (Figure 1), from 29th of May to 14th of August 2011. The survey areas formed 26 clusters, each consisting of three habitat types: i) Barren land that had been eroded during the past few centuries and where secondary succession is still in its early stages due to physical or biological pressures. ii) Heathland restored on formerly barren land sometime during the past 50 years, either with passive methods that enhance the secondary succession, such as management of grazing and river regulation, or intial fertilization that may have included seeding with grass species. iii) Areas covered by the exotic N-fixing Nootka lupin, where barren land has been revegetated by active methods in the past 40 years. All three habitat types within each cluster were in the vicinity of each other, at similar height above sea level, climate and other physical conditions, apart from the difference in vegetation and soil properties. For further information about the three habitat types, see Table 1 and Figure 2.

Habitats within each cluster were usually visited during the same day (77% of clusters), or during consequent days (23% of clusters) depending on weather conditions. The habitat types were surveyed in a random order each day, to eliminate possible systematic effects of diurnal rhythms in animal behavior. At each study site birds were counted on transects and invertebrates were caught in sweep nets (details below). Date, time of day, wind speed, air temperature and cloud coverage were recorded and the plant successional stage of heathland and Nootka lupin was given a grade on a scale of 0 to 4 (Table 2). Photos were taken of each transect and the GPS location of the starting and finishing point of transects noted as well as the location of sweepnetting points.

Survey methods

Bird surveys were carried out from 29th May to 25th June 2011, which is the period of highest breeding activity of the most common terrestrial bird species in sub-arctic and arctic conditions (Meltofte 2001; Gunnarsson 2006; Davidsdottir 2010). One to two sets of habitat-clusters were monitored per day, either before noon or between four and eleven pm., which are the periods when most terrestrial bird species show a peak in detectability (Bibby et al. 2000; Hoodless et al. 2006; Davidsdottir 2010). To obtain site specific density estimates, birds were recorded on transects (Bibby et al. 2000) using a 50 m inner belt and a 100 m outer belt which was suitable for the sizes of the survey patches (often linear from strip sowing with machinery) and the species surveyed (Gunnarsson & Indridadottir 2009). The mean transect length was 0.74 km (SE 0.12 km) and was often restricted by the size of homogenous habitat patches (Table 3). All birds were recorded, at the distance from where they were first seen to the transect line, and their behavior noted. Birds further than 100 m from the transect line and those overflying were recorded but excluded from further analysis. Binoculars (Leica Ultravid 8x32; Leica, Germany) were used together with a rangefinder (icaddie G-543; Magadoro Ltd, Neatherlands) to verify the observer's ability of accurate evaluation of distances. The unit calculated was individual birds, of each species, per km^2.

Insects were sampled directly following the bird counts with a hand-net on three random points placed within or adjacent to one end of each of the bird surveying transects. The net, of diameter 39 cm, mesh size 0.3 mm, was swept over the surface of every survey points with ten, non overlapping, 2 m long strokes. The number of caught diptera, moths and spiders (>3 mm) was counted and the animals then released. These groups made up the near entire invertebrate catch (>95%). We used the average invertebrate number of the three catches per area as a measurement of invertebrate abundance per site.

Data and statistical analyses

We first estimated the overall differences in bird density between the three habitat types (heathland, lupin, barren land) using habitat as a predictor of bird density. We constructed species-specific generalized linear models with a poisson distribution and a log link function for the nine species which occurred on ≥ 7 transects. To account for the large number of zeros in the data and adjust for overdispersion we corrected the standard errors using a quasi-model (quasi-poisson in program R) (R Development core team 2011).

We carried out a Principal Components Analysis (PCA) with the nine most commonly occurring species to assess difference in species composition between the three habitat types. The difference in species composition between habitats was estimated by comparing the mean scores of extracted factors between habitats with an ANOVA and Tukey post-hoc tests. Difference in invertebrate abundance between habitats was assessed with a Generalized linear Model (negative binomial with log link function in SPSS 20) (IBM) and the overall relationship between bird and invertebrate abundance with a Spearman nonparametric correlation. Habitats will inevitably be of different succession stages around the country, but as we were interested in an overall effect for management purposes we analysed the overall effect of habitat on bird density. We then explored the effect of successional stage within lupin (four stages, Table 2) and heathland (three stages, Table 2) on bird density. Models of the effects of succession stage on bird densities in lupin and on heathland were comparable to the overall models (quasi-poisson Generalized linear models) but were only built for species which occurred on more than 50% of transects due to sample size restrictions.

RESULTS

The effect of revegetation on bird density

Over all a total distance of 59 km of transects was walked and 1511 birds were detected of 19 species (Table 3 and Table 4). A low density of birds was generally found on barren land and both revegetation methods increased bird density greatly from the unvegetated state (Table 3). Of the nine most commonly occurring species none were most abundant on barren land compared to the two other habitat types (Table 5). Golden Plover and Dunlin were significantly most abundant on heathland (Table 5). Ringed Plover and White Wagtail were most abundant on heathland, but not significantly so. Snipe, Redshank and Meadow Pipit were significantly most abundant in lupin and Whimbrel and Redwing most abundant there, but not significantly (Table 5).

The effect of revegetation on bird diversity

Both revegetation methods had a strong positive effect on all different measures of diversity. Over all, 12 species of birds occurred on barren land, 16 on heathland and 15 in lupin (Table 3). There were significantly fewer bird species on average on barren land than in heathland and in lupin stands (ANOVA: $F_{2.77}$=37.25; P<0.001), but the average number of species did not differ significantly between the two revegetation methods (ANOVA - $F_{4.03}$ = 1.7616; P = 0.1904; Figure 3).

Species composition was different between habitats (Table 4) and detected presence of species varied within and between habitat types. All species detected on barren land occurred on less than 50% of transects on barren land. On heathland, Golden Plover, Dunlin, Whimbrel and Meadow Pipit occurred on over 50% of transects and in lupin Meadow Pipit and Snipe had an over 50% occurance (Table 4). A Principal Components Analysis (PCA) was conducted with the 9 most common species (same species as in Table 5). Four components were extracted from the PCA, where component one explained 27% of the variation in the data and the next three 22%, 17% and 11%, respectively (Table 6). Overall, the species that occurred on barren land were not clearly distributed on any single component, but species which were common in lupin tended to load positively on component one (Meadow Pipit, Snipe and Redshank most strongly) and species more common on heathland loaded positively on component 2 (Dunlin, Golden Plover and Ringed Plover most strongly) (Figure 4). Mean factor scores of components 1 and 2 varied significantly between habitat types (ANOVA - Factor 1: $F_{2.77}$ = 25.67, P<0.0001; Factor 2: $F_{2.77}$ = 7.45, P = 0.001). Tukey's post-hoc tests (alpha = 0.05) showed that factor 1 was significantly higher in lupin than in other habitats but factor 2 was higher in heathland than in others. Mean scores for factors 3 and 4 did not vary significantly between any habitats.

The effect of succession within revegetated areas on bird density

Although sample sizes were small when habitat types were split up by succession stages some variation in density was evident with succession stage (Figure 5, table 7). In heathland, densities of Golden Plover and Dunlin were highest in intermediate vegetation succession and Whimbrel increased with advancing vegetation succession. Both Snipe and Meadow Pipit were more common in the most advanced heathland than at earlier successional stages. In lupin both Snipe and Meadow Pipit increased their density as lupin succession advanced. Of the species most common on heathland (Golden Plover and Dunlin), both were relatively rare in lupin and of similar density in all its successional stages. Whimbrel was also found at similar density in advancing and retreating lupin (stages 1, 2 and 4), but was absent in the densest lupin patches (stage 3). Other bird species occurred too rarely to make inferences about the effects of succession on their abundance on heathland or in lupin.

The relationship between the abundance of birds and invertebrates

The total invertebrate catch by sweepnet was 75, 141 and 594 individuals on barren land, heathland and in lupin respectively. There was no significant difference between the abundance of caught invertebrates on barren land and on heathland but invertebrate abundance was significantly higher in lupin than in other habitats (GLM, negative binomial with log link function: Test of model effects, Wald Chi-square = 39.901, DF = 2, $P < 0.0001$, deviance/df = 1.640, with pairwise comparsions) (Figure 6). There was a significant positive relationship between the total abundance of birds counted and the total abundance of invertebrates caught by sweepnet on all transects, when compared across all habitat types, indicating that bird density and invertebrate abundance were both higher on the same sites (Spearman rank correlation with untransformed data: Rho = 0.592, $P<0.001$) .

DISCUSSION

The current study compared and assessed the effects of two revegetation methods of barren land on bird density and diversity in Iceland; the revegetation with introduced Nootka lupin vs. restoration of native vegetation. Both methods had a substantial positive effect on avifauna and increased both density and diversity of birds.

Some bird species thrive on barren land in Iceland (Gunnarsson et al. 2006; Gunnarsson & Indridadottir 2009, this study) although at very low density (Magnusson et al. 2009). In our study bird density on barren land was on average 31bird/km^2. Revegetation with introduced lupin has been shown to have a positive effect on birdlife while other methods of revegetating with monocultures on barren land, such as *Leymus arenarius* (lyme grass), have little effect on birdlife (Gunnarsson & Indridadottir 2009). Our results showed that bird species responded strongly and positively both to the restoration of native heathland vegetation and to revegetating with lupin with average densitys of 337 birds/km^2 on heathland and 627 in Nootka lupin. Bird densities on heathland and grassland in lowland Iceland have been shown to vary between 109 and 270 pairs/km^2 (Magnússon et al. 2006) with a total bird density of

274 birds/km^2 on poor heathland and around 500 birds/km^2 on rich heathland and grassland (Jóhannesdóttir 2013). Our results correspond well with Jóhannesdóttir (2013) density of poor heathland. Of common lowgrowing vegetation habitats in Iceland, bird diversity and densities have been shown to be highest in wetlands and semi-wetlands with up to 640 birds/km^2 (Jóhannesdóttir 2013) wich is similar to here detected bird densities in Nootka lupin. Each revegetation method did however support different bird communities with Golden Plover and Dunlin being significantly most common in heathland but Snipe, Redshank and Meadow Pipit in lupin.
Restored habitats and revegetation efforts have been shown to provide valuable habitat for birds (Williams et al. 2012) even though the assembly of bird species is rarely the same in restored areas as in original or remnant habitats, at least during the first decades (Munro et al. 2011). Studies have shown that restored habitats that have evolved by spontaneous succession in a complete succession series inhabit a higher bird species diversity and tend to sustain a larger number of rare bird species compared to sites that are reclaimed with methods which „skip“steps of natural succession (Šálek 2012). Our results were partly in coherence with these findings as species numbers were not different between the native heathlands or introduced lupin stands. These two revegetated habitat types attracted mostly different species. Golden Plover, Dunlin and Ringed Plover, all of which show a preference to open low growing vegetation (Gunnarsson et al. 2006) and characterized the bird fauna of mature heathland vegetation, avoided lupin stands. Meadow Pipit, Snipe, Redwing and Redshank on the other hand, showed a preference for lupin stands. The fact that there were rather subtle differences in bird species numbers and composition between the two vegetation types was a somewhat unexpected finding, but might indicate the effect of different successional stages within the two habitat types and the fact that lupin stands were in some instances close to other vegetated habitats.

Early successional areas and shrubland have become scarce in Europe and in North America (Dettmers 2003; Oehler 2003) and avian early successional specialists are subsequently rarer than generalists and woodland birds (Šálek 2012). Iceland is globally an important nesting ground for ten wader species (Gunnarsson et al. 2006), including the Golden Plover, Ringed Plover and Dunlin, which all prefer open heathland habitats. This suggests that heathland restoration on barren land in Iceland is of great value for the conservation of these heathland species which generally have internationally decreasing populations (International Wader Study Group 2003; MacKinnon et al. 2012).

As with many revegetation actions which show positive effects on birdlife (Williams et al. 2012), our results show positive effects of revegetating barren lands with the imported Nootka lupin on bird density. The most responsive bird species have all been associated with taller wet swards, shrubland or woodlands in Iceland, namely Snipe, Meadow Pipit and Redwing (Jónsson et al. 2006; Nielsen et al. 2007). Redshank and Black-tailed Godwit were found in some lupin stands, but these species were less abundant on heathland in the present study. The presence of Redshank in lupin stands was in accordance with earlier reports in lupin in Iceland (Gunnarsson & Indridadottir 2009) and may indicate a higher adaptability of the Redshank and Black tailed-Godwit to this novel habitat. It is likely that the presence of wetland species in lupin stands is also dependent on wet features nearby, which are important feeding habitats for adults (Gunnarsson et al. 2006). Further studies on the effect of nearby vegetation and habitat features and isolation of revegetation areas are needed to better understand the occupancy of the revegetated patches by individual species.

Although the structural complexity of an ecosystem has been shown to have a positive effect on bird species richness (e.g. Munro et al. 2011), areas of early succession host decreasing numbers of rare bird species with site age (Šálek 2012). In our study, bird species responded differently to various successional stages within vegetation types. In the very early stages of heathland succession, which lacked woody shrubs, early successional specialists (Gunnarsson et al. 2006), such as Ringed plover, Golden plover and Dunlin, were most abundant. Woody plants and shrubs, became more noticeable in the later stages of heathland succession where Whimbrel, Snipe and Meadow pipit were increasingly abundant. Lupin stands on the contrary tended to have more structural complexity in earlier and latter successional stages (referred to as successional stages 2 and 4 in this study) in the form of mosaics of tall lupin plants/patches with gravel or low vegetation in between plants, compared to their densest stage which was dominated by tall dense lupin (stage 3 here). There were indications that the densest stage of lupin stands had a negative effect on some bird species, such as Whimbrel and Redshank which were absent in these patches, whereas in scattered lupin stands there appeared to be a necessary structural complexity for the foraging of various bird species of foliar and terrestrial invertebrates.

The observed increase in invertebrate abundance where barren land had been transformed into lupin stands was in accordance with other studies on invertebrate abundance in the same habitat types (Sigurdardottir 2002; Oddsdottir et al. 2008; Davidsdottir et al 2013). When the two revegetation methods were compared, a difference in the overall density of birds and foliar invertebrates was evident. Numbers of birds and invertebrates were lowest on barren land, higher on heathland and highest in lupin stands, which had almost a double bird density compared to heathlands. When compared across all habitat types the total abundance of birds and invertebrates, caught by sweepnet, showed a significant positive relationship, indicating that bird density and invertebrate abundance were both higher on the same sites. The fact that invertebrates were not significantly more abundant on heathland than barren land , wich corresponds to another study of poor heathland in Iceland (Jóhannesdóttir 2013), was possibly also influenced by varying successional stages within habitats and foremost, the differences in weather conditions within the country at the time of sampling. Temperatures in the North of the country were colder than average in June with snowfall in late May (Vedurstofa Íslands 2013) wich might have influenced invertebrate life in low growing vegetation.

While revegetation with excotic species can provide important habitat for birds (Munro et al. 2011; this study) restoration of native plant communities has become a priority in the protection of biodiversity (MacMahon & Holl 2001). In the process of restoration, modification of environmental factors can be necessary to aid in overcoming restricting environmental barriers and speed up natural succession. Application of fertilizers, sowing of seeds and providing of safe sites for seedlings are methods used to speed up succession or to turn around the actual degradation aiding the recovery of the degraded land (Elmarsdottir et al. 2003; Petursdottir et al. 2012; Arnalds et al. 2013), especially in Iceland where harsh winds, a short growing season and frequent freeze-thaw cycles causing ice-needles all hinder or slow natural succession of barren land considerably.

Many of Iceland's heathland birds feed on berries and seeds as well as various invertebrates (van de Kam et al. 2004; Green & Sanches 2006) and are likely to contribute to the reestablishment of restored ecosystems. Seed dispersal by highly mobile animals such as birds is considered of central importance in vegetation recovery during restoration (Garcia et al. 2010). Avian dispersal of seeds and invertebrate larvae is worth taking into consideration (Kaiser-Bunbury et al. 2010) when aiming for fast and successful reclamation of heathland fauna and flora in Iceland. It has been shown that the abundance of seed dispersing birds as well as the vicinity of the to-be-restored ecosystem to an established resource of seeds and invertebrates (Garcia 2010; Knop et al. 2011; Gardali & Holmes 2011) are driving forces in ecological engineering and in the recovery of degraded land increasing species richness. This should be taken into account when accessing the costs of revegetation projects, and deciding between reclamation of native vegetation and revegetating with an introduced N-fixing plant, which might have a lower initial cost but uncertain ecological trajectories (Petursdottir et al.

2012) and probably resulting in exteme coverage of alien vegetation in the future (Thoroddsen et al. 2009).

Implications for management

Change in land use such as changing grazing pressure on former agricultural land leads to an alteration in plant communities (Skórka et al. 2010; Sutherland et al. 2012; Amar et al. 2011). With less grazing pressure tall woody plants or invasive plants often take over prairie or heathland and globally rare birds which are dependent on preexisting grassland habitats have been replaced with more common woodland birds (Jónsson et al. 2006; Skórka et al. 2010; Sutherland et al. 2012; Amar et al. 2011). In Iceland the future successional development of both heathland and lupin stands, and the density and communities of bird species within these ecosystems, is largely dependent on land use in coming decades. With less intensive grazing pressure combined with the detected increase in plant growth associated with increasing temperatures in the arctic and subartic (IPCC 2007; Pearce-Higgins, 2011; Elmendorf et al. 2012), much of Icelandic heathland is likely to increase in canopy height and advance in succession to shrubland or birch woodlands (Elmendorf et al. 2012). This is likely to have a negative effect on many of the breeding wader species which breed in internationally important numbers in Iceland (Gunnarsson et al. 2006). Further detailed studies comparing bird and invertebrate life on recently restored heathlands versus ‘old’ heathlands would give important information on the difference in species composition and density through natural succession. These, in addition to studies on the effect of livestock grazing on birds, would indicate the desired future grazing intensity for the maintenance and management of important breeding grounds of the internationally important wader populations of Iceland (Banks-Leite et al. 2011).

Where invasive plants invade meadow bird communities, these communities have been shown to greatly decrease in bird species richness (Skórka et al. 2010). It should be considered that lupin areas expand with time and they have presently invaded some existing heathlands in Iceland (Magnusson et al. 2002). Although lupin stands in Iceland attract and sustain a high density of some bird species and invertebrates, the future direction of succession of lupin stands is unclear as they seem to develop a novel ecosystem (Petursdottir et al. 2012). There is evidence that lupin patches can make favorable growing conditions for another exotic invasive plant, cow parsley, to create stands in which few other plant coexists (Magnusson 2011; Thoroddsen et al. 2009), even though it is more common for grassland to replace the lupin after some decades (Magnusson et al. 2003). If, however, the former successional trajectory becomes common, this would place a serious question on the effect on heathland birds in the future. Thus future monitoring of the ecological succession of the new ecosystems, originally reclaimed with lupin, and the plant-animal associations within, will give important information on the effect of lupin stands on multitrophic development and the lupins value as a tool for conservation of biodiversity.

Our results showed that heathland reclamation in Iceland has a substantial value for the maintenance of biodiversity of some waders and heathland birds, possibly more so than the sowing of lupin, as many wader species found on heathland have declining numbers world wide (Birdlife International 2004). Although lupin stands in Iceland support a high desdity of a few bird species, these species are commonly found on a wider range of habitats with a wider distribution world wide than early successional heathland.

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TABLES AND FIGURES

Table 1. Description of habitat types.

Barren land	Very sparsely vegetated land on sand or gravel.	*Agrostis vivealis*, *Festuca rubra*, *Phleum pratensis*, *Thymus praecox* ssp. *arc*
Heathland	Dry young heath land on prior sand plains re-vegetated by fertilisation and sowing of grass seeds or by self regeneration. Cover of native species, varying from biological crust with spares grasses, rushes and sedges, moss and lichen to a homogenous coverage of grasses and/or moss with sparse small shrubs. Often subject to grazing.	Moss, lichen, grasses, rushes,, sedges sparse low *Empetrum nigrum*, *Vaccinum* spp. and *Salix* ssp.
Nootka lupin	Fields consisting of varying ages and densities of introduced and sowed *Lupinus nootkatensis* with bare patches or native grasses amongst lupin plants.	Nootka lupin *Lupinus nootkatensis*

Table 2. Description of succession stages which heathland and lupin habitats were classified into. Heathland has three stages but lupin four. NA = no fourth group for heathland succession

Succession class	Heathland	Nootka lupin
1	Soil organic crust with sparse grasses	Sparse low lupin plants on barren land
2	A shallow mat of low vegetation or a dominating cover of moss and lichen	Tall lupin with barren land between plants
3	A homogenous coverage of grasses,rushes and sedges, moss and forbes with sparse low growing shrubs.	Tall very dense lupin with little coexcisting flora.
4	NA	Tall lupin started to retreat with dense grass between plants.

Table 3. Calculated mean bird density (individuals/km^2) on 26 transects within each habitat type (with standard error). Species are listed in taxonomic order. Species with a mean density of over 10 individuals/km^2 are indicated in bold letters.

	Barren land		Heathland		Lupin		
Greylag Goose *Anser anser*	0.0	(0.0)	0.0	(0.0)	>0.0	(0.0)	
Mallard *Anas platyrhynchos*	0.0	(0.0)	0.9	(0.9)	1.6	(1.6)	
Ptarmigan *Lagopus mutus*	0.0	(0.0)	1.3	(1.3)	0.0	(0.0)	
Oystercatcher *Haematopus ostralegus*	1.5	(1.5)	2.7	(1.9)	4.4	(4.4)	
Ringed Plover *Charadrius hiaticula*	**11.3**	(5.7)	**18.8**	(6.7)	3.6	(2.7)	
Golden Plover *Pluvialis apricaria*	2.8	(2.0)	**74.2**	(34.1)	9.8	(3.4)	
Dunlin *Calidris alpina*	4.4	(3.1)	**72.4**	(23.1)	**22.1**	(7.6)	
Redshank *Tringa totanus*	>0.0	(0.0)	1.8	(1.8)	**53.1**	(25.6)	
Black-tailed Godwit *Limosa limosa*	0.0	(0.0)	0.0	(0.0)	**11.8**	(8.4)	
Whimbrel *Numenius phaeopus*	0.9	(0.9)	**26.4**	(6.1)	**29.9**	(11.1)	
Snipe *Gallinago gallinago*	2.8	(2.2)	**12.0**	(5.3)	**96.6**	(22.2)	
Great Skua *Catharacta skua*	>0.0	(0.0)	**10.7**	(7.4)	0.0	(0.0)	
Arctic Skua *Stercorarius parasiticus*	3.8	(3.8)	5.4	(3.1)	1.1	(1.1)	
Lesser Black-backed Gull *Larus fuscus*	0.0	(0.0)	0.0	(0.0)	3.1	(3.1)	
Meadow Pipit *Anthus pratensis*	2.4	(1.7)	**83.4**	(25.9)	**337.2**	(43.5)	
White Wagtail *Motacilla alba*	1.1	(1.1)	**14.8**	(7.6)	7.1	(4.0)	
Wheatear *Oenanthe oenanthe*	0.0	(0.0)	1.2	(1.2)	0.0	(0.0)	
Redwing *Turdus iliacus*	0.0	(0.0)	0.6	(0.6)	**45.3**	(21.5)	
Snow Bunting *Plectrophenax nivalis*	1.5	(1.5)	**10.8**	(7.9)	0.0	(0.0)	
Grand total	31		337		627		
No. Of species detected	12		16		15		19
Total transect length (Km)	17		27		15		59

Table 4. The proportional occurance of bird species per transect within habitats (each consisting of 26 transects), unrelated to species density. The occurance of a species which were found on 50% or more of the transects is indicated in bold letters.

	Barren land	Heathland	Lupin
Greylag Goose *Anser anser*	-	-	0.08
Mallard *Anas platyrhynchos*	-	0.04	0.04
Ptarmigan *Lagopus mutus*	-	0.08	-
Oystercatcher *Haematopus ostralegus*	0.08	0.19	0.08
Ringed Plover *Charadrius hiaticula*	0.23	0.35	0.12
Golden Plover *Pluvialis apricaria*	0.12	**0.77**	0.42
Dunlin *Calidris alpina*	0.15	**0.65**	0.35
Redshank *Tringa totanus*	0.04	0.12	0.27
Black-tailed Godwit *Limosa limosa*	-	-	0.15
Whimbrel *Numenius phaeopus*	0.08	**0.73**	0.46
Snipe *Gallinago gallinago*	0.08	0.46	**0.77**
Great Skua *Catharacta skua*	0.08	0.15	-
Arctic Skua *Stercorarius parasiticus*	0.08	0.27	0.12
Lesser Black-backed Gull *Larus fuscus*	-	-	0.04
Meadow Pipit *Anthus pratensis*	0.12	**0.81**	**0.96**
White Wagtail *Motacilla alba*	0.04	0.23	0.12
Wheatear *Oenanthe oenanthe*	-	0.04	-
Redwing *Turdus iliacus*	-	0.08	0.38
Snow Bunting *Plectrophenax nivalis*	0.04	0.08	-

Table 5. Poisson Generalized linear models (adjusted for overdispersion, quasi-poisson) comparing density of the most common 9 species between three habitats. Estimates of Lupin and Unvegetated are relative to heatland (intercept model).

Species	Habitat	Estimate	SE	t	P	Model predicted mean values
	Intercept	4.3067	0.2863	15.044	<0.0001	74.19
Golden Plover	Lupin	-2.0196	0.8363	-2.415	0.0182	9.85
	Unvegetated	-3.2743	1.4990	-2.184	0.0321	2.81
	Intercept	2.9322	0.3604	8.135	<0.0001	18.77
Ringed Plover	Lupin	-1.6470	0.8967	-1.837	0.0702	3.62
	Unvegetated	-0.5033	0.5872	-0.857	0.3941	11.35
	Intercept	2.4849	0.5053	4.918	<0.0001	12.00
Snipe	Lupin	2.0854	0.5358	3.892	0.0002	96.58
	Unvegetated	-1.4663	1.1667	-1.257	0.2127	2.77
	Intercept	3.2728	0.2847	11.496	<0.0001	26.38
Whimbrel	Lupin	0.1233	0.3908	0.315	0.7533	29.85
	Unvegetated	-3.3528	1.5478	-2.166	0.0335	0.92
	Intercept	0.5921	1.6148	0.367	0.7149	1.81
Redshank	Lupin	3.3790	1.6420	2.058	0.0431	53.03
	Unvegetated	-15.8946	2769.7252	-0.006	0.9954	0
	Intercept	4.2836	0.2367	18.101	<0.0001	72.50
Dunlin	Lupin	-1.1908	0.4901	-2.430	0.01751	22.04
	Unvegetated	-2.8055	0.9909	-2.831	0.00595	4.38
	Intercept	4.4221	0.2439	18.134	<0.0001	83.27
Meadow Pipit	Lupin	1.3985	0.2723	5.136	<0.0001	337.15
	Unvegetated	-3.5693	1.4730	-2.423	0.0178	2.37
	Intercept	2.6977	0.4037	6.682	<0.0001	14.85
White Wagtail	Lupin	-0.7464	0.7119	-1.048	0.2978	7.04
	Unvegetated	-2.6236	1.5525	-1.690	0.0952	1.08
	Intercept	-0.4855	2.4201	-0.201	0.8415	0.62
Redwing	Lupin	4.2998	2.4365	1.765	0.0817	45.35
	Unvegetated	-14.8171	2422.0044	-0.006	0.9951	0

Table 6. Species loadings of four components from a Principal Components Analysis. Species with the three highest loadings in component one and two are indicated in bold letters.

	Component			
	1	2	3	4
Ringed Plover	-0.223	**0.559**	0.417	0.434
Golden Plover	-0.061	**0.745**	0.084	-0.546
Dunlin	0.087	**0.872**	0.12	-0.211
Redshank	**0.693**	0.244	-0.442	0.308
Whimbrel	0.634	0.411	-0.466	0.169
Snipe	**0.752**	-0.206	0.393	-0.143
Meadow Pipit	**0.829**	-0.084	0.113	-0.005
White Wagtail	0.071	0.177	0.719	0.476
Redwing	0.472	-0.261	0.527	-0.342

Table 7. Results of Poisson Generalized linear models (corrected for overdispersion, quasi-poisson) predicting the abundance of individual species at different successional stages in lupin and heathland. Lupin has four succession stages and heathland three (Table 2). Only species which occurred on more than 50% of study plots were analysed (Table 4). Estimates of stages 2-4 are relative to stage 1 (intercept). See figure 2 for direction of relationships.

LUPIN

Species	Succession	Estimate	SE	T	P
Golden Plover	1 (Intercept)	31.061	0.7215	4.305	<0.001
	2	-0.8692	0.9269	-0.938	0.358
	3	-0.5804	11.037	-0.526	0.604
	4	-16.02	12.204	-1.313	0.203
Snipe	1 (Intercept)	1.992	2.193	0.909	0.373
	2	2.152	2.227	0.966	0.344
	3	3.188	2.226	1.432	0.166
	4	2.917	2.215	1.317	0.201
Whimbrel	1 (Intercept)	3.526	0.978	3.606	0.002
	2	0.018	1.101	0.017	0.987
	3	-17.828	3821.189	-0.005	0.996
	4	0.00743	1.135	0.05	0.948
Dunlin	1 (Intercept)	-14.3	3452.27	-0.004	0.997
	2	17.51	3452.27	0.005	0.996
	3	16.7	3452.27	0.005	0.996
	4	17.78	3452.27	0.005	0.996
Meadow Pipit	1 (Intercept)	43.263	0.7392	5.852	<0.0001
	2	14.675	0.7621	1.926	0.067
	3	16.651	0.79	2.108	0.047
	4	17.043	0.764	2.231	0.036

HEATHLAND

Species	Estimate	SE	T	P
Golden Plover	3.0796	0.9451	3.258	0.003
	1.88	10.208	1.842	0.078
	0.4269	17.957	0.238	0.814
Snipe	1.9924	0.6705	2.972	0.007
	-0.1418	10.073	-0.141	0.889
	1.9459	0.8405	2.315	0.029
Whimbrel	23.979	0.4735	5.064	<0.0001
	11.258	0.551	2.043	0.053
	17.02	0.6227	2.733	0.012
Dunlin	31.023	0.7577	4.095	<0.001
	17.135	0.8288	2.067	0.049
	13.597	10.787	1.261	0.22
Meadow Pipit	39.286	0.3336	11.775	<0.0001
	-0.1737	0.5057	-0.343	0.734
	19.622	0.417	4.705	<0.0001

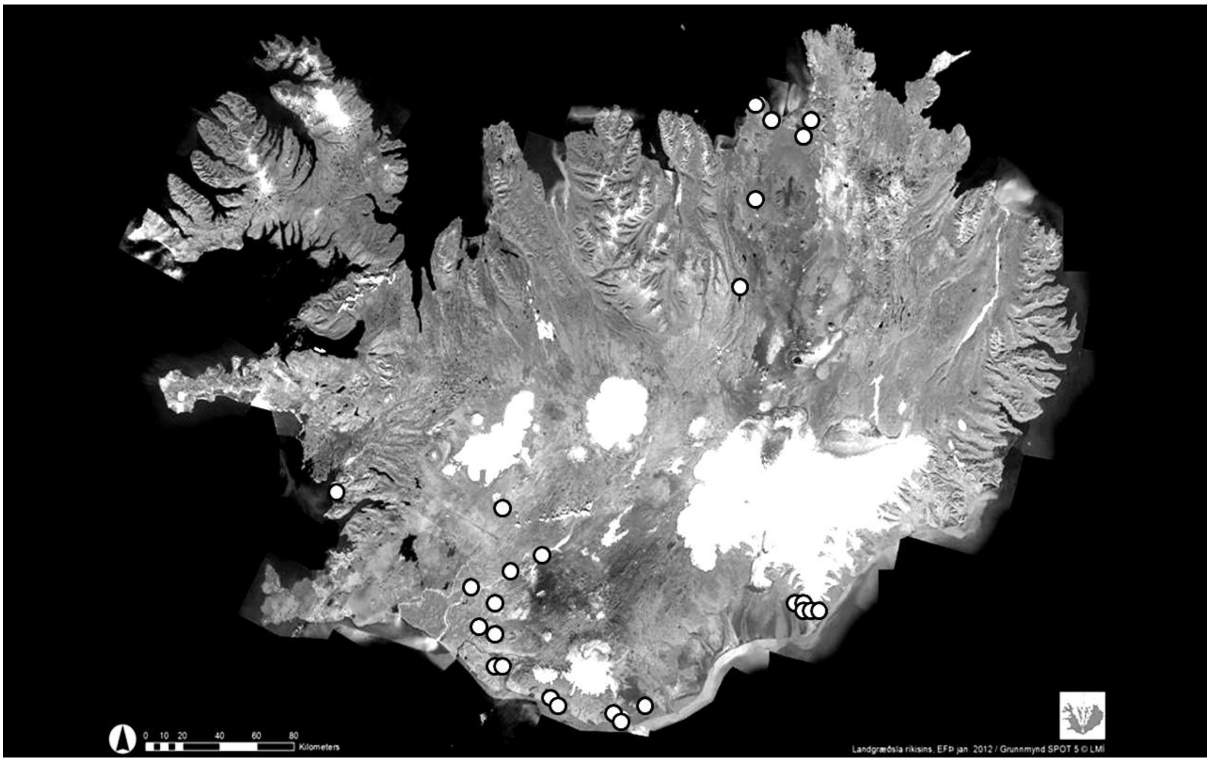

Figure 1. Positioning of study plots where birds were counted on transects and invertebrates caught by sweepnet. Each dot stands for three habitat types studied as a cluster.

Figure 2. Photographic samples of the three habitat types. To the left: restored heathland, top right: lupin stand, bottom right: barren land.

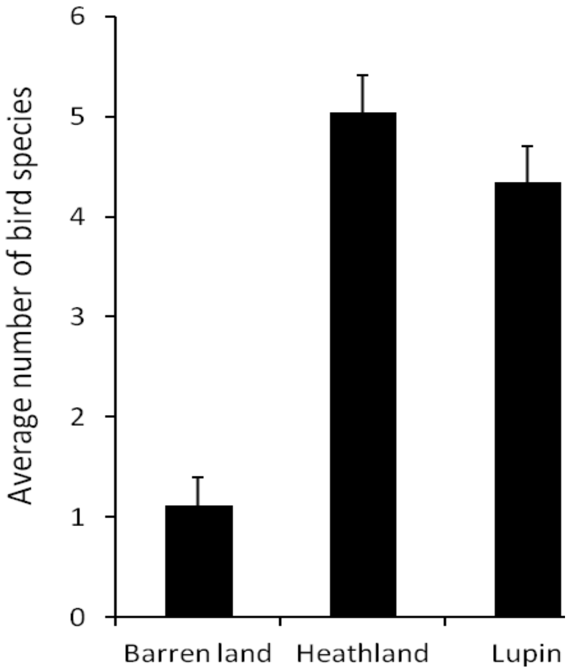

Figure 3. Average number of bird species per transect within three different habitat types, with standard error bars.

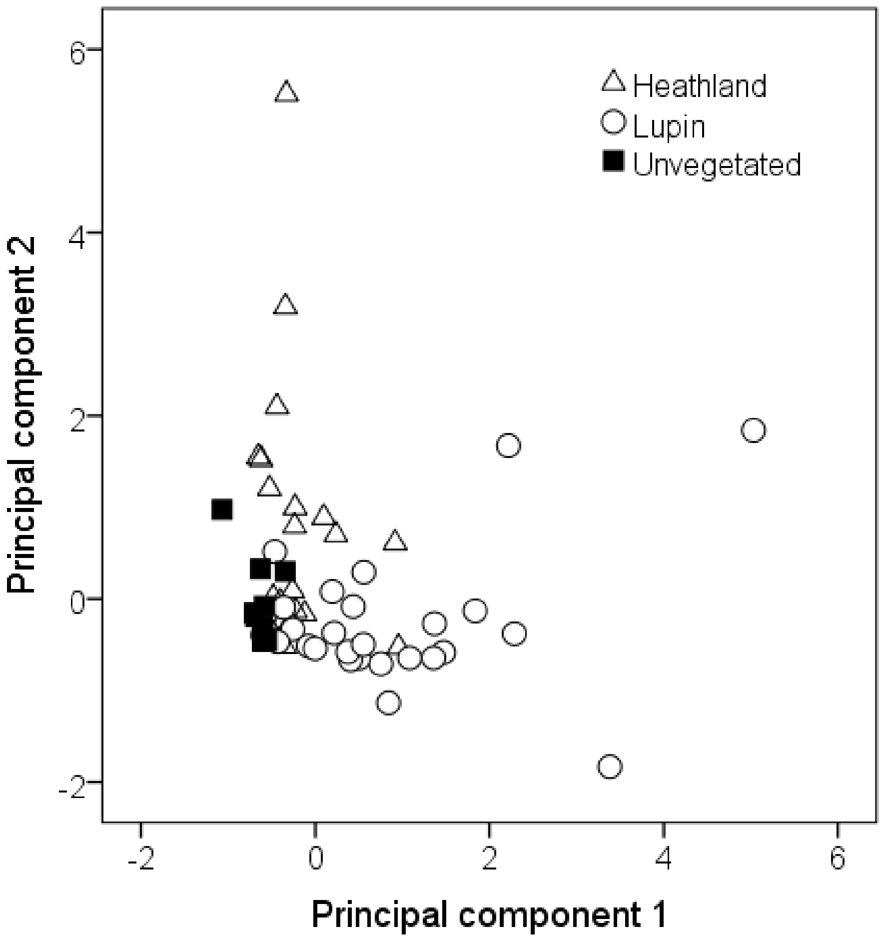

Figure 4. Principal components plot of the first two factors of the 9 most commonly occurring species with habitats overlaid. See table 6 for components scores.

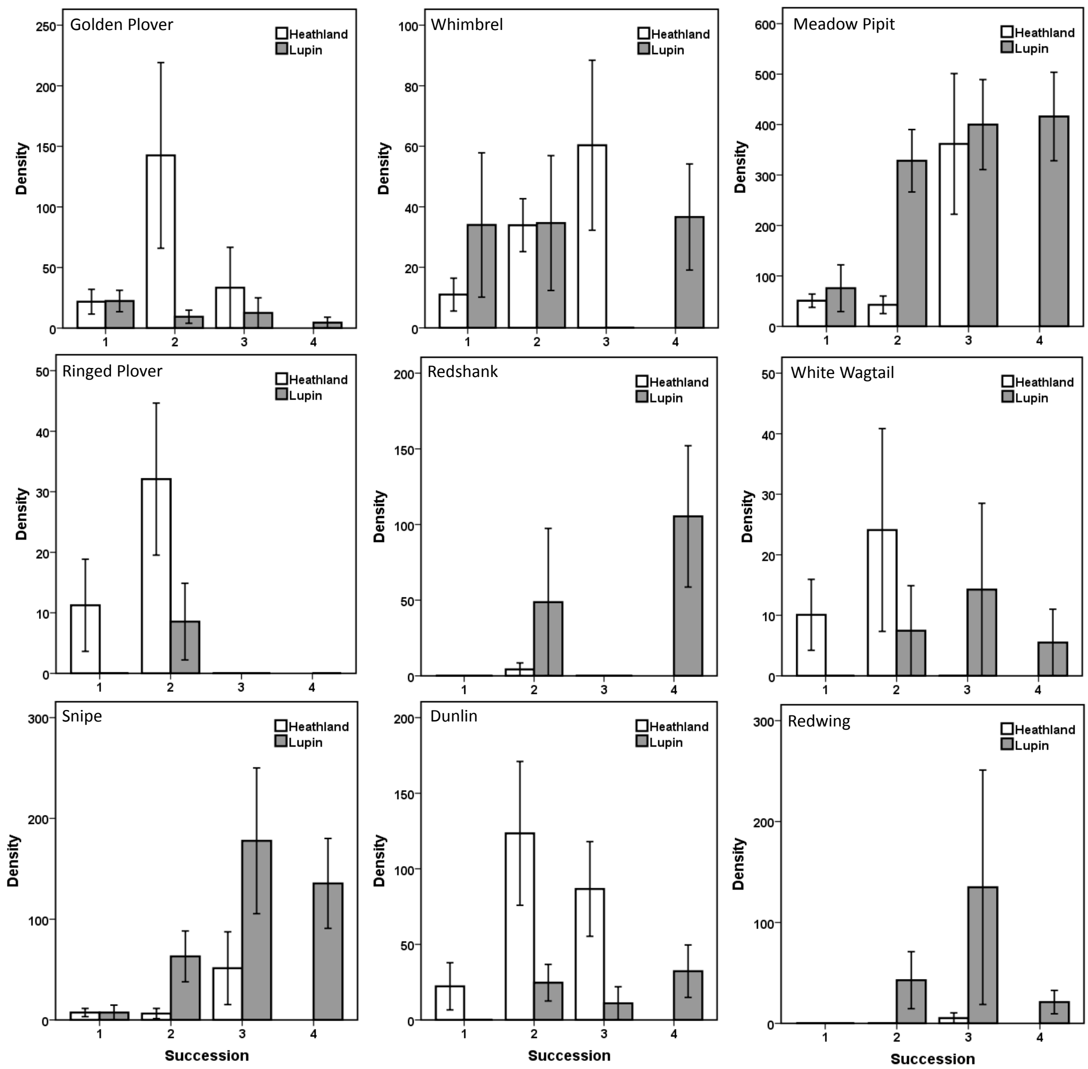

Figure 5. Densty (individuals/km2) of the nine most commonly occurring birds species in relation to vegetation succession on heathland and in lupin. Lupin has four (1-4) defined succession stages but heathland has only three (1-3) (table 2). Note the different scales on the y-axis. Bars are 1 SE.

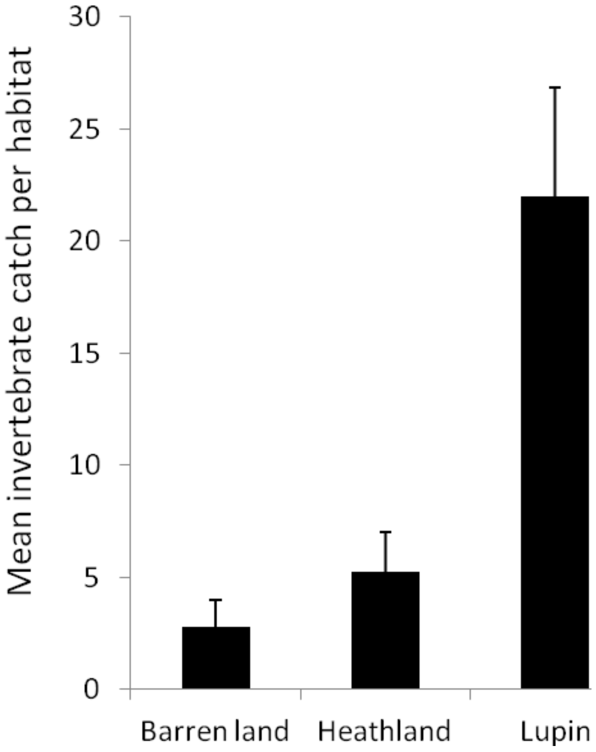

Figure 6. The mean catch of foliar invertebrates by sweepnet in barren land, heathland and in lupin. Bars are 1 SE.

Effect of revegetation with exotic versus native plant species on invertebrate fauna

BRYNJA DAVIDSDOTTIR[1], GUDMUNDUR HALLDORSSON[2], TOMAS GRETAR GUNNARSSON[3] AND BJARNI D. SIGURDSSON[1]

[1] *Agricultural University of Iceland, Hvanneyri, IS-311 Borgarnes, Iceland (brynjad@live.com)*
[2] *Soil Conservation Service of Iceland. Gunnarsholt, IS-381, Hella Iceland (gudmundur.halldorsson@land.is)*
[3] *University of Iceland, South Iceland Research Centre. Tryggvagata 36, IS-800 Selfoss and Gunnarsholt, IS-851 Hella, Iceland (tomas@hi.is)*

ABSTRACT
Iceland has the highest rate of soil erosion and desertification in Northern-Europe. In order to combat this extensive areas have been revegetated with different methods. We studied the effect of revegetation on invertebrate density and group composition, comparing: a) unvegetated eroded areas, b) native heathlands restored on eroded land and c) exotic Nootka lupin (*Lupinus nootkatensis*) stands established on eroded land. Invertebrates were collected by two methods, in pitfall traps and by sweep net. Revegetation was shown to positively affect invertebrate densities. The average invertebrate numbers per sweepnet were 1.9 on barren land, 22.3 on heathland and 58.2 in Nootka lupin. The average numbers of invertebrates per pitfall trap per day were 0.8, 1.6 and 3.3 individuals on barren land, heathland and Nootka lupin, respectively.Catches in pitfall traps and sweep nets were strongly correlated. The composition of invertebrate groups was found to be strongly affected by the revegetation method; mites and spiders dominated on restored native heathlands but beetles, spiders and snails were most abundant in the exotic lupin stands. Only few invertebrates, mostly beetles and spiders, were found on unvegetated eroded land.
Keywords: Barren land, heathland, invertebrates, lupin, rehabilitation, restoration.

YFIRLIT

Áhrif landgræðslu á smádýralíf: samanburður á lúpínu og endurheimt staðargróðurs.

Á Íslandi hefur átt sér stað ein mesta jarðvegseyðing og eyðimerkurmyndun sem finnst í Norður-Evrópu. Til að sporna gegn áhrifum jarðvegseyðingar hafa mikil landsvæði verið grædd upp með mismunandi aðgerðum. Gerður var samanburður á smádýralífi í: a) ógrónu landi, b) mólendi sem endurheimt hafði verið á ógrónu landi og c) lúpínubreiðum sem ræktaðar höfðu verið á ógrónu landi. Smádýrum var safnað í fallgildrur og háf. Smádýrum fjölgaði verulega í kjölfar landgræðsluaðgerða. Meðalveiði smádýra í háf var 1.9 dýr á ógrónu landi, 22.3 í mólendi og 58.2 í alaskalúpínu. Meðalveiði í fallgidru á dag var 0.8, 1.6 og 3.3 smádýr á ógrónu landi, á mólendi og í alaskalúpínu.Marktæk jákvæð fylgni var milli smádýrafjölda sem veiddist í fallgidrur og háf. Samsetning smádýrahópa var breytileg milli gróðurlenda. Mítlar og köngulær voru algengust í endurheimtu mólendi en bjöllur, köngulær og sniglar voru algengust í lúpínu. Fá smádýr fundust á ógrónu landi, algengustu hóparnir þar voru bjöllur og köngulær.

INTRODUCTION

Iceland currently has the highest rate of erosion in Northern-Europe, eroded land and deserts now cover 40% of the country's surface as opposed to an estimate of 5 – 15% at the time of settlement (Arnalds 2011). Unaided, repair of eroded areas through natural succession can take decades to hundreds of years in Iceland (Gretarsdottir et al. 2004). Organized revegetation efforts started in Iceland in 1907 (Crofts 2011) following a law on combating erosion inacted the same year and the foundation of The Soil Conservation Service of Iceland (UOA 2013). The most common method is protection from grazing alone or combined with top dressing of fertilizers and sowing of mixed grass seeds (Halldorsson et al. 2011a). With time, this results in the restoration of local vegetation cover of native heathland species, as the seeded species disappear (Gretarsdottir et al. 2004, Aradottir et al. 2008).

Sowing of the introduced, nitrogen-fixing Nootka lupin (*Lupinus nootkatensis* Donn ex Sims) has also been successfully used in Iceland for revegetation and sand binding (Halldorsson et al. 2011). In Iceland the Nootka lupin forms vast fields on eroded areas resulting in a novice ecosystem dominated by lupin with few coexisting plant species, at least for some decades before it often is replaced by either native or other exotic plant species (Magnusson et al., 2001, 2002; Magnusson 2010). The use of this exotic plant has been controversial and is increasingly questioned by the public and authority in recent years (IINH & SCS 2010; Petursdottir et al. 2013). The Nootka lupin can disperse over established heathland in Iceland reducing the number of plant species (Magnusson et al. 2001, 2002) To date, Nootka lupin can be found in all parts of the country (IINH & SCS 2010) and has recently been recognized as an invasive species in Iceland (Magnusson 2010; Nobanis 2012). It has been shown in Iceland (Magnusson et al. 2001, 2002) and abroad (Bishop 2002) that lupins can influence successional rates and directions.

Considering and increasing the understanding of ecosystem functioning such as food webs and the interactions among species, makes restoration and revegetation efforts more likely to become successfull (Richardson et al. 2000; Memmot, J. 2009; Ása Aradóttir 2011). Invertebrates have important roles in ecosystem functioning. They participate in nutrient cycling as detrivores and herbivores, but they also have key roles as seed dispersers, predators, parasites, ecosystem engineers and pollinators (Forup et al. 2008; Losey & Vaughan, 2006; Weisser & Siemann 2004). Invertebrates are also an important link in the food chain for birds (Robel & Xiong 2001) and small mammals.

Invasive plant species can disrupt and change established ecosystem function between invertebrates or animals and native plants, with a cascading negative effect on population growth of native plants and pollinators or other animals (Traveset & Richardson 2006). In Iceland Nootka lupin stands are known to attract and sustain a high abundance of birds, invertebrates and soil arthropod life compared to eroded land in Iceland (Sigurdardottir 2002; Oddsdottir et al. 2008, Gunnarsson & Indridadottir 2009). Few surveys have been made on the opposed difference in faunal composition and density in restored habitats with native plant species opposed to revegetated areas with exotic species in Iceland.

The present study was a part of a larger study on the effect of different revegetation methods on invertebrate fauna and birdlife in Iceland (Davidsdottir et al. 2013). That study used solely sweep net to to sample invertebrates in 26 sites around Iceland (Davidsdottir et al. 2013). The scope of the present study was to compare invertebrate density in subset of the sampling areas used by Davidsdottir et al. (2013) using two different sampling methods: sweep net and pitfall traps. The sweep net method is known to catch only certain groups of invertibrates (Majer et al 2007; Davis & Ustrup 2010; Standen 2000), whereas other groups which are often important food source of birds are not caught. It was, however, an open question if catches in pitfall traps would correlate with catches in sweep nets under Icelandic conditions. Furthermore, the pitfall trap method was used to gather information on invertebrate group composition in habitats revegetated by different methods. We were interested in comparing the effect of restoration of native heathlands and revegetation with exotic species, such as Nootka lupin, on invertebrate group-assembly and abundance.

MATERIALS AND METHODS

Iceland (63-66°N) is a volcanic island of about 100.000 km^2 in the North-Atlantic Ocean. It has an oceanic climate, with 0 to -3 °C mean temperature during winter and 8-10 °C during summer in areas < 400 m a.s.l. (Björnsson et al. 2007). The annual precipitation comes rather evenly throughout the year with an annual average of 1226 mm at Hella, the local weather station of the survey area (Vedurstofa Íslands 2013). The soil consists mainly of volcanic Histic, Gleyic and Brown Andosols (>50% of the area) and Virtisols (30%; barren areas) (Arnalds 2004).

Comparative invertebrate studies were carried out in 5 different survey areas in S-Iceland, Bolholt, Dímon, Geitasandur, Gilsbakki and Markarfljótsaurar, from 29 May to 14 August 2011. Each survey area consisted of three habitat types (Table 1.): i) Barren land, a result of erosion in past centuries, still in early stages of secondary succession. ii) Young heathland on formerly barren land, in the process of restoration, either by passive measures that enhance secondary succession or by initial application of fertilizers and/or grass seeds during the past 50 years. iii) Areas revegetated with the introduced Nootka lupin within the past 50 years.

The three habitat types within each survey area were all close to each other (< 5 Km) and at similar elevation. The sequence of visits to habitat types was at random each day. At each visit, date, time of day, wind speed, temperature and cloud coverage was recorded. Photos were taken of each habitat type and the gps location of sweep netting and trapping points were noted.

Invertebrate sampling and analysis

Sampling took place both with sweep nets and pitfall traps in each survey area. During sweep-netting invertebrates were sampled at every habitat type in a standardized fashion with three repetitions during each sampling (cf. Davidsdottir et al. 2013). The hand held sweep net had a diameter of 39 cm and mesh size 0.3 mm. The net was swept over the surface of each habitat type with ten, non-overlapping 2 m long strokes within a 50 m radius of the pitfall-traps (see later). This was repeated three times over the summer in every habitat type. The weather conditions during sweep net sampling varied from 1.0 to 10 °C, with wind speeds of 1-8 m/sec. The number of caught diptera, moths and spiders (>3 mm) were recorded and the animals then released. Other very occasional invertebrates such as caterpillars and those smaller than 3 mm in diameter were excluded from counts. We used the total sum of the three catches per area/day for further calculations of the average number of invertebrates caught over the summer in each of the three habitat types.

Pitfall traps were laid out from 14 and 15 June and retrived on 14 August 2011, during which they were emptied three times. Each trap was a 250 ml cup with an opening of 100 mm in diameter. Approximately 100 ml of anti-freeze was poured into each cup to kill and preserve the caught invertebrates. The cups were dug into the ground so their rim was level to the surface. Plastic lids were fixed with metal rods 15-20 mm above the cups to stop rain, sand

and undesired objects from falling into the traps (Olafsson & Ingimarsdottir 2007). Two traps were laid out in Nootka lupin and heathland habitats, but four in every barren area. This was done since wind was expected to blow the lids off some of the traps in the barren areas but two traps, chosen at random, were used for analysis of invertebrate catch. Where livestock had interfered with traps, these were excluded from analysis, resulting in 21 pitfall counts from heathland compared to the total of 30 pitfall counts in Nootka lupin and barren land. The total catch from each study site was summed up and divided by the number of days each trap had been active, to then obtain the mean catch per trap-day per habitat type. Invertebrates smaller than 3 mm were excluded from analyses. Also dipteral flies were excluded from analyses as the traps were aimed at surface active invertebrates (Standen 2000).

RESULTS

Relationship between invertebrate cactches by sweep-net and pitfall traps

The average daily catch of invertebrates, caught in sweep-net at the same location where the pitfall traps were placed, was used to estimate the correlation between the two techniques (Figure 1). There was a significant positive correlation of invertebrate numbers between the two methods ($r = 0.850$, $P < 0.001$; Figure 1).

The effect of revegetation on invertebrate density

We first estimated the over all differences in the total invertebrate numbers and group sizes between the three habitat types (barren land, heathland and Nootka lupin). Since the data did not always meet the requirement of normal distribution, we used a non-parametric Kruskal-Wallis test to compare invertebrate density of all groups, both from pitfall traps and sweepnet, and Mann-Withney U-test to make pairwise comarisons between habitat types. A significance limit of $P<0.10$ was used.

The overall invertebrate abundance increased significantly by revegetation irrespective of revegetation method and sampling method (Figures 2 and 3; Tables 2 and 3). When caught with sweep net, the invertebrate numbers increased 12 and 33 fold from barren land to restored heathland and with revegetation by Nootka lupin, respectively (Figure 2). When caught in pitfall traps, the increase from barren land was 2.1 and 4.4 fold higher for restoration of heathland and revegetation by Nootka lupin, respectively (Figure 3). Total catches of invertibrates were also significantly higher in Nootka lupin than in restored heathland, both when measured in sweep nets or pitfall traps (Tables 2 and 3).

The effect of revegetation on invertebrate group composition

Three main groups of invertebrates were caught by sweep net: flies (Diptera), spiders (Arachnida) and moths (Lepidoptera). Flies were the most abundant group (Table 4). There was a significant difference in the increase of all three invertebrate groups beteen habitat types, ($P < 0.001$) both where barren land had been restored to heathland and where revegetated by Nootka lupin (Table 3). No spiders or moths were caught on unvegetated land and spiders were almost exclusively caught in Nootka lupin (35 in total but only one on heathland). Flies were 2.7 times more abundant in lupin than on heathlands with a significant diference between the two vegetation types (Table 3, Table 4).

The invertebrates caught in pitfall traps were devided into seven groups: spiders, beetles (Coleoptera), mites (Acari), slugs and snails (Gastropoda), moths, earthworms (Lumbricus) and a group including other invertebrates (Table 5). The proportion and composition of invertebrate groups in pitfall traps differed between the three habitat types (Table 2, Table 5, Figure 4).

On unvegetated land beetles and spiders were the most abundant groups, on heathland spiders and mites were most abundant where as in Nootka lupin beetles, spiders and gastropods were the most abundant invertebrates (Figure 4). There was no significant difference in the abundance of mites between habitats (Table 2). Significantly more moths were found in heathland than on barren land. Beetles, slugs and moths were significantly more abundant in lupin than on barren land (Table 2). Significantly higher number of beetles and slugs were in Nootka lupin revegetations compared with heathland restorations (Table 2).

DISCUSSION

Sampling methods

It has been shown that more than one method of invertebrate sampling is often needed to access the relative effects of restoration on different invertebrate groups (Standen 2000; Majer et al 2007; Davis & Ustrup 2010). Here two methods were used, sweepnet for sampling foliar and flying invertebrates and pitfall traps for sampling surface active invertebrates. The results, with highly significant positive correlation between total catch by the two methods, show that sampling by sweep-net through vegetation is an indicator of the abundance of surface invertebrates. As sampling by sweepnet is a fast method, giving single visit estimates of invertebrate abundance, this finding has practical implications for studies comparing invertebrate abundance between sites and habitats in Iceland.

Invertebrate group composition on native barren land and heathland

The composition of invertebrate groups on barren land was in coherence with other studies in Iceland (Magnusson et al. 2009) and our results showed lowest numbers of invertebrates on barren land with none of the caught invertebrate groups being most common on barren land.

The aboveground invertebrate fauna in mature Icelandic heathlands consists largely of dipteral flies, spiders and beetles (Ingimarsdottir et al. 2007; IINH 2009). In our study heathland was in the early successional stages from barren land, but the composition of invertebrates still differed significantly in the two habitats.

In restored heathlands flies were significantly more abundant than on barren land and the abundance of surface active invertebrates was double in numbers compared to that of barren land. The dominating invertebrate groups resembled that of what has been described as mature heathland invertebrate group assembly (Ingimarsdottir et al. 2007), indicating a positive restoration process of invertebrate fauna. Such changes are clear signs of successful ecological restoration (Forup 2008).

Effects of revegetation on invertebrates and higher trophic levels

Restoration methods have varying effects on the establishment of invertebrate fauna, depending on timescale, dispersability of invertebrates (Majer et al. 2007; Woodcock et al. 2012a), distance to the pool of import species (Sunderman et al. 2011) and methods used during the restoration process (Davis & Utrup 2010; Woodcock et al. 1012b). Given the importance of functional groups of invertebrates in ecosystem services, we found it important to access the effect of different revegetation actions on invertebrate numbers and group compositions between habitats in this study.

Our results showed that while both revegetation methods had positive effects on invertebrate abundance, group composition of invertebrate fauna showed different development between the two methods. Similar findings were recored by Davidsdottir et al. (2013) on bird population sizes and composition in a larger study, which also included the same study sites.

Other studies on invertebrate life in revegetated habitats in Iceland have shown an increase in beetle and soil arthropod numbers compared with unvegetated reference sites (Friðriksson et al. 1976; Oddsdóttir et al. 2008; Halldorsson et al. 2004). Oddsdottir et al. (2008) also showed that the group composition of soil arthropods on barren land changes with revegetation action and differs between revegetation methods. While mites have been shown to be codominant with springtails in grass sowings, springtails dominated in Nootka lupin areas (Oddsdottir et al. 2008). Prior studies on earthworms in Nootka lupin stands also show a significant increase in earthworm density and diversity compared with barren land (Sigurdardottir 2004).

Although invasive plants have been shown to decrease biodiversity they can have a boosting effect where none is left of the native vegetation (Richardson et al. 2000). The latter was evident in our study, as invertebrate numbers were significantly highest in Nootka lupin stands. Invertebrate group assembly also differed in Nootka lupin stands to that of heathland. The main difference being a higher presence of slugs and snails and three times higher beetle numbers in Nootka lupin than on heathland and more moths and spiders. These results were mirrored in higher total bird densities in Nootka lupin patches than restored heathlands in Iceland (Davidsdottir et al. 2013). Another comparative study on bird density on barren land and Nootka lupin in Iceland show an increase in bird density and diversity with the revegetation of lupin (Gunnarsson & Indridadottir 2009). These studies suggested a successional gradient in colonisation of birds, with Nootka lupin patches first occupied by species such as Meadow Pipit which exploit foliar arthropods, later followed by some wader species exploiting earthworms in older established Nootka lupin stands (Sigurðardóttir 2004; Gunnarsson & Indridadottir 2009).

In Iceland flies serve an important role of pollination but in the larval state many of them are detrivores and grazers (IINH 2013a). Fly numbers were higher in restored heathland and in Nootka lupin stands than on barren land. Moths were also more abundant in restored sites, although not found in high numbers. Catterpillars of some moth species in Iceland are known to be voracious grazers both in Nootka lupin (IINH 2013a) and heathland, at times drasticly affecting leaf cover of Nootka lupin and woody heathland plants in occasional outbreaks (Halldórsson et al. 2011b).

Mites, either detrius feeding or predatory forms are one of the first colonisers on virgin ground/ new surfaces in Iceland and appear within 60 years after glaciers retreat (Ingimarsdottir et al. 2012). In restored habitats mites tend to have a higher species number and density in older restoration areas than in young ones (Cuccovia & Kinnear 1999). This has been related to higher plant species richness, increased canopy height and litter cover (Cuccovia & Kinnear 1999). The abundance of mite on heathland did, however, not differ significantly to that of barren land in this study. The lack of a response might be explained by the fact that our heathland habitats were still in early stages of succession, but also that mites smaller than 3 mm were excluded from analysis.

The functional roles of beetles found in Iceland can be detrivorous, herbivorous, omnivorous or predators (IINH 2013b) as well as pollinators. Halldorsson et al. (2004) describe a higher abundance of beetles in restoration sites and Nootka lupin fields in Iceland than on unvegetated control sites. This is also known to occur with time within forest plantations in the same area as the present study (Jonsson et al. 2005). Our results did not reflect this in the restored heathlands. We, however, found beetles to become more common in Nootka lupin stands than on barren land, which was in accordance with prior findings (Halldorsson et al. 2004).

Reflections on the effect of slugs and snails in Nootka lupin revegetation areas

Lupins are highly accepted by slugs (Brooks et al. 2003), which can affect various states of lupin growth (Ferguson 1994). Slug grazing has been shown to change plant species assembly, enriching forb cover with time and increasing plant species richness (Buschmann et al. 2005).

Nootka lupin stands in Iceland commonly retreat with time, often replaced by grasses and flowering plants (Magnusson 2002; 2003), but the successional trjajectory differs between different parts of Iceland (Magnusson et al. 2001). We would like to suggest that slugs may have an important, but currently overlooked effect on succession of Nootka lupin in Iceland. The effects of slugs may be different with Nootka lupin stand age: Firstly: Slugs in younger Nootka lupin stands may have some effects on the low number of coexisting vascular plant species (Magnusson 2001) through selective grazing (Hanley et al. 1996; Buschmann et al. 2005; Lanta 2007; Strauss et al 2009; Hitchmough & Wagner 2011). Secondly: Varying slug densities could influence the regeneration possibilities of Nootka lupin in older stands, which again could affect how fast Nootka lupin is replaced by native plant species, and also could possibly partly explain the different successional trjajectories of Nootka lupin in different parts of Iceland (Magnusson et al. 2001). Thirdly: Slug density possibly diminishes again in retreating Nootka lupin stands, resulting in the reappearance of common native plants found in the seedbank (Magnusson 2001, Eyþórsdóttir 2009) or can easily recolonize the new area. Some of these same plant species have been shown to reappear after the removal of slugs in other ecological studies (Hanley et al. 1996).

CONCLUSIONS

The two invertebrate sampling methods, pitfall traps and sweepnet, showed a significant positive correlation. Meaning that invertebrate numbers caught by sweepnet can indicated the over all productivity of surface active invertebrates, not commonly caught by this method.

The significant increase of invertebrate density and the group assembly found on restored heathlands compared with barren lands indicated a succsessfull restoration process of early successional native heathland.

Where barren lands had been revegetated by Nootka lupin, an extremely productive but novice ecosystem had developed, with great numbers of beetles and snails.

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TABLES AND FIGURES

Table 1. Description of study sites.

Habitat	Description	Dominating/characteristic plants
Barren land	Very sparsely vegetated land on sand or gravel.	*Agrostis vivealis*, *Festuca rubra*, *Phleum pratensis*, *Thymus praecox* ssp. *arc*
Heathland	Dry young heath land on prior sand plains re-vegetated by fertilisation and sowing of grass seeds or by self regeneration. Cover of native species, varying from biological crust with spares grasses, sedges and rushes, moss and lichen to a homogenous coverage of grasses and/or moss with sparse dwarf shrubs. Often subject to grazing.	Moss, lichen, grasses, sparse low *Empetrum nigrum*, *Vaccinum* spp. and *Salix* ssp.
Nootka lupin	Fields consisting of varying ages and densities of introduced and sowed *Lupinus nootkatensis* with bare patches or native grasses amongst lupin plants.	Nootka lupin *Lupinus nootkatensis*

Table 2. Results of statistical analysis comparing daily catches of pitfall traps (P-values) of differences between eroded barren lands (B), restored heathlands (H) and revegetated Nootka lupin stands (L). As presented in Figure 3 (mean number of invertebrates) and Figure 4 (proportional composition). The tests used were Kruskal-Wallis test (KW test) to compare all groups and Mann-Withney U-test (MW-U test). Significant differences (P<0.10) are indicated in bold font.

Vegetation	Test	Density	Relative catch					
			Arachnea	Coleoptera	Gastropoda	Acari	Lepidoptera	Lombricus
All groups	KW test	**0.01**	0.11	**0.01**	**0.002**	0.57	**0.02**	0.10
B-H	MW-U test	**0.07**	-	0.12	0.32	-	**0.01**	-
B-L	MW-U test	**0.009**	-	**0.009**	**0.007**	-	**0.04**	-
H-L	MW-U test	**0.08**	-	**0.03**	**0.005**	-	0.42	-

Table 3. Results of statistical analysis comparing sweepnet catches (P-values) between eroded barren lands (B), restored heathlands (H) and revegetated Nootka lupin stands (L). As presented in Figure 2 (mean number of invertebrates). The tests used were Kruskal-Wallis test (KW test) to compare all groups and Mann-Withney U-test (MW-U test). Significant differences (P<0.10) are indicated in bold font.

Vegetation	Test	Density	Relative catch		
			Diptera	Arachnea	Lepidoptera
All groups	KW test	**<0.001**	**<0.001**	**<0.001**	**<0.001**
B-H	MW-U test	**0.002**	**0.002**	**0.005**	**0.006**
B-L	MW-U test	**<0.001**	**<0.001**	**<0.001**	**<0.001**
H-L	MW-U test	**0.03**	**0.045**	**0.04**	**0.048**

Table 4. Total sum of individual invertebrates, by taxonomic group, caught in sweep-nets on three occasions in each habitat type on the five survey areas in each habitat.

Habitat	Diptera	Arachnea	Lepidoptera	Grand total
Barren land (5)	29	0	0	29
Heathland (5)	338	1	3	342
Lupin (5)	912	35	4	951

Table 5. Mean numbers of individuals of the most common invertebrate groups per pitfall trap per day (with standard error).

	Arachnea	Coleoptera	Gastropoda	Lepidoptera	Lombricus	Acari	Other
Barren land	0.2 (0.08)	0.4 (0.08)	0.0 (0)	0.0 (0.01)	0.0 (0)	0.1 (0.03)	0.0 (0.01)
Heathland	0.5 (0.09)	0.3 (0.16)	0.0 (0)	0.0 (0)	0.0 (0)	0.7 (0.31)	0.0 (0.01)
Lupin	0.5 (0.09)	1.2 (0.30)	0.4 (0.16)	0.0 (0)	0.0 (0.03)	0.0 (0.04)	0.1 (0.04)

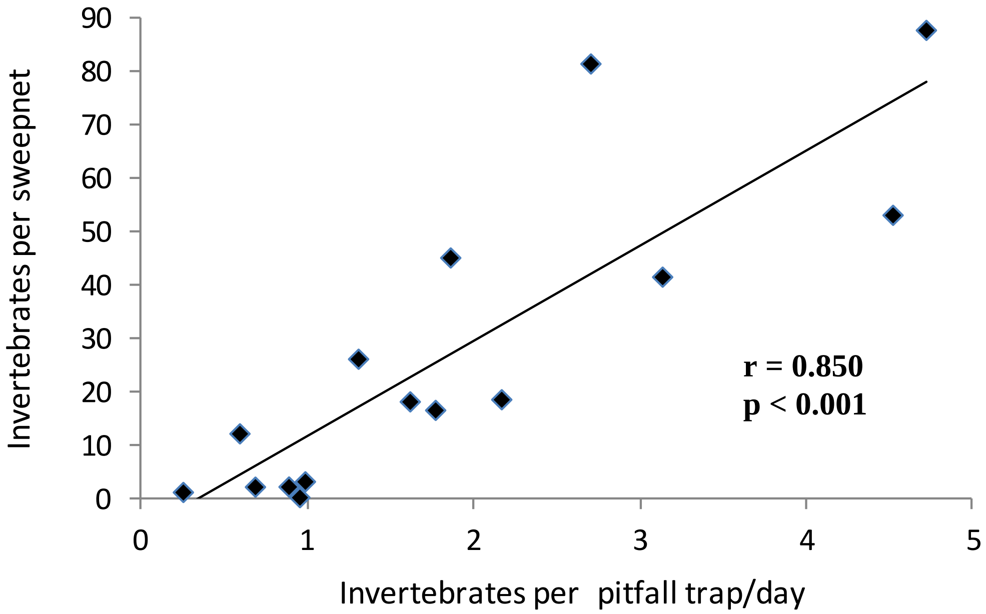

Figure1. Correlation between the mean number of invertebrates caught by pitfall traps per day (excluding diptera) and the mean number of invertebrates caught by sweep-net over three occasions in the same study plots on barren land, heathland and in lupin stands. The line is fitted by least squares (y = 17.893x – 6.0776).

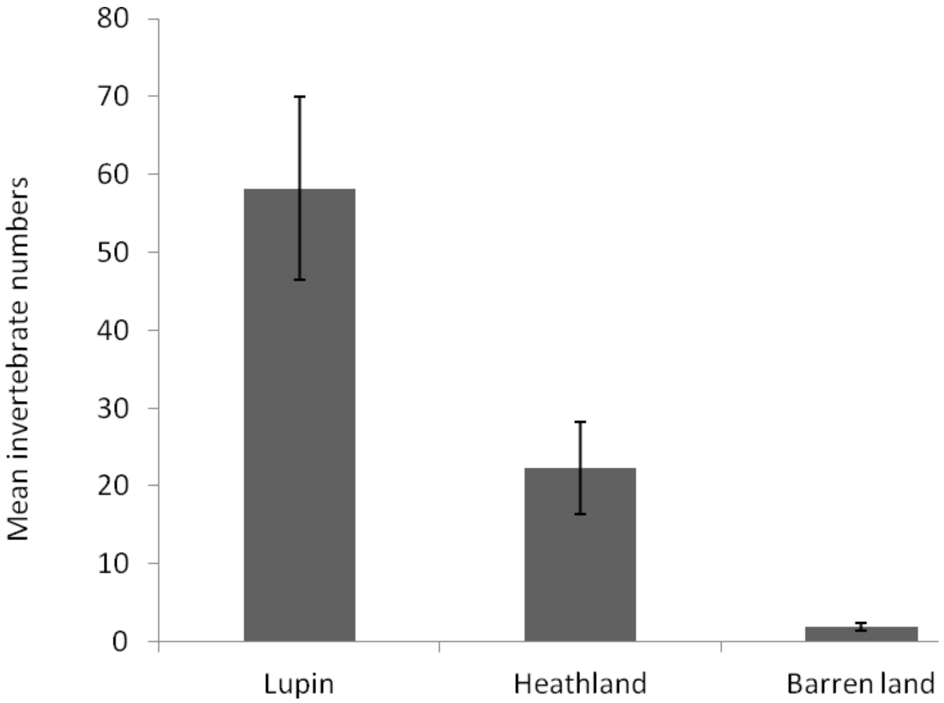

Figure 2. The mean number of invertebrates caught by sweepnet in each habitat. With standard error bars.

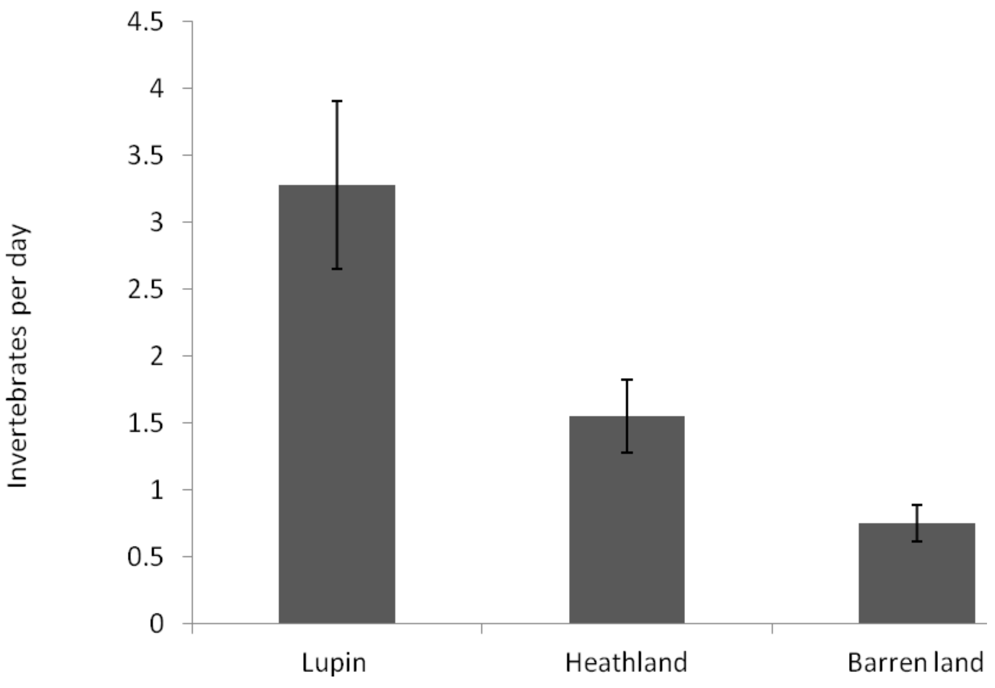

Figure 3. The mean numbers of invertebrates caught in a pitfall trap per day per study site, in each habitat type. With standard error bars.

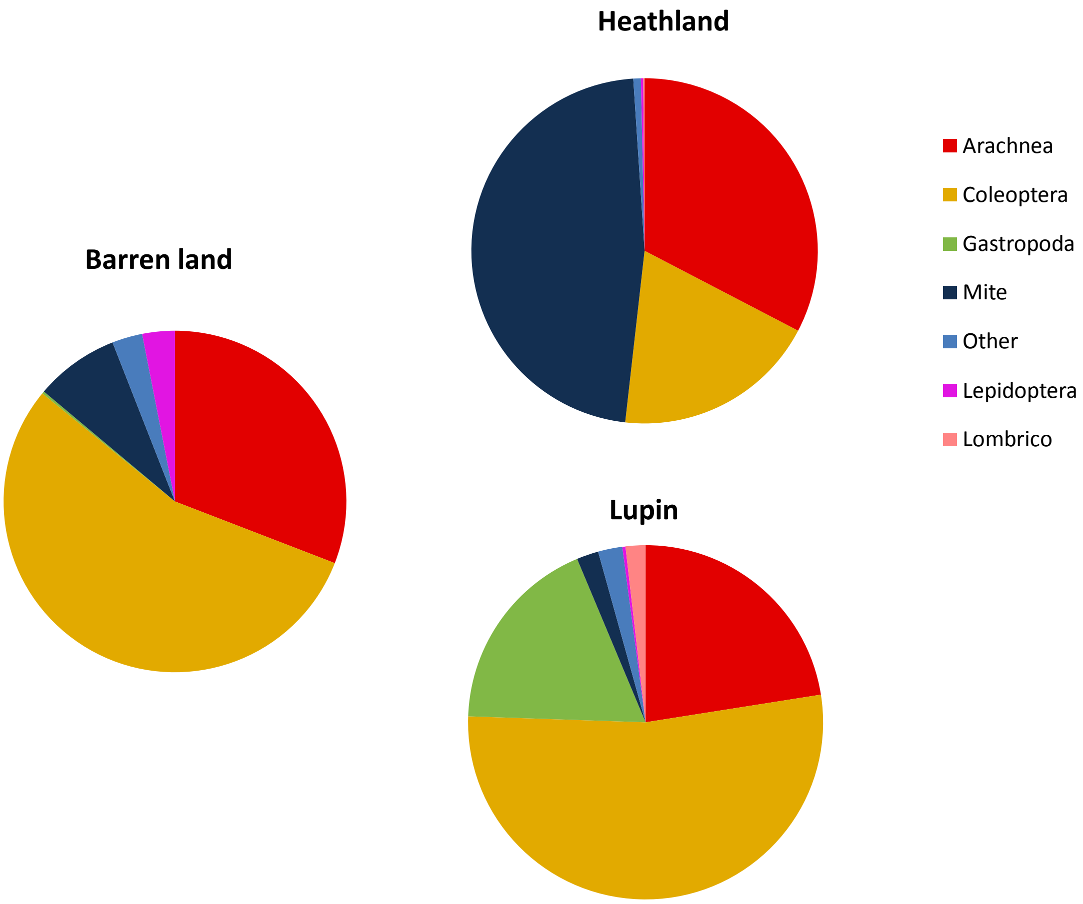

Figure 4. The proportional composition of invertibrate catch in pitfall traps in each habitat.