Animal diversity around Mt Hekla: roles of land degradation and succession

Heiða Gehringer

Faculty of Life and
Environmental Sciences
University of Iceland
2013

Animal diversity around Mt Hekla: roles of land degradation and succession

Heiða Gehringer

90 ECTS thesis submitted in partial fulfillment of a
Magister Scientiarum degree in biology

Advisors
Tómas Grétar Gunnarsson
Hreinn Óskarsson

Faculty of Life and
Environmental Sciences
School of Engineering and Natural Sciences
University of Iceland
Reykjavik, 14 may 2013

Animal diversity around Mt Hekla: roles of land degradation and succession
90 ECTS thesis submitted in partial fulfillment of a *Magister Scientiarum* degree in biology

Faculty of Life and Environmental Sciences
School of Engineering and Natural Sciences
University of Iceland
Askja, Sturlugata 7
101, Reykjavík
Iceland

Telephone: 525 4000

Bibliographic information:
Heiða Gehringer, 2013, *Animal diversity around Mt Hekla: roles of land degradation and succession*, Master's thesis, Faculty of Life and Environmental Sciences, University of Iceland, pp. 53.

Printing: Háskólaprent
Reykjavik, Iceland, June 2013

Abstract

Land degradation is one of the major environmental issues of the 21st century, caused mainly by overgrazing, agricultural practices and deforestation that often lead to soil erosion. Soil erosion results in the loss of soil nutrients and water holding capacities and in decreasing biodiversity and maintenance of soil erosion. These cycles can be reversed by adding nutrients to the soil and re-establishing vegetation.

About 40% of Iceland is severely eroded and soil- and vegetation conservation is a priority. Vegetation reclamation supports vegetation succession and restoration of biodiversity. The abundance and communities of animals, like birds and invertebrates, are strongly linked to vegetation succession and reflect reclamation success. In this large-scale study, animal biodiversity was linked to vegetation types at different stages of succession in the vicinity of Mt. Hekla which is one of the most severely eroded areas in Iceland. The study area, which covers 1% of Iceland is under great impact from the very active Hekla volcano and is a venue for a large scale birch woodland restoration program (Hekluskógar).

The aim of the study was to explore the links between animal biodiversity and erosion/succession patterns which are poorly known in Iceland and to serve as yardstick on which to estimate the effect of restoration efforts and volcanism in the area.

Birds were counted on transects in total of 59 study sites in 6 habitat types, at different stages of vegetation succession (barren land, moss, grassland, heathland, wetland and tall vegetation) and invertebrates were caught in pitfall traps in 36 sites. Density and communities of birds and the abundance, diversity and biomass of invertebrates were estimated.

The density of birds increased with vegetation succession, from 22.6 birds/km^2 (SE= 11.3) on barren land to 201.3 birds/km^2 (SE= 106.4) on wetland. Invertebrates catches varied from 6.4 animals/trap/day (SE= 0.83) on barren land to 19.5 animals/trap/day (SE= 2.32) in grassland. Bird diversity was lowest in barren land and highest in wetland but invertebrate diversity was lowest in moss and highest in tall vegetation. Invertebrate biomass was on the other hand lowest in barren land (2.99 mg/trap/day, SE= 1.25) but highest in wetland. (23.1 mg/trap/day, SE= 9.74). In all, wetland supported the most animal density and diversity, although habitats overlapped to some extent. Although there was a relatively high variation in measurements within habitats, the study showed a clear general increase the abundance and diversity of birds and invertebrates with increasing vegetation cover and succession.

Útdráttur

Landeyðing er eitt af stærstu umhverfisvandamálum 21. aldarinnar. Helstu drifkraftar landeyðingar eru ofbeit, landbúnaður og skógarhögg, sem getur orsakað jarðvegsrof. Jarðvegsrof getur á móti valdið því að næringarefni tapast úr jarðvegi og vatnsheldni minnkar. Þannig minnkar líffræðilegur fjölbreytileiki og jarðvegsrofið viðhelst. Hægt er að sporna við þessu með því að auka næringarefnamagn jarðvegsins og endurheimta gróðurþekju.

Jarðvegsrof á Íslandi er mikið á um 40% landsins og er landgræðsla og endurheimt vistkerfa forgangsatriði. Uppgræðsla styður við framvindu gróðurs og endurskapar líffræðilega fjölbreytni. Gróðurframvinda hefur mikil áhrif á þéttleika og samfélög dýra eins og fugla og hryggleysingja og því geta mælingar á þeim verið metill á framvindustig eða árangur vistheimtar. Þessi rannsókn tengir saman fjölbreytni dýra við gróðurfar á mismunandi framvindustigum á svæði sem hefur hvað mest jarðvegsrof á Íslandi. Rannsóknarsvæðið er um 1% landsins og er í nágrenni Heklu og afmarkast af starfssvæði Hekluskóga þar sem stendur yfir umfangsmikið skógræktarverkefni. Á svæðinu eru mikil áhrif af eldvirkni Heklu og fleiri virkra eldstöðva.

Markmið rannsóknarinnar var að rannsaka lítt kunn tengsl dýrafjölbreytni við rof- og framvinduferla á Íslandi, en einnig til samanburðar í framtíðinni til að meta áhrif skógrækar og eldvirkni á lífríki svæðisins.

Fuglar voru taldir á samtals 59 sniðum í 6 mismunandi búsvæðagerðum á mismunandi gróðurframvindustigum (lítt gróið, mosi, graslendi, mólendi, votlendi og kjarr-og lúpína). Hryggleysingjar voru veiddir í fallgildrur á 36 stöðum í sömu búsvæðum og fuglar. Þéttleiki, fjölbreytni og samfélög fugla ásamt þéttleika, fjölbreytni og lífmassa hryggleysingja voru metin.

Þéttleiki fugla jókst með gróðurframvindu, úr 22,6 fuglum/km^2 (SE= 11,3) í 201,3 fugla/km^2 (SE= 106,4) og veiðni hryggleysingja frá 6,4 dýrum/gildru/dag (SE= 0,83) í lítt grónu landi í 19,5 (SE= 2,32) í graslendi. Fjölbreytileiki fugla var lægstur í lítt grónu landi og hæstur í votlendi en fjölbreytileiki hryggleysingja var lægstur í mosa og hæstur í kjarri- og lúpínu. Lífmassi hryggleysingja var samt sem áður minnstur í lítt grónu landi (2,99 mg/gildru/dag, SE= 1,25) en hæstur í votlendi (23,1 mg/gildru/dag, SE= 9,74). Í heildina var þéttleiki og fjölbreytileiki dýra mest í votlendi, þó skörun á milli búsvæða hafi verið talsverð. Þrátt fyrir breytileika á mælingum innan búsvæða, sýnir rannsóknin greinilega aukningu á þéttleika og fjölbreytileika fugla og hryggleysingja með aukinni gróðurþekju og framvindu.

Table of Contents

List of Figures

List of Tables

Acknowledgements

I wish to express my deepest gratitude to Dr. Tómas Grétar Gunnarsson and Dr. Hreinn Óskarsson for their patient guidance, enthusiastic encouragement and useful critiques of this research work. Their willingness to give their time so generously has been very much appreciated.

Special thanks go to Guðmundur Halldórsson and Erling Ólafsson for their help with invertebrate identifications and to landowners in the Hekluskógar area, for their kind cooperation.

The generous financial support from Hekluskógar and Landsvirkjun is truly appreciated.

Last but not least I would like to thank my family, especially Dagbjört Sævarsdóttir, Erla Þorsteinsdóttir, Kristbjörg Bjarnadóttir and Svava Friðriksdóttir for taking care of my children during field work and long hours at school, and of course my wonderful soon to be husband, Róbert Aron Pálmason, for all his support and understanding.

1 Introduction

1.1. Land degradation

Land degradation is one of the major environmental issues of the 21st century because of its impact on food security and environmental quality (Millennium Ecosystem Assessment, 2005).

The term “Land degradation” is often described as a biophysical process by which productivity in both land and water resources is negatively impacted, resulting from an increasing anthropogenic pressure on the land rather than from natural events (H. Eswaran, Lal, & Reich, 2001; Johnson & Lewis, 2007) while other definitions integrate the two processes (Reynolds, Maestre, Kemp, Stafford-Smith, & Lambin, 2007). Drylands or lands characterized by low rainfall, extreme air temperatures, and seasonally high evaporation rates, are especially prone to land degradation. These lands cover about 40% of the Earth, and suffer often from soil erosion, shifts in natural fire cycles and vegetation loss (Reynolds et al., 2007).

The three main causes of land degradation are overgrazing, destructive agricultural practices and deforestation (Hari Eswaran & Dumanski, 1994). The main consequence of these drivers is soil erosion (Ravi, Breshears, Huxman, & D'Odorico, 2010); the detachment and transport of soil particles and subsequent redeposition in near or distant areas, driven by the forces of wind and water (e.g. (Oldeman, 1992). These processes can reduce the productivity of the soils either or both physically or chemically (Oldeman, 1992). Recently, studies have shown an interaction between these aeolian and fluvial drivers (e.g. (Field, Breshears, & Whicker, 2009; Ravi et al., 2010) and they often occur in association with other weathering processes like freezing and thawing (Ó. Arnalds et al., 1997; Morgan, 2005).

Water erosion is thought to be a dominant erosive factor in more humid environments (Ravi et al., 2010). Generally, if annual precipitation is between 450 and 650 mm, vegetation cover increases, leading to a better protection of the soil. Further increase in precipitation can overcome the protection provided by vegetation and cause soil erosion (Morgan, 2005). Water erosion deforms the terrain or removes the topsoil, thereby reducing the productive capacity of the soil. This kind of erosion occurs almost everywhere and is often preceded by compaction of the soil which decreases the infiltration capacity (Oldeman, 1992) although differences are seen between natural vegetation, cultivated land and bare soil (Morgan, 2005).

The second category is erosion by wind forces. Wind erosion is generally thought to be more dominant in arid environments, particularly where intense winds occur in a dry season (Ravi et al., 2010). The forces required to move particles by air are much stronger than by water (Morgan, 2005) since the specific density ratio between sand and water is lower than between sand and air (Bagnold, 1988). Because of the roughness imparted by soil, stones and vegetation, wind velocity is lower at the surface (Morgan, 2005). Wind erosion is therefore nearly always caused by a decrease of vegetation cover (Oldeman, 1992).

Human induced land degradation can also affect the environment more directly. This refers to chemical degradation, particularly the loss of nutrients and organic matter, changes in the salinity and acidity or pollution of the soil by industries or mining (Oldeman, 1992; Woods, 1987). Physical degradation is another example, e.g. the compaction of soil by heavy machinery, waterlogging and subsidence of organic soils by drainage or oxidation (Oldeman, 1992).

On the whole, soil erosion results in loss of soil nutrients, the capacity of soil to hold water, and in an overall decrease in the ability of land to sustain vegetation (Ravi et al., 2010). Land degradation can be perceived as a downward spiral where prolonged loss of vegetation cover will lead to decreased infiltration and reduced availability of soil-water for plant growth. Plant production and organic inputs into the soil decrease and temperatures become more extreme. This will negatively affect the soil fertility and deterioration of soil structure, again leading to increased erosion (Whisenant, 1999).

1.2. Drivers of land degradation

1.2.1. Anthropogenic activities

To a large extent, soil degradation is caused by the actions of people. This applies for example to deforestation or removal of the natural vegetation for e.g. agriculture, commercial forestry or urbanisation (Oldeman, 1992; Ravi et al., 2010).

Globally, overgrazing causes about 60% of the global wind erosion and 30% of water erosion, estimated by area (Oldeman, 1992). This is a result of exposing the soil to the aggressive forces of rainfall or cultivating on steep slopes without proper anti-erosion measures (Oldeman, 1992). Some studies suggest that moderate grazing increases plant species richness in productive habitats (S. H. Magnússon & Svavarsdóttir, 2007). Moderate grazing produces a degree of herbage utilization that allows the palatable species to maintain themselves but usually does not permit them to improve their productivity (Klipple & Bement, 1961). Moderate grazing means that about half of the plant material is used in well vegetated areas, but in less productive areas, moderate and sustainable grazing drops down to 35-45% use of plants (Holechek, Gomez, Molinar, & Galt, 1999). This is the result of grazing animals tearing plants out of the soil or damaging them more than in dense vegetation (S. H. Magnússon & Svavarsdóttir, 2007). Moderate grazing inhibits dominant and often tall species from blocking others. Also, grazing animals increase habitat mosaic by trampling and fertilizing (S. H. Magnússon & Svavarsdóttir, 2007), inducing nitrogen mineralization and litter decomposition (Shariff, Biondini, & Grygiel, 1994). Grazing can affect local plant species composition, through cutting of the plants or because grazers prefer some species to others (S. H. Magnússon & Svavarsdóttir, 2007). Grazing also positively affects other animals, which are adapted to open areas, by retaining the height of the vegetation (Tichit, Durant, & Kernéïs, 2005) but if grazing is intense, trampling or reduction of vegetation cover can result in decreasing density of some species like shorebirds (Norris et al., 1998).

People have been utilizing wood for at least 5000 years, but with increasing agriculture and urbanization, deforestation has also increased (Chew, 2001). This intensifies surface runoff and river discharge (Costa, Botta, & Cardille, 2003) causing nearly half of all water erosion on Earth (Oldeman, 1992). Deforestation alters elements of the ecosystems such as microclimate, soil and aquatic conditions (Yasuoka & Levins, 2007). Other kinds of land cover conversions are also distinctive drivers of land degradation. Wetland drainage for agricultural purposes is an example. These kinds of land-cover changes can e.g. affect biodiversity, trace gas emissions and hydrological balance, alter the soil and promote climate change (Meyer & Turner, 1992).

Agricultural intensification is a cause of ever growing human population with limited land for agriculture. These methods use excessive amounts of chemical fertilizers and pesticides and can increase erosion, reduce biodiversity (Giller, Beare, Lavelle, Izac, & Swift, 1997) and cause ground water pollution and eutrophication (Matson, Parton, Power, & Swift, 1997). Industrial activities have also a profound impact on land degradation (Oldeman, 1992), taking materials derived from the land and leaving waste products (Woods, 1987).

1.2.2. Environmental factors

The vast majority of studies have focused on the anthropogenic impacts on land degradation. Land degradation is of course also a natural phenomena and a number of environmental factors contribute to it. Well studied examples include climatic changes, seasonal fires and volcanism. Climatic changes that increase aridity can increase the rates of soil erosion with consequent losses of biodiversity (Ravi et al., 2010). Seasonal wildfires cause loss of nutrients, especially nitrogen and carbon, while other nutrients, like ammonium and organic nitrogen are added to the soil as ash in a readily available form (Christensen & Muller, 1975). Volcanic activity is a more intense factor, creating barren substrates by destroying vegetation. The effects can be quite diverse, depending on many factors (Dale, Delgado-Acevedo, & MacMahon, 2005). Some areas are affected by lava and some by ash and tephra depositions that contribute to soil erosion (Jost, 2006). Wind erosion has a distinctive effect on vegetation and vice versa, for plants fundamentally influence air flow patterns (Breshears, Whicker, Zou, Field, & Allen, 2009) and produce shelter. This results in increasing aeolian deposition when moving from grassland to shrubland (Breshears et al., 2009).

1.3. Natural revegetation and role of biodiversity

Disturbances and succession, that is the creation and refilling of gaps in vegetation, are two important factors that interact and often oscillate through time (Raven, Evert, & Eichhorn, 1999). Studies generally assume that there are one or more factors that constrain the growth and/or survival of organisms, leading to a change in the composition of the community through time (Tilman, 1994). These processes can be very slow if the disturbances are great (Hlynur Óskarsson, Arnalds, Guðmundsson, & Guðbergsson, 2004).

In spite of about 200 countries intention to reduce the rate of biodiversity loss by 2010 (Convention on Biological Diversity, 2002), biodiversity is still decreasing (Butchart et al., 2010). Biodiversity loss has been related to a decrease in ecosystem resilience; the ability of the ecosystem to recover from disturbances (Elmqvist et al., 2003), causing greater destruction from disturbances.

Primary succession can begin on newly formed surface or where former soil structure and perhaps nutrients and organic matter have been lost as a result of degradation (Walker & del Moral, 2003). Primary succession often happens slowly and is therefore hard to observe and experiment with. It operates more slowly than secondary succession, which is initiated from at least a vestige of an existing ecosystem (Matthews, 1992). An example of this are surviving plant propagules sprouting after a natural disaster (Raven et al., 1999).

In 1963 an opportunity arose for investigating primary succession when a new island was born south of Iceland: Surtsey. This island was far from other terrestrial ecosystems, with Vestmannaeyjar islands being about 20 km away. On the barren lava, nitrogen was the most limiting factor for life and soil formation (Schwabe, 1974). Nitrogen-fixing cyanobacteria populations were brought to the island with wind and birds (Schwabe, 1974). Mosses started colonizing the island after four years (S. Magnússon & Friðriksson, 1974) and lichens six years after the eruption (Kristinsson, 1974). Seeds of vascular plants, like sea rocket (*Cakile edentula*) and other shore plants, were washed ashore from the first year onwards and seedlings formed, but could not survive the harsh conditions for long. Gradually, stress tolerant pioneer species improved the soil conditions. Generally, plants that form symbiotic associations with nitrogen-fixing microbes, are among the first colonizers of fresh substrate (Matthews, 1992). Because of their ability to fix nitrogen, microorganisms are clearly central to early ecosystem development, and some studies even suggest that microbial activities promote plant establishment and growth (reviewed in Nemergut et al., 2007). Other, more demanding plants were transported to Surtsey, mainly with seabirds. In 2008, 32 vascular plant species had formed viable communities on the island (B. Magnússon, Magnússon, & Friðriksson, 2009). Willows (*Salix* spp.) reached the island by wind some 23 years after the eruption (B. Magnússon et al., 2009).

Like in the example of Surtsey, pioneer species which have evolved “colonizing” characteristics, enabling them to germinate in unoccupied places and grow quickly to maturity, usually appear first. They are not adapted for growth in occupied sites so that offspring seldom survive the presence of their parents. Following succession is more complicated and depends on how the early colonizers allow or inhibit other species to recruit the area (Connell & Slatyer, 1977). Changes occur with the first colonizers and other species alter the conditions so new species are more successful. This is for example the case when a forest matures and the pool of species growing there are more and more shade tolerant. This is also the case with other environmental factors, like moisture, nutrients, grazing etc. (Connell & Slatyer, 1977). The successional processes are complex and many processes may operate simultaneously. We can therefore predict more accurately on the rate of succession rather than the final outcome (Walker & Chapin, 1987). Theoretically, the process of succession should ultimately slow down or nearly stop and terminate in a so-called climax community, related to the specific climatic conditions present. In reality, climatic conditions often change, natural disturbances occur and animals modify the environment (Raven et al., 1999).

In order to prevent further degradation and to restore degraded lands, a number of countries have enacted environmental policies to establish management actions to combat desertification. These actions include avoidance of further land degradation, monitoring the current state and restoring destructed areas (Reynolds et al., 2007). Soil degradation can be halted, for example with small check dams that pool surface water back into the ground water (Hooke & Sandercock, 2012) or reversed by adding nutrients to nutrient-depleted soil, rebuilding topsoil through soil amendments, re-establishing vegetation or buffering soil acidity (Scherr & Yadav, 1996). By increasing vegetation, the stability of the ground increases too. This is e.g. due to above-ground vegetation increasing the surface roughness and acting as a wind brake and sediment trap (Gray & Sortir, 1996) and below-ground root systems forming anchors in the soil (Pohl, Alig, Körner, & Rixen, 2009).

1.4. Land degradation in Iceland and its effect on biodiversity

Iceland, an island located in the North Atlantic Ocean, is subject to high volcanic activity and intense land degradation. More than 60% of the land is sparsely or very sparsely vegetated land (with less than 5% vegetation) (Ministry for the Environment & the Icelandic Institute of Natural History, 2001; National Land Survey of Iceland, 2013a). Soil erosion adds large amount of aeolian additions to the unique Icelandic soils and cryoturbation is more pronounced in Iceland than in most other sub-arctic regions (Ó. Arnalds, 2004).

Species diversity is low in Iceland, more so due to the young geological age (the oldest bedrock being about 16 million years), isolation (Ministry for the Environment & the Icelandic Institute of Natural History, 2001) and relatively short time since the last ice age (Einarsson, 2005) than land degradation. Before the settlement of Iceland in AD 874, much of the lowlands were covered in arctic birch (*Betula pubescens*) (e.g. McGovern et al., 2007). Land degradation, particularly soil erosion, began after the settlement. A major decline in birch began in around 1200 and around 1500 only about 5% of the original forests remained and that has not changed much (Gathorne-Hardy, Erlendsson, Langdon, & Edwards, 2009). The first settlers were sedentary farmers that depended on livestock, mainly sheep, cattle, goats, horses and even pigs (McGovern et al., 2007; Streeter, Dugmore, & Vésteinsson, 2012). The farmers cut down or burned wood to provide space for agriculture. Later, wood was cut for use as fuel and to make charcoal. Livestock was supported through the winter with fodder as well as some winter grazing. In the summertime, outfields and rangelands were exploited (Streeter et al., 2012). Overgrazing and wood utilization continued through the middle ages, gradually using up the Icelandic woods. In addition, the climate was colder in the 17th and 18th century, so firewood, as well as peat and dung, was almost essential for survival in Iceland (Kristinsson, 1995).

At present, forests and shrub-land covers approximately 1.7% of the land (Hallsdóttir, Wöll, Guðmundsson, Snorrason, & Þórsson, 2013). The only native woody species in Iceland that forms woodlands is birch but other native trees include rowan (*Sorbus aucuparia*), willows (*Salix phylicifolia* and *S. lanata*) and juniper (*Juniperus communis*). Natural birch woods and shrubs grow beneath 300-550 m a.s.l. and are key areas of terrestrial biodiversity in Iceland (Jónsson, 2001). About 28% of the land area is within the climatic species limit of birch woods and it is believed that at the time of settlement (1,100 years ago) birch may have covered at least 25 per cent of the land (Aradóttir & Arnalds, 2001). Climate change and anthropogenic activities have caused this major decline (Jónsson, 2001; Ministry for the Environment & the Icelandic Institute of Natural History, 2001).

Livestock grazing, particularly the winter grazing, had a profound negative influence on the Icelandic vegetation cover. Grazing above the treeline caused the land to slide and produced open scars, sensitive to soil erosion, one of the most serious environmental problems facing the country today (Kristinsson, 1995). Uncontrolled grazing and unsustainable land use in the past have had a substantial impact on the environment by altering the conditions for flora and fauna and are the main cause why the birch and willow forests could not regenerate naturally (Kristinsson, 1995). Despite the land degradation, there is still some vegetation in eroded areas, and they continue to be grazed (Streeter et al., 2012).

1.4.1. Environmental factors

Most Icelandic soils are so called andosols; dark-coloured volcanic soils. These soils are highly susceptible to erosion, due to low specific density and active aeolian, fluvial- and cryogenic processes. Erosive processes were mapped by Ó. Arnalds et al. (1997), where soil erosion in Iceland was categorized from 0 (no erosion) to 5 (very severe erosion). The survey showed that about 40% of Iceland suffered erosion from 3 to 5. This is by far the most serious erosion that a country with such a moist and a cold climate has suffered (Aradóttir & Arnalds, 2001).

Icelandic volcanoes cause a great pressure on ecosystems with ash and tephra damaging the sward and exposing the soil and vegetation to further soil erosion (A. Arnalds & Runólfsson, 2007). This is especially true were forests have been cut and have lost their resilience, for the trees buffer the volcanic effects (Þórarinsson, 1961). The spread of volcanic tephra and sandy deserts in Iceland is an environmental threat, for large amount of materials are transported during storms (Grétarsdóttir, Aradóttir, Vandvik, Heegaard, & Birks, 2004; Ólafur Arnalds, Gísladóttir, & Sigurjónsson, 2001; Þórarinsdóttir & Arnalds, 2012) and storms, among the most extreme on Earth, have been recorded (Schuh & Slater, 1995). With such a severe degradation large amounts of organic carbon and nutrients have been lost from the soil (Hlynur Óskarsson et al., 2004), ecosystems are ruined and result in barren deserts (Aradóttir, Arnalds, & Archer, 1992) with slim prospects for natural revegetation . This has led to drastic reductions in several species of plants and animals and there may have been inevitable (but unknown) extinctions (Sadler, 1999).

1.5. Measures to prevent land degradation in Iceland

Soil and vegetation conservation has been a priority in Iceland for several decades. In the past, nature conservation focused on the protection of areas but is now being diverted towards the protection of species and their habitats, habitat-types and ecosystem conservation (Ministry for the Environment & the Icelandic Institute of Natural History, 2001).

The first action against soil erosions in Iceland was the *Act on Forestry and Protection against Soil Erosion*, passed by the Icelandic Parliament in 1907. The Iceland Forest

Service (IFS) was in charge of forest protection and erosion control from 1907, but in 1914 the erosion control and revegetation was split from the IFS and later the Soil conservation Service (SCS) was founded. Both institutions have emphasized conservation of soils and vegetation; the SCS is primarily concerned with soil erosion control and revegetation, but the IFS is responsible for protection of the remaining birch woodlands, reforestation and afforestation (A. Arnalds & Runólfsson, 2007). Extensive recovery programmes have succeeded in halting and reversing erosion in many of the most severely affected areas. To date more than 1,500 km^2 of heathland and grassland and 200 km^2 of native birch woodlands have been restored (Halldórsson et al., 2012).

1.5.1. Protection from Grazing

In the late 19th century, a peak of Icelandic ecosystem destruction may have been reached, caused by the interaction of increasing livestock numbers and climatic fluctuations (A. Arnalds & Runólfsson, 2007). The number of sheep has declined after 1980 and the grazing of woodlands, especially winter grazing has almost been eliminated (Ministry for the Environment & the Icelandic Institute of Natural History, 2001). Still, the most common method for revegetating barren land in Iceland is protection from grazing (Halldórsson et al., 2012).

1.5.2. Reclamation

Presently, reclamation methods in Iceland depend more and more on stimulating natural recovery using fertilizers, like manure or minerals (Aradóttir, 2007a; A. Arnalds & Runólfsson, 2007), but more interventive methods like seeding grass and planting trees are used too. Pioneer grass species like lyme grass (*Leymus arenarius*) have been seeded for their ability to stabilize drifting sand and are key plants for sand reclamation (Greipsson & Davy, 1994). The nitrogen-fixing Nootka lupin (*Lupinus nootkatensis*) has been seeded to improve soil qualities and serve as nurse species for natural revegetation on barren areas (Davíðsdóttir, 2013; B. Magnússon, 2006). Alien tree species like Russian larch (*Larix sukaczewii*), Lodgepole pine (*Pinus contorta*) and Black cottonwood (*Populus trichocarpa*) (Ministry for the Environment & the Icelandic Institute of Natural History, 2001) have been planted but also native trees mentioned above. Birch and willows are key species in many Icelandic ecosystems and can help restore former ecosystem function and biodiversity (Aradóttir, 2007a). The long-term effects of reclamation in Iceland have been beneficial in the sense of forming a persistent plant cover and promoting plant colonization (Grétarsdóttir et al., 2004) and increasing animal species richness (Davíðsdóttir, 2013; Oddsdóttir, Svavarsdóttir, & Halldórsson, 2008).

1.6. The study area

The study area is a large scale birch woodland restoration area, called Hekluskógar. Hekluskógar is mostly barren land under great impact from the very active Hekla volcano and other volcanoes in the vicinity. Despite these natural disasters, most of the area was covered with birch forests at settlement around year 870 and in the following centuries. Large volcanic eruptions in the past and forest depletion by land owners reduced the forests in only 200-500 years (Sigurmundsson, 2011) and presently, about half of the area suffers great erosion (Aradóttir, 2007a). In spite of that, patches of different habitats, like grassland, heath, moss and wetland, exist scattered around the area and these habitats are home to different ecosystems. Large-scale revegetation of birch woodlands is being undertaken in Hekluskógar area since 2006. This heterogeneous area, under influences of natural disturbances and reclamation attempts, gives an opportunity to investigate the long-term changes in ecosystem succession from barren land to forest.

This study gives information on the status of biodiversity in 2011 and 2012 in different ecosystems within Hekluskógar area, and will serve as a baseline to follow the effect of birch woodland restoration on invertebrates and birds into the future, and also a baseline to follow the effect of a possibly near future eruption in Hekla or other volcanoes in the vicinity. The effects of forestry have been investigated to some extent in Iceland, especially the use of foreign tree species (Elmarsdóttir et al., 2011; Halldórsson & Oddsdóttir, 2007; Ólafsson & Ingimarsdóttir, 2007) and birch (Aradóttir, 2007a; Aradóttir & Arnalds, 2001; Oddsdóttir et al., 2008). On the other hand, there is less known about the effects of volcanic activities on ecosystems. Lack of pre-disturbance data for comparison could be the reason for this.

1.7. Objectives of the study

a) Evaluate the effects of vegetation succession on erodible volcanic soils on biodiversity by comparing diversity measures between habitat types at different stages of succession.

b) Provide a baseline on which to assess the future effects of afforestation and volcanic activity on biodiversity in the area.

Land degradation due to human influences have to a large extent ceased in the Hekluskógar area, apart from sheep grazing, so erosive forces can be thought of being the current biggest factor influencing organisms in the area.

Birds are commonly used as indicators of biodiversity, especially where numbers are high (Larsen, Bladt, Balmford, & Rahbek, 2012). Birds are widespread around the world, diverse and sensitive to changes lower down in the food chain and persistent pollutants. Furthermore, bird ecology is on the whole well understood, making it easier to interpret their fluctuations (Gregory, 2006). Using other taxa as biodiversity indicators can also be valuable (Larsen et al., 2012) and common invertebrates have also been used as indicators (Andersen, Fisher, Hoffman, & Read, 2004), although only a small proportion of invertebrates has been thoroughly studied (Gregory, 2006).

The effects of animals on primary ecosystem succession have not been investigated to a large extent, but some studies show that invertebrates provide valuable information about succession and restoration success, having roles in decomposition and nutrient turnover (Majer, 1997). In later successional stages, root feeding soil invertebrates can enhance vegetation succession by reducing the biomass of the dominant plant species (Deyn et al., 2003).

A generalized pathway of community succession which can apply to Hekluskógar is represented in figure 1. Erosive forces are represented by influences of nearby volcanoes, weather conditions and human activities like livestock grazing and wood cutting. These factors interact to influence the environment, resulting ultimately in a state of barren land, sustained by further erosion. If the erosion ceases for some reason, and if the damage done is not so severe that the life supporting capacity of the ground is destroyed, the ecosystems get stabilized. It starts with nitrogen-fixing microbes (Nemergut et al., 2007), low nutrient demanding vascular plants (Greipsson & Davy, 1994) or mosses (Matthews, 1992). When these pioneer plants have altered the conditions, other species are able to colonise and take over the habitat (Connell & Slatyer, 1977). It is then a question of influencing environmental factors, like moisture, that affect the succession either to wetland or heathland surroundings. Ultimately, shrubs and trees are able to colonise, forming shrub-lands or forests which are thought to be important for terrestrial biodiversity in Iceland (Jónsson, 2001). At all stages, erosive factors can influence the ecosystems again and induce complicated cycles.

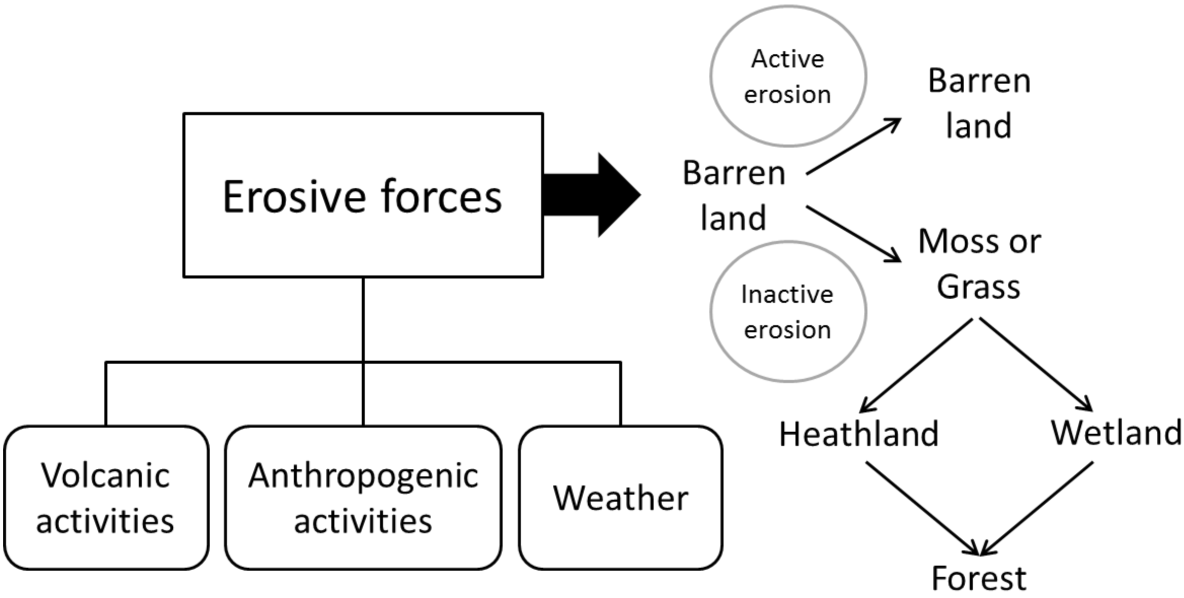

Figure 1. Generalized effects of erosive forces (i.e. volcanic- or human activities or weather) on plant succession in Hekluskógar. Erosive forces keep barren land deserted, but when erosion is halted, moss and grass colonize the substrate and succession leads finally to forested land.

2 Methods

2.1. Study area and layout

Mt. Hekla and Hekla forest project (HFP) are located in South Iceland (Figure 2). The revegetation/afforestation program started in 2006 and is currently the largest ecological restoration project in Iceland (Halldórsson et al., 2012). The project is an association of many organizations, like landowners in the area, the SCS and the IFS. The project area covers about 92,000 hectares, or ca. 1% of Iceland (Hreinn Óskarsson, 2011), surrounding Mt. Hekla from north to south. The range in altitude is from 100 m to 600 m a.s.l. (Hreinn Óskarsson, 2011). The area was once greatly forested but was deforested by anthropogenic activities in the past, climate changes and eruptions from the very active Hekla volcano (Hreinn Óskarsson, 2011). Between AD 1587-1938 the woodlands in the area declined by 93.4% (Sigurmundsson, 2011). Presently a vast area of the HFP is covered with pumice from the volcanoes Hekla, Katla and others in the vicinity (Hreinn Óskarsson, 2011). More than half of Hekluskógar suffers from active or very active erosion (Þórarinsdóttir & Arnalds, 2012) and sparse vegetation (<33%, often <5%) (Aradóttir, 2007a) (Figure 2). In vegetated parts, willows grow on about half of that land and birch to some extent (Þorsteinsdóttir et al., 2006).

Prior to the HFP, there has been some reclamation and reforestation in the area. Lyme grass has been seeded for halting erosion. In less erosive parts, nootka lupin and grass species have been seeded, to improve habitats for tree species (Þorsteinsdóttir et al., 2006).Since the HFP started, about 675 ha have been planted with trees and vast areas of barren land is now covered with grass (Hreinn Óskarsson, 2011). The aim of the HFP is to continue revegetation by fertilizing and seeding lyme grass in the most severely eroded areas and planting birch and willows in more fertile habitats. This is accomplished by the procedure of planting trees in patches serving as seed sources and promoting natural reclamation of the former forests (Þorsteinsdóttir et al., 2006). It is anticipated that the project will reduce soil erosion, restore ecosystem function and biodiversity, increase carbon sequestration and improve options for future land use (Aradóttir, 2007a; Hreinn Óskarsson, 2011).

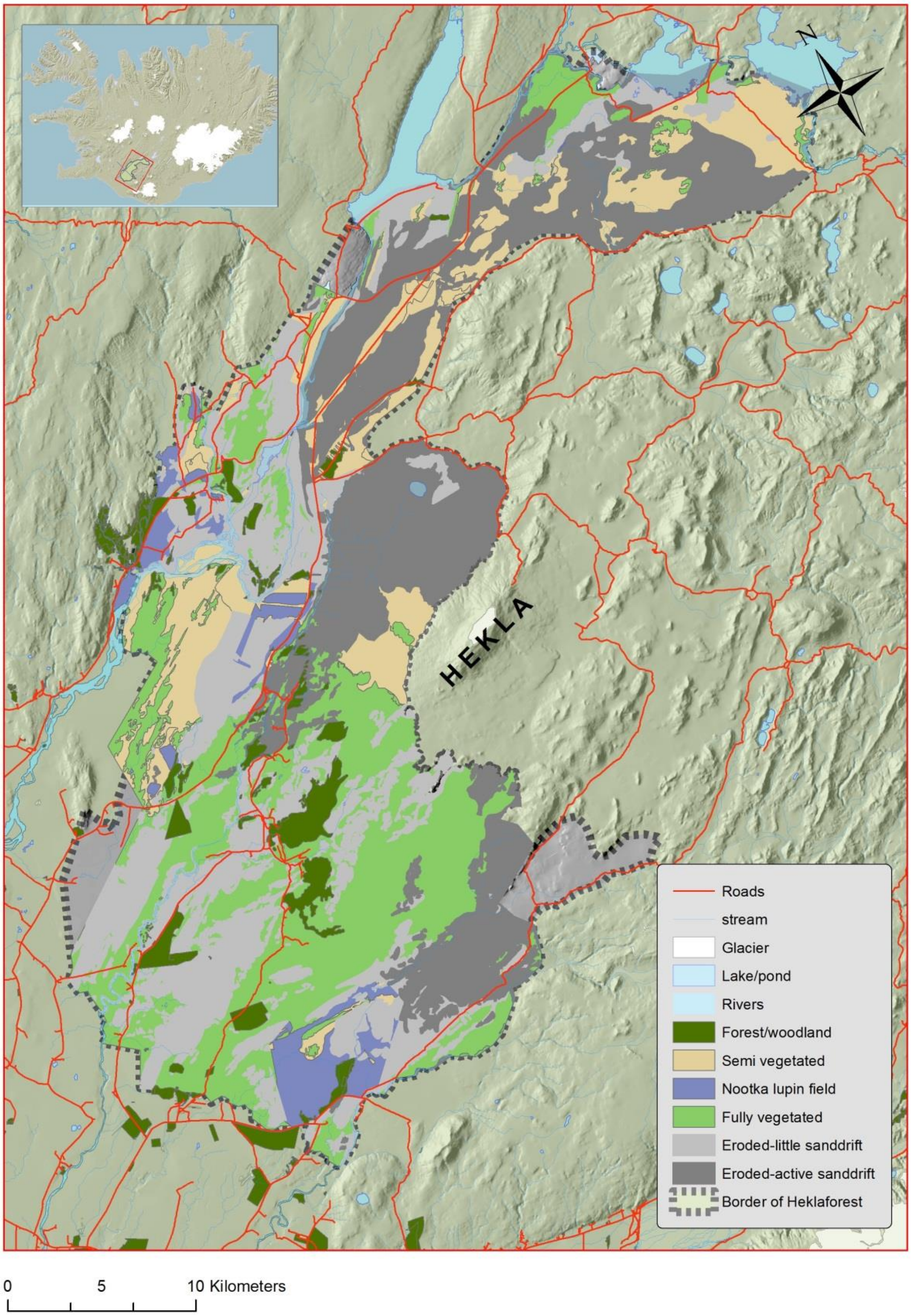

Figure 2. Vegetation cover and distribution of main habitat types in Hekluskógar: forests, semi vegetated (50% vegetation cover), nootka lupin fields, fully vegetated and eroded land (vegetation cover < 5%). The vegetation cover of the map was prepared by Arna Björk Þorsteinsdóttir and modified by Hreinn Óskarsson (2013). Background elevation model was done by Björn Traustason. Roads, rivers, lakes and glaciers are from National Land survey of Iceland.

2.1.1. Volcanism and erosion in the study area

Over the past 1100 years an apparent increase in eruption frequency has been observed in Iceland, 80% of which took place where the four most active volcanic systems (Hekla, Katla, Grímsvötn and Bárðarbunga- Veiðivötn) are but they all impact the study area (Thordarson & Larsen, 2006). Hekla has erupted at least 22 times since 1104, latest in 2000 (Guðmundsson, 2001) and compared to recent eruption intervals, another eruption is due. Hekla accounts for about 13% of volcanic eruptions in Iceland in historical times (Thordarson & Larsen, 2006). Katla is situated about 50 km away from the study area (National Land survey of Iceland, 2013b) and about twenty eruptions have been recorded for the volcano in historical times, accounting for 12% of the total number of eruptions (Thordarson & Larsen, 2006). Grímsvötn has the highest eruption frequency of all volcanoes in Iceland, between 60 or 70 in historical times (Guðmundsson, 2001) or 38% of the total number in the period (Thordarson & Larsen, 2006). The adjoining Laki fissure erupted over an eight-month period between 1783 and 1784, producing the largest lava flow in historical times and causing the great dry fog/blue haze in Europe (Sigurðsson, 1982). Bárðarbunga- Veiðivötn is responsible for about 14% of total number of eruptions and in AD 1477 it produced the largest Icelandic tephra fall in historical times (Thordarson & Larsen, 2006).

The mountainside of South Iceland, where HFP is situated is one of the most severely eroded places in Iceland. Sand drift from the area has long been a problem but about 100 years ago, farmers started actively managing the sand drift with good results, but the area is still susceptible to sand erosion (Ó. Arnalds et al., 1997).

2.2. Survey design

In total 59 study sites were visited in June and July, 29 in 2011 and 30 in 2012. These included eight sites for birds and five for invertebrates, spread across habitat types, which were repeats to explore inter-annual variation in abundance. Study sites were selected randomly in a stratified manner (Bibby, Burgess, & Hill, 1992), taking into account that the habitats barren land and heathland were far more abundant than the other four. The two most common habitats were surveyed on 14 study sites but other habitat types on eight each (Table 1). Location of study sites within each habitat type was selected at random in a digitised manner. The digital selection was constrained to keep study plots within 1 km of roads and tracks for logistical reasons but no closer than 100 m.

Table 1. Description of habitats types in the study area where sampling of biodiversity took place (Nytjaland, 2013).

Habitat type	**Habitat description**
Barren land	Contains less vegetation than 50% with variable species composition.
Moss	At least 2/3 parts covered with moss. Other vegetation is restricted, but often grass, sedges (*Carex* spp.) and small bushes grow among the moss.
Grassland	Dominated by grasses and sometimes flowers like buttercups (*Ranunculus spp.)* and dandelions (*Taraxacum spp*). Productivity is high and grassland is commonly found where conditions are favourable, e.g. near streams.
Heathland	Characteristic species include small shrubs like black crowberry (*Empetrum nigrum*), flowering plants, grasses, moss and lichens. Heathlands are dry and hummocky.
Wetland	Characterized by sedges, horsetails (*Equisetum* spp.), grasses and heathland vegetation. Vegetation is dense and ground water level high.
Tall vegetation	Refers to natural birch woods, low growing shrubs, cultivated forests or lupin patches. At least 50% coverage of knee high shrubs. Common species include birch and but also flowering plants, grasses and dwarf-shrubs.

To explore inter-habitat variation in vegetation and to relate to surveys of birds and invertebrates, vegetation cover and type was estimated into 3-5 broad categories on each study site: total vegetation cover (%) and percentage cover of grasses, lichens, mosses, herbs, dwarf bushes, lupine and bushes. At each site photos were taken for future reference (Figure 4).

2.2.1. Bird census

Bird surveys were performed either in the morning or in the evening, when birds are most active (Figure 3). To avoid conditions of low bird detectability, censuses were only made if wind velocity was lower than 7 m/s and precipitation was very low or none (Bibby et al., 1992). Birds were counted on transects. Transects are an efficient means of deriving bird densities of scattered species in open habitats with sufficient detail (Bibby et al., 1992). Mean transect length was 642 m (SD 235 m) in homogenous habitats, and a total length of 37.9 km was walked. Five distance bands were used for recording bird distance from the transect line, 0-25, 25-50, 50-75, 75-100 and > 100 meters. The number of individuals per km^2 of each species was calculated (details below) and used for further analysis. Birds further than 100 m away were excluded from calculations, as their unbounded category is difficult to interpret (Normann, Harris, & Newson, 2012).

2.2.2. Invertebrate sampling

Surface active invertebrates were sampled by pitfall traps, (95 mm in diameter) on 18 plots each year 2011 and 2012, a total of 36 (Figure 3). Three traps were set up on every site and number of individual invertebrates of each group/site/day was used for calculations. The traps were set up from 7 June to 24 June in 2011 and from 11 June to 27 June in 2012. Traps were emptied between 21 July and 24 July in 2011 and 11 July to 24 July in 2012. Average sampling period was 33 days (SD 6.2) from early June to late July and gives a measure of active invertebrates during that time of summer. The traps were made of a plastic cup, filled up to a couple of centimetres high with anti-freezing agent (ethylene glycol) and dug into the ground so that the rim of the cup was level with the surface. The traps were covered with a tin plate that was held up by wire, approximately one cm above ground, to prevent them from filling up with water or airborne debris.

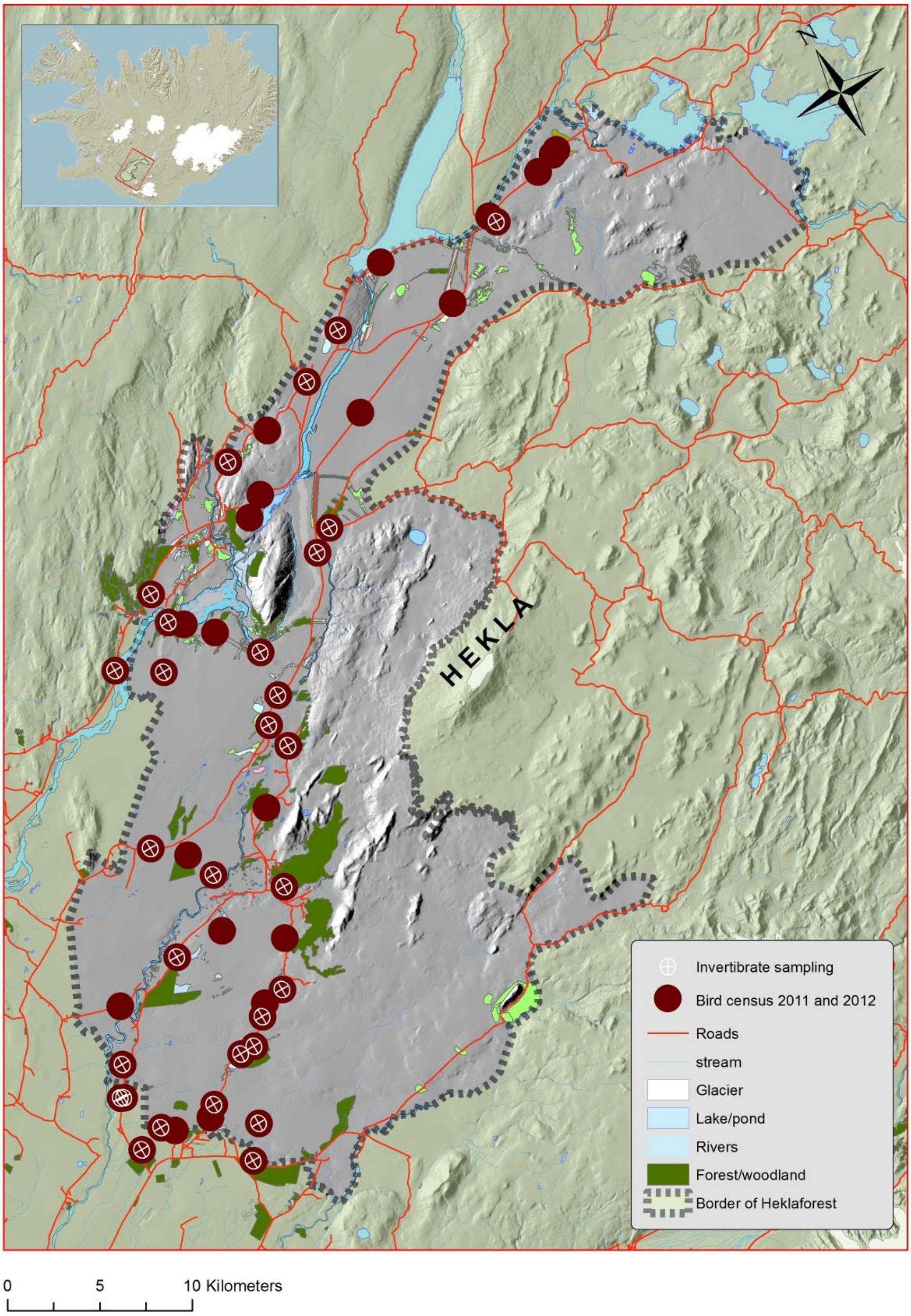

Figure 3. Sampling sites of birds and invertebrates in Hekluskógar 2011-2012. Sites where birds were counted are marked by a red dot and sites where invertebrates were sampled with a white cross. Hekla forest borders were digitized by Arna Björk Þorsteinsdóttir and modified by Hreinn Óskarsson (2013). Background elevation model was done by Björn Traustason. Roads, rivers, lakes and glaciers are from National Land survey of Iceland.

Samples were washed in a sieve with mesh size of 0.5 mm. Invertebrates were identified with a stereoscope, most often into genera, but some into species and some into classes (Table 2). Additionally, the animals were classified into length categories: < 3, 3-6, 6-9 and >9 mm (length from head to abdomen, length of legs excluded). Some animals had additional length groups: 9-12, 12-15, 15-20, 20-30 mm and larger. Only adult individuals were included in most of the data analysis, but all animals in biomass calculations. Nine major groups were used for calculations: Identified into orders: True flies (Diptera), Hymenoptera, True bugs (Hemiptera), Beetles (Coleoptera), Moths (Lepidoptera). Class: Arachnida. Subclasses: Springtails (Collembola) and Earthworms (Oligochaeta). Informal group: Snails and slugs (Pulmonata). The different groups are described in table 2. Other groups, like Thrips (Thysanoptera), caddisflies (Trichoptera) and centipedes (Chilopoda) were recorded to but were not abundant enough to be included in most calculations, except in diversity estimations.

The length from head to end of abdomen of invertebrates was measured. Invertebrate biomass was subsequently calculated with following formula (Collins, 1992; Sample, Cooper, Greer, & Whitmore, 1993).

$$\ln(\mathit{weight}) = \ln(a) - b * \ln(\mathit{length})$$

where a and b were given for each family. Biomass was measured in mg/trap/day, wet weight.

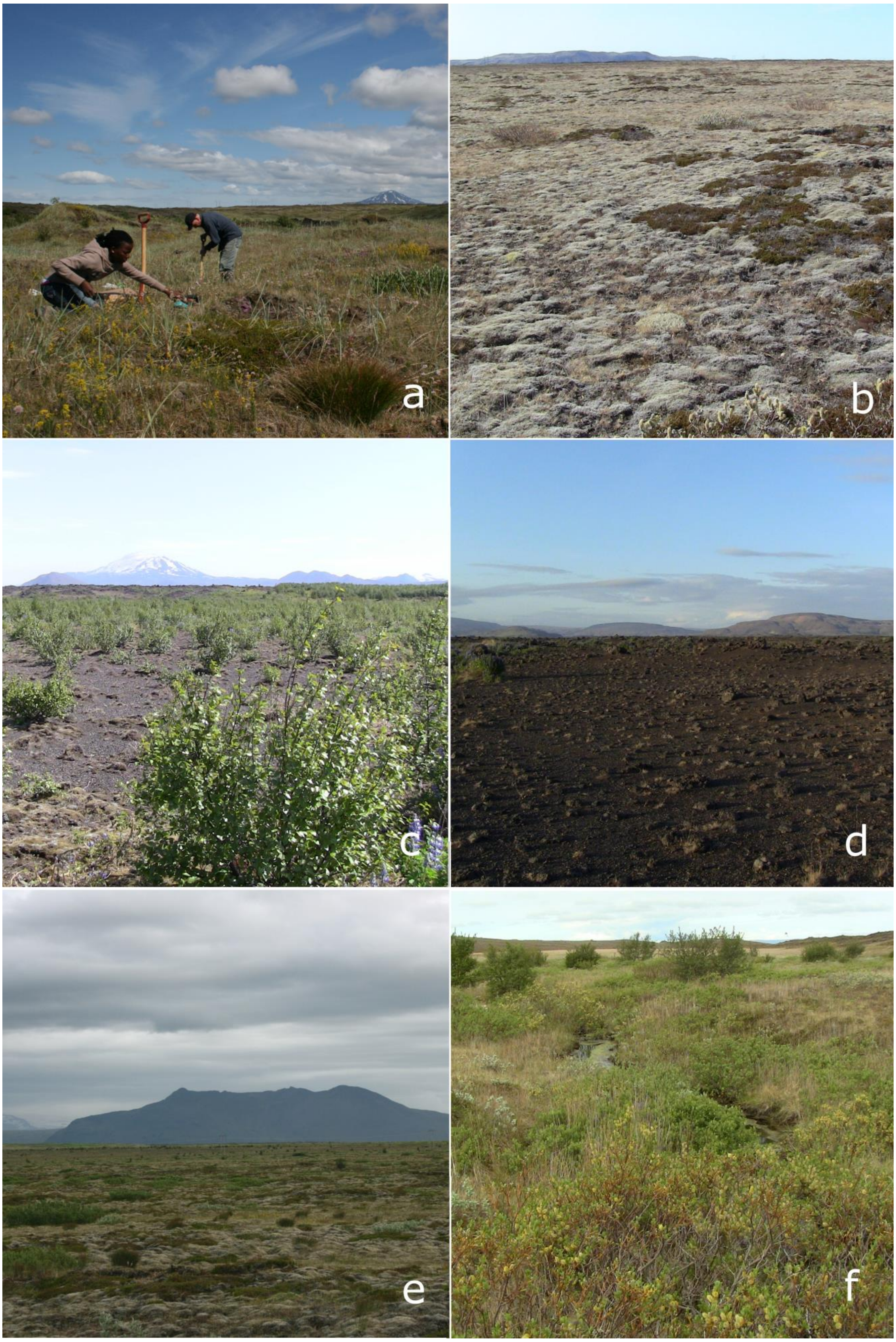

Figure 4. The six habitats of bird census and invertebrate sampling sites in Hekluskógar 2011-2012. a) Grassland (with Lahya Tjilumbu and Úlfur Óskarsson), b) Moss, c) Tall vegetation (reclamation site), d) Barren land, e) Heathland and f) Wetland. Photos taken by Heiða Gehringer 2011 and 2012.

Table 2. Description of invertebrate groups in samples collected in Hekluskógar 2011-2012.

Major group	Classification levels in relation to invertebrates found on study sites.
True flies (Diptera)	Include Brachycerans (House flies (Muscidae), March flies (Bibionidae) and Crane flies (Tipulidae)), Nematocerans (Midges (Chironomidae, Cecidomyiidae and Ceratopogonidae), Black flies (Simulidae) and Gnats (Sciaridae)).
Hymenoptera	Sawflies (Symphyta) and wasps (Apocryta), especially parasitic wasps. Bees and ants were not found on the study sites.
True bugs (Hemiptera)	Leafhoppers (Cicadellidae), Plant lice (Aphidoidea), Scale insects (Coccoidea) and Heteroptera („Typical bugs“ like Shore bugs (Saldidae), Lace bugs (Tingidae) and Seed bugs (Ligaeidae)).
Arachnids	Spiders (Araneae), Mites (Acari) and Harvestmen (Opiliones).
Beetles (Coleptera)	Ground beetles (Carabinae), Rove beetles (Staphylinidae), Weevils (Curculionidae), Pill beetles (Byrrhidae), Ladybirds (Coccinellidae) and relatives. In very few cases, predaceous diving beetles (Dytiscidae) and their larvae were recorded.
Springtails (Collembola)	Springtails were not divided into genera, but classified into „oblong”-like Entomobryomorpha and „round“, like Sminthuridae.
Moths (Lepidoptera)	Owlet moths (Noctuidae) and Geometer moths (Geometridae).
Snails and slugs (Pulmonata)	Only land snails and slugs were found on the study sites and not classified further.
Earthworms (Oligochaeta)	Earthworms were not classified further.

2.2.3. Data analysis

All statistical analyses were made to detect variation with declining erosive influence on the habitats. Bird densities of the most numerous species (Golden Plover (*Pluvialis apricaria*), Whimbrel (*Numenius phaeopus)* and Meadow Pipit (*Anthus pratensis*)) were calculated with program DISTANCE 6.0. The software models the decline in detectability of birds with increasing distance from the transect line (Buckland et al., 2001). For species which were recorded too rarely to allow a detection curve to be calculated with Distance, an uncorrected density (number of birds divided by the area of the transect) was calculated. The software R (R Development Core Team, 2008) was used for all remaining data analysis. To compare bird density between habitats, Generalized Linear Models (GLM) with Poisson error distribution and a log link were fitted and corrected for over dispersion by adjusting the standard errors (with quasipoisson in program R). Number of birds per transect were modelled with transect area as an offset variable. Logistic regression models were applied to predict bird densities with increasing vegetation cover. Identical GLM's were also applied to the invertebrate catch data. For both bird and invertebrate community analysis, a Principal Component Analysis (PCA) was used. For both birds and invertebrates, Shannon Entropy indices and Effective species Number (Jost, 2006) were calculated. A Detrended Correspondance Analysis (DCA) (R package Vegan 2.0-5) was applied to bird density and invertebrate catch for community estimates. Alpha level was 0.05 for all statistical tests.

3 Results

3.1. Birds

3.1.1. Bird density

A total of 697 birds of 28 species were recorded on the 59 sites surveyed (Appendix A). Sites which were surveyed both in 2011 and 2012 had generally a similar overall density of birds (Pearson $r = 0.687$, $P < 0.0001$). Three species, Golden Plover, Whimbrel, Meadow pipit were the most abundant species (59 % of all birds) and the only ones which occurred often enough to allow calculation of their density with program Distance (Figure 2). The density of these three species was compared between habitats with a generalized linear model (Table 3). Overall, the density of these three increased from the barren state and they occurred in higher density at higher succession stages but peak density varied between habitats (Figure 5). For species which occurred in too low a density to account for detectability with the program Distance, density was calculated by dividing the number of individuals by the area of the transect. The uncorrected densities (sum of all species) were lowest in barren land (22.6 birds/km^2, SE = 11.3) and highest in wetland (201.3 birds/km^2, SE = 106.4) (Figure 6).

Table 3. Results of generalized linear models (GLM) with Poisson distribution, adjusted for over dispersion (quasipoisson) with area (km^2) as offset, for birds in 2011 and 2012. n= 31. Significant differences from Intercept (barren land) are in bold.

Species	Habitat	Estimate	SE	t	P
Golden	(Intercept)	-1.388	1.013	-1.370	0.178
Plover	Grassland	1.695	1.143	1.483	0.145
	Heathland	1.836	1.080	1.700	0.096
	Moss	1.693	1.143	1.481	0.146
	Tall vegetation	1.745	1.143	1.527	0.134
	Wetland	**2.461**	**1.077**	**2.285**	**0.027***
Whimbrel	(Intercept)	-1.388	1.266	-1.096	0.279
	Grassland	2.005	1.387	1.446	0.155
	Heathland	2.574	1.307	1.969	0.055
	Moss	-0.012	2.002	-0.006	0.995
	Tall vegetation	0.040	2.002	0.020	0.984
	Wetland	1.118	1.551	0.721	0.475
Meadow	(Intercept)	-0.695	0.685	-1.014	0.316
Pipit	Grassland	**2.070**	**0.747**	**2.771**	**0.008****
	Heathland	**2.041**	**0.722**	**2.825**	**0.007****
	Moss	0.999	0.852	1.173	0.247
	Tall vegetation	**2.265**	**0.739**	**3.066**	**0.004****
	Wetland	1.198	0.829	1.446	0.155

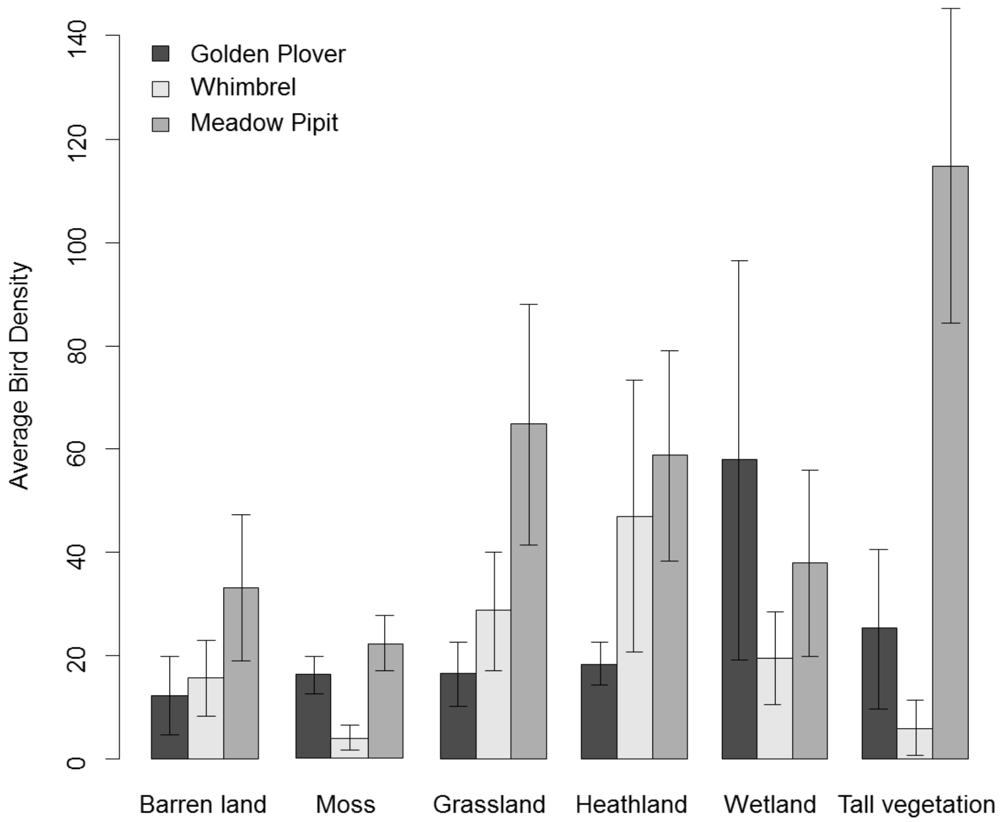

Figure 5. Mean individual density (± SE) of the three most common species in Hekluskógar area in 2011-2012. Golden plover, Whimbrel and Meadow pipit are adjusted for variation in detectability with program Distance.

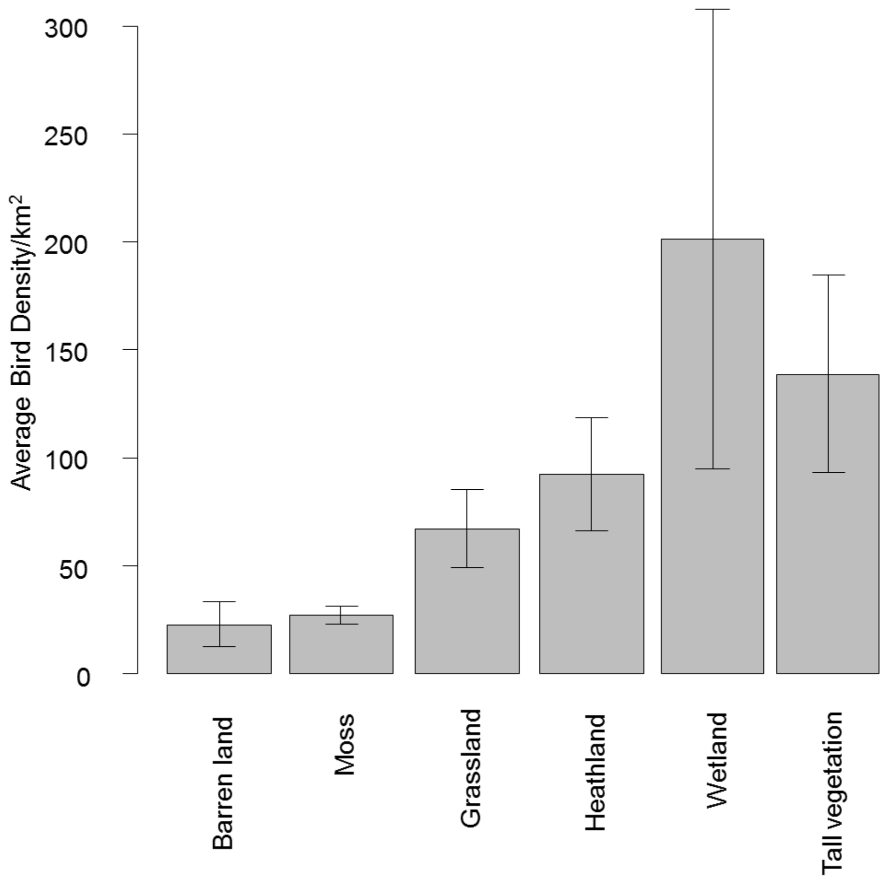

Figure 6. Average individual density (± SE) for all bird species in the six different habitats in Hekluskógar in 2011-2012. n= 51.

3.1.2. Relationship between bird occurrence and vegetation

As breeding density of birds at early succession stages is often low and susceptible to high levels of measurement and random error, the occurrence of birds was also related to vegetation types. This was done for shorebirds (Charadrii) as a group (including Golden plover, Whimbrel, Common Snipe, Redshank, Dunlin, Black- tailed godwit (*Limosa limosa*) and Red-necked phalarope) and for Meadow pipit, which was the far most numerous passerine, by modelling bird occurrence as a function of vegetation cover with a logistic regression, including all habitats.

The occurrence of both shorebirds ($\chi^2_{1,49}$= 55.428, P= 0.002, Figure 7a) and Meadow Pipit ($\chi^2_{1,49}$= 45.510, P< 0.001) were strongly related to vegetation cover (Figure 7b).

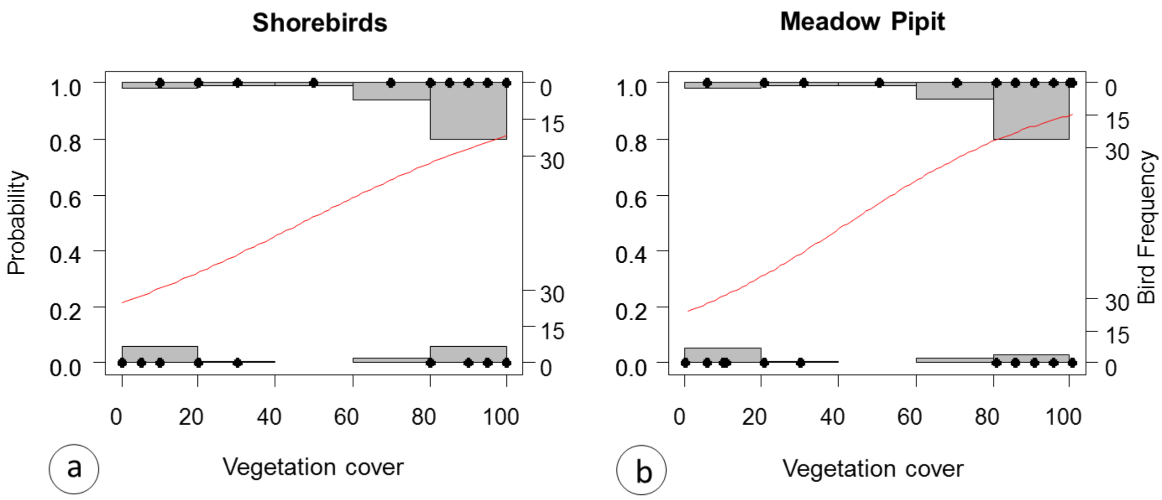

Figure 7. Relationship between bird occurrence (a: shorebirds, b: Meadow pipit) and vegetation cover in Hekluskógar area in 2011-2012. n= 51. Bars are a histogram of occurrence and the lines show a modelled (logistic regression) change in occurrence with increasing vegetation cover.

3.1.3. Bird communities

To identify different bird communities and relate to habitats, species were grouped with a Principal Component Analysis (PCA) of bird species with more than 20 individuals in total, a total of seven species (Table 4). High correlations were found between Red necked phalarope and Greylag goose (*Anser anser*) (r= 0.9865) and between Golden plover and Red necked phalarope (r = 0.7689) and Greylag goose (r = 0.7985) respectively.

The first two components accounted for 70.0% of the total variance in the data and were retained. Variables and corresponding factor loadings are presented in Table 4 and Figure 8. PC1 (characterized by Golden plover, Red-necked phalarope, Greylag goose and (weakly) by Ringed plover) was not correlated with any vegetation (Table 5). PC2 (characterized by Common snipe, Whimbrel and Meadow pipit) were related to bushes and lupins (r= 0.46, P < 0.001) (Table 5).

Table 4. Mean counts per transect on all habitat types for the seven most abundant bird species in Hekluskógar 2011-2012. Factor loadings > 0.5 are shown in bold.

Variable	Mean count	Standard deviation	PC1	PC2
Common snipe	0.588	0.639	-0.09	**0.65**
Golden plover	1.588	2.729	**0.86**	0.15
Whimbrel	1.451	4.012	-0.10	**0.73**
Meadow pipit	3.000	3.583	-0.02	**0.93**
Ringed plover	0.471	1.461	**0.59**	-0.22
Red-necked phalarope	1.078	5.868	**0.96**	0.08
Greylag goose	0.667	4.213	**0.97**	0.08
% Variance explained			42.3	27.7

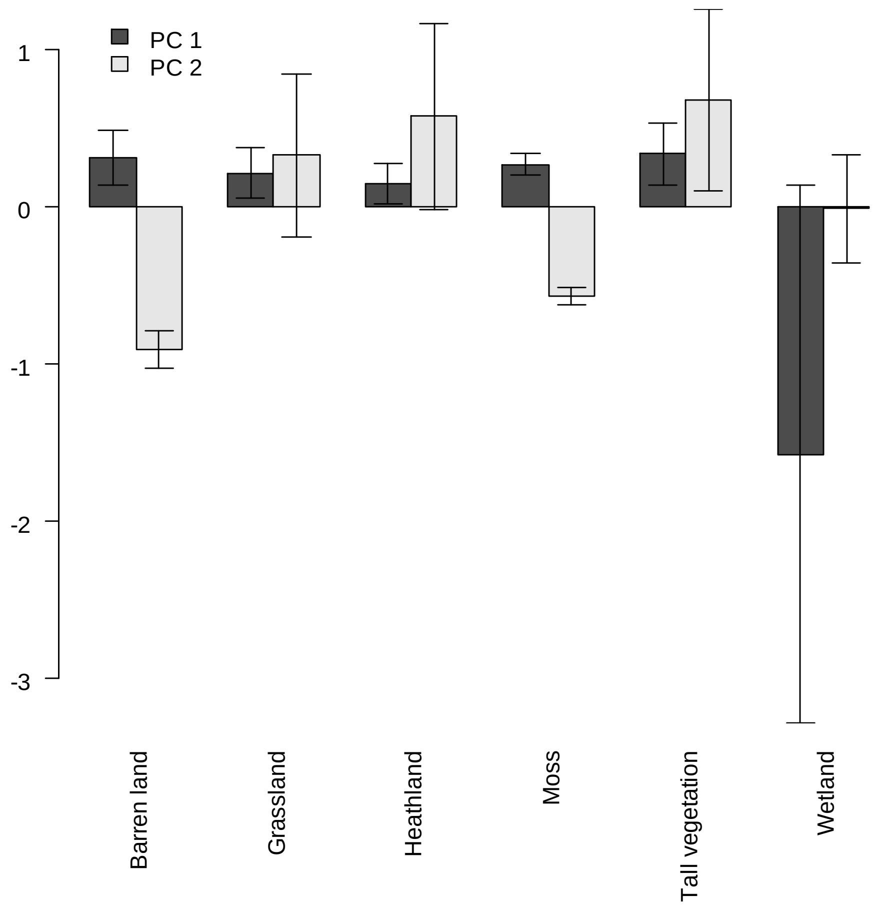

Figure 8. Mean (± SE) factor scores of the two factors from a principal components analysis of bird density for each of the six habitat types in Hekluskógar 2011-2012. n= 51 sites.

Table 5. Correlation (Pearson r) between the first two principal components and vegetation variables across habitats in Hekluskógar 2011-2012.

	Moss		**Grass**		**Bushes and lupin**		**Dwarf shrubs and herbs**	
	r	P	R	P	r	P	r	P
PC1	0.0182	0.8989	0.1128	0.4306	0.0925	0.5183	0.0310	0.8291
PC2	0.0284	0.8430	0.1228	0.3908	**0.4572**	**0.0007**	-0.0422	0.7687

3.1.4. Bird Diversity

Heathland and wetland had the highest bird species richness and average species number (Table 6). The "True diversity" or effective species number (Jost, 2006) in the habitats was mostly lower than the average number of species. The average number of species was significantly different between habitats (Kruskal-Wallis test: H = 12.9, 5 d.f., P = 0.025). Pair-wise differences showed that barren and moss habitats had lower average number of species than other habitats but were not significantly different from each other.

Table 6. Species richness and diversity of birds in Hekluskógar 2011-2012. Effective number of species ("True diversity" (Jost, 2006)) is the exponential of the Shannon entropy.

	Total number of species	**Average number of species**	**Average Shannon entropy index (±SD)**	**Effective number of species**
Barren land	12	1.364	0.380 ± 0.620	1.463
Moss	6	2.429	0.765 ± 0.458	2.149
Grassland	12	3.000	0.893 ± 0.438	2.441
Heathland	20	4.250	1.027 ± 0.610	2.792
Wetland	20	5.571	1.103 ± 0.907	3.013
Tall vegetation	8	2.857	0.807 ± 0.493	2.242

3.2. Invertebrates

3.2.1. Invertebrate density

In total 46 families belonging to 12 groups of invertebrates were found in pitfall traps. Of these, nine groups were 99.8% of the total number of animals and were used for calculations (Table 7 and Figure 9, see also Appendix B). To explore annual variation, five sites were sampled both in 2011 and 2012 and the correlation between the total catches within sites between years was $r = 0.70$, $P < 0.001$.

Table 7. Mean number of invertebrate individuals/trap/day in Hekluskógar 2011-2012, which were active from early June to late July.

Variable	Mean	Standard deviation
Diptera	1.0423	0.8306
Hymenoptera	0.4564	0.3962
Hemiptera	0.9558	1.4691
Arachnida	6.7136	5.5404
Coleoptera	0.6404	0.6224
Collembola	3.3119	3.9951
Lepidoptera	0.0146	0.0197
Pulmonata	0.2901	0.9957
Oligochaeta	0.0290	0.1239

The total sum of invertebrates per trap per day ranged from 6.4 (SE= 0.83) in barren land to 19.5 (SE= 2.32) in grassland (Figure 9). No significant difference was found when the total sum of invertebrates was compared (GLM with Poisson distribution, adjusted for overdispersion (quasipoisson)). When comparing the catch of individual groups between habitats, True flies ($F_{5,25}$ = 7.1114, P < 0.001) and Hymenoptera ($F_{5,25}$= 6.0315, P < 0.001), showed a significant difference between barren land and vegetated habitat classes. Hymenoptera and True bugs ($F_{5,25}$= 8.8121, P < 0.001) were also different between vegetated habitats, between grassland and heathland and moss and tall vegetation respectively (Table 8 and Figure 10).

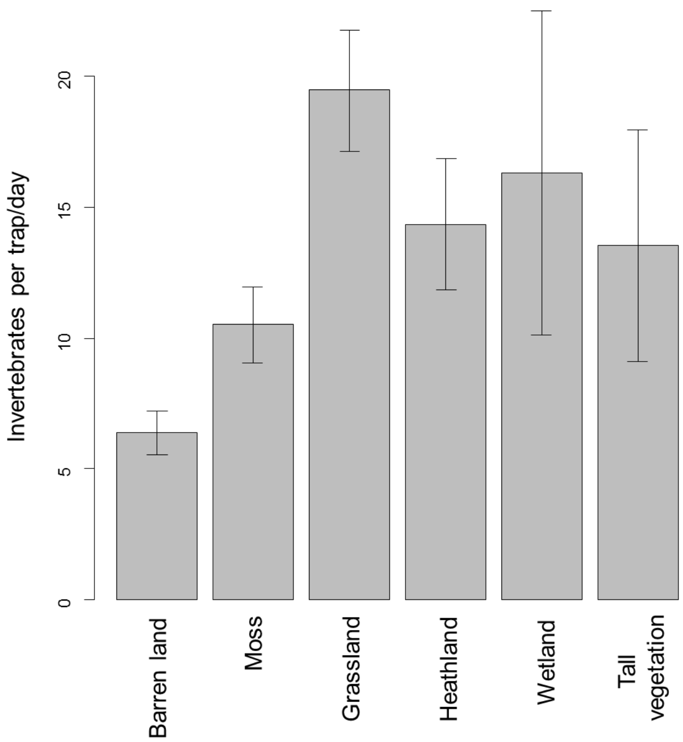

Figure 9. Mean catch, total number of individuals/trap/day (± SE) of the nine most abundant invertebrate groups in Hekluskógar 2011-2012. n= 31 sites.

Table 8. Generalized linear models (GLM) with Poisson distribution, adjusted for over dispersion (quasipoisson), for invertebrate catches per day in 2011 and 2012. n= 31. Significant differences from the Intercept (barren land) are shown in bold.

Species	Habitat	Estimate	SE	T	P
Diptera	(Intercept)	**0.926**	**0.155**	**5.986**	**2.99e-06 *****
	Grassland	**-0.893**	**0.287**	**-3.112**	**0.005****
	Heathland	**-1.174**	**0.297**	**-3.947**	**0.001*****
	Moss	**-1.289**	**0.333**	**-3.873**	**0.001*****
	Tall vegetation	**-1.181**	**0.319**	**-3.700**	**0.001****
	Wetland	**-1.624**	**0.381**	**-4.260**	**0.0003 *****
Hymenoptera	(Intercept)	**-2.406**	**0.611**	**-3.940**	**0.001*****
	Grassland	**2.339**	**0.639**	**3.658**	**0.001****
	Heathland	**1.958**	**0.645**	**3.034**	**0.006****
	Moss	1.133	0.702	1.613	0.119
	Tall vegetation	1.355	0.688	1.979	0.059
	Wetland	**1.506**	**0.674**	**2.232**	**0.035***
Hemiptera	(Intercept)	**-1.740**	**0.835**	**-2.084**	**0.048***
	Grassland	**2.948**	**0.857**	**3.441**	**0.002****
	Heathland	1.077	0.946	1.138	0.266
	Moss	1.092	0.965	1.132	0.269
	Tall vegetation	1.455	0.927	1.569	0.129
	Wetland	1.073	0.967	1.109	0.278
Arachnida	(Intercept)	0.564	0.658	0.858	0.399
	Grassland	**1.761**	**0.712**	**2.473**	**0.021***
	Heathland	**1.717**	**0.706**	**2.434**	**0.022***
	Moss	1.162	0.754	1.541	0.136
	Tall vegetation	1.181	0.752	1.570	0.129
	Wetland	1.313	0.741	1.771	0.089
Coleoptera	(Intercept)	-0.143	0.373	-0.384	0.704
	Grassland	-0.008	0.529	-0.016	0.987
	Heathland	-0.338	0.549	-0.615	0.544
	Moss	-1.066	0.737	-1.446	0.161
	Tall vegetation	-0.379	0.585	-0.647	0.523
	Wetland	-0.350	0.580	-0.603	0.552
Collembola	(Intercept)	-0.143	0.373	-0.384	0.704
	Grassland	-0.008	0.529	-0.016	0.987
	Heathland	-0.338	0.549	-0.615	0.544
	Moss	-1.066	0.737	-1.446	0.161
	Tall vegetation	-0.379	0.585	-0.647	0.523
	Wetland	-0.350	0.580	-0.603	0.552
Lepidoptera	(Intercept)	**-4.547**	**0.643**	**-7.074**	**2.05e-07 *****
	Grassland	1.254	0.729	1.721	0.098
	Heathland	0.052	0.860	0.061	0.952
	Moss	0.334	0.842	0.396	0.695
	Tall vegetation	-0.017	0.913	-0.019	0.985
	Wetland	-0.935	1.211	-0.773	0.447

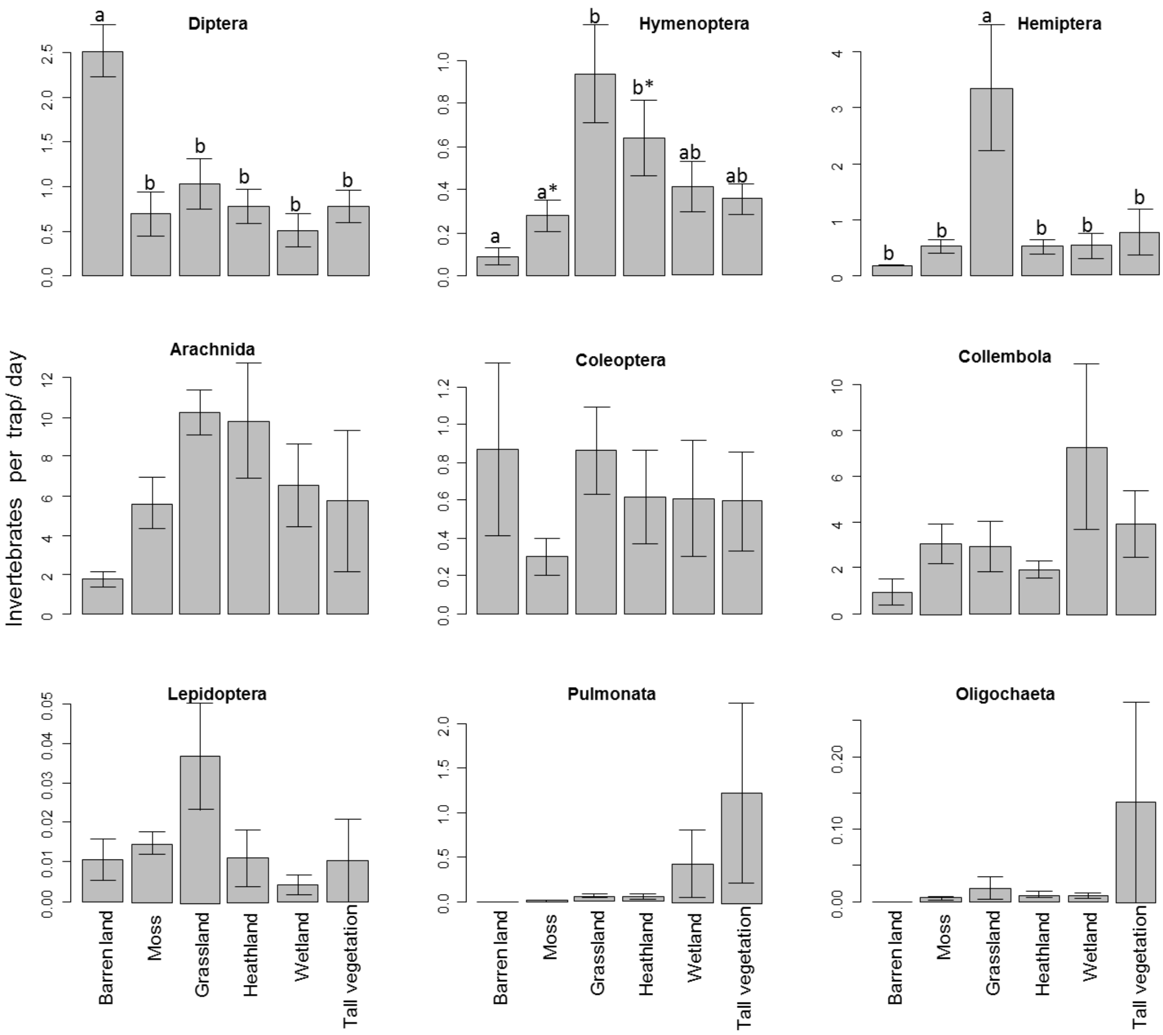

Figure 10. Mean catch of invertebrates (animals/per/day) by group (± SE) in Hekluskógar 2011-2012. n= 31 sites. Note the different scales on y-axis. The three groups on top showed significant differences between habitats, the others not. Different letters indicate significant differences between habitats.

3.2.2. Invertebrate biomass

Mean biomass per unit catch (mg/trap/day, wet weight) of all invertebrates ranged from 2.99 (SE= 1.25) in barren land to 23.1 (SE= 9.74) in wetland and tended to increase with increasing vegetation succession. A significant difference was among mean ranks of barren land and wetland (Kruskal-Wallis test, H= 11.22, 5 d.f., P = 0.047, Figure 11).

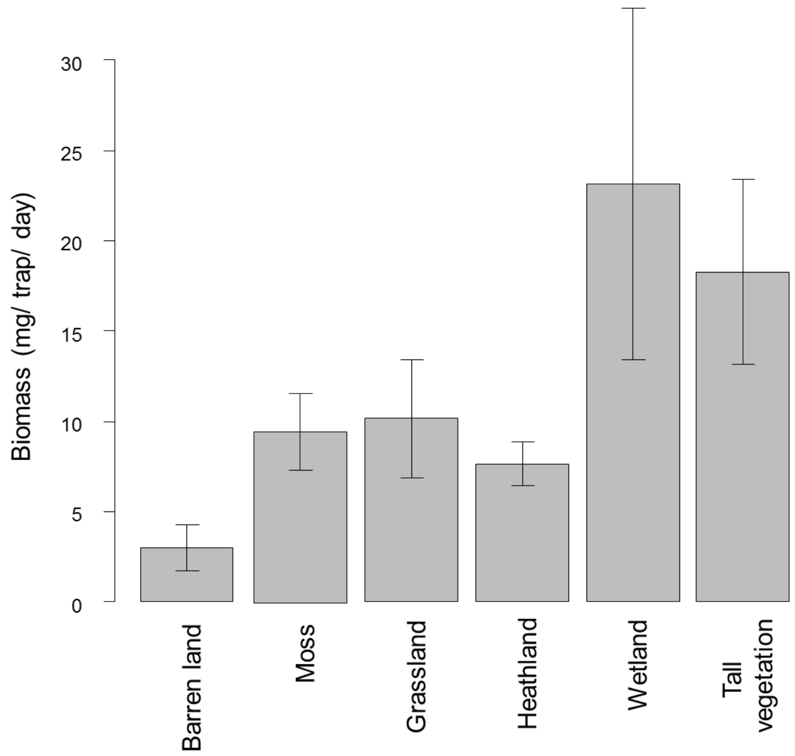

Figure 11. Mean invertebrate biomass (mg/trap/day) in pitfall traps (±SE) in Hekluskógar 2011-2012. n= 31 sites.

3.2.3. Invertebrate communities

To identify different communities for invertebrates, a Principal Components Analysis (PCA) was made for the nine invertebrate groups similarly as for birds. The first four components explained 71% of the variation (Table 9) and were retained. The four components are shown in Figure 12.

Scores from the PCA were correlated with vegetation variables to assess the prevalence of different invertebrate groups in relation to habitat (Table 10). PC1 (characterised by True bugs, Arachnids and Moths) was positively correlated with cover of grass (r = 0.3616, P= 0.0456). There was a negative relationship between PC2 (characterised by Hymenopterans, Beetles and Springtails) and cover of moss (r = -0.4234, P = 0.0176). True flies (PC3) were negatively correlated to grassland (r = 0.4075, P = 0.0229) and tall vegetation (r = 0.3551, P = 0.05). Earthworms (PC4) correlated with tall vegetation (r = 0.3541, P = 0.05).

Table 9. PCA loadings with 4 components for invertebrates caught in pitfall traps in Hekluskógar. Factor loadings < -0.5 and > 0.5 are shown in bold.

	PC1	**PC2**	**PC3**	**PC4**
Diptera	-0.04	0.15	**-0.86**	-0.16
Hymenoptera	0.55	**0.51**	-0.09	0.45
Hemiptera	**0.80**	-0.08	-0.19	0.27
Arachnida	**0.70**	-0.18	0.44	-0.29
Coleoptera	0.06	**0.88**	-0.11	0.04
Collembola	0.32	**0.50**	0.37	-0.25
Lepidoptera	**0.81**	-0.33	-0.13	0.01
Pulmonata	-0.22	0.34	0.42	0.02
Oligocheata	-0.24	-0.19	0.21	**0.80**
% Variance explained	25.5	17.8	15.2	12.0

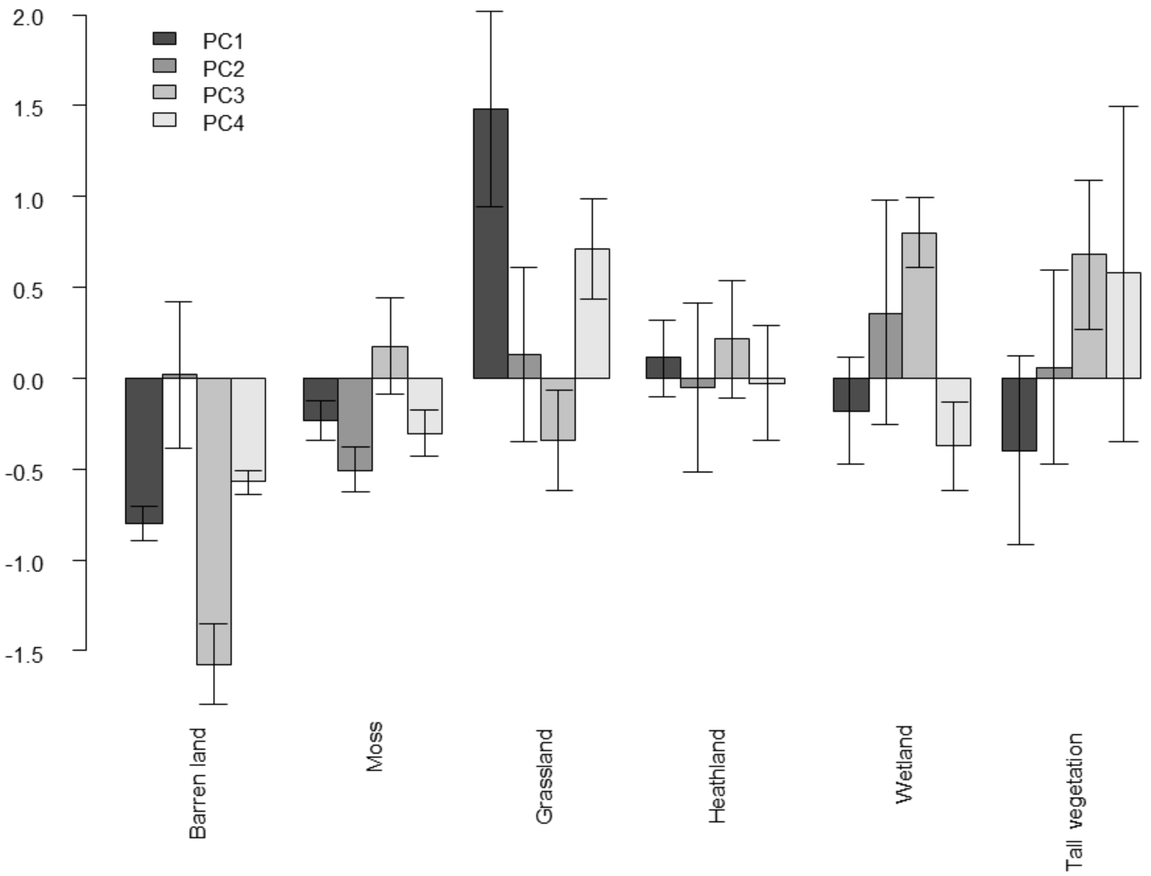

Figure 12. Mean (± SE) factor scores of the two factors from a principal components analysis of the invertebrate catches for each of the six habitat types in Hekluskógar 2011-2012. n= 31.

Table 10. Correlations between principal component factors and growth variables in Hekluskógar. Significant relationships are shown in bold.

	Moss		Grass		Bushes and lupin		Dwarf shrubs and herbs	
	r	P	r	P	r	P	r	P
PC1	0.2286	0.2161	**0.3616**	**0.0456**	-0.2125	0.2512	0.1783	0.3372
PC2	**-0.4234**	**0.0176**	0.1141	0.5410	0.2170	0.2410	-0.0960	0.6075
PC3	0.2725	0.1381	**0.4075**	**0.0229**	**0.3551**	**0.0500**	0.1542	0.4074
PC4	0.2979	0.1036	0.0071	0.9699	**0.3541**	**0.0506**	-0.0163	0.9307

Mean PCA scores were compared between habitat types to explore habitat related differences in invertebrate communities. PC 1 and PC 3 had significant differences among them (ANOVA on mean factor scores for invertebrates; Factor 1: $F_{5,25}$= 5.296, P= 0.002, Factor 3: $F_{5,25}$= 8.53, P< 0.001).

3.2.4. Invertebrate diversity

Different measures of invertebrate diversity were generally similar between habitat types with average number of families caught per habitat (standardized by effort) ranging between ca. 16 and 20 (Table 11). Average number of families was lowest on barren land and highest in tall vegetation, although the Shannon entropy index was lowest in moss (Figure 14b). No significant differences were found between habitats when comparing the average number of families per trap.

Table 11. Total number and diversity of invertebrate families in the six different habitats in Hekluskógar 2011-2012. Effective number of families ("True diversity") is the exponent of the Shannon entropy.

Habitat	**Average number of families recorded per trap**	**Average Shannon entropy index and SD**	**Effective number of families**
Barren land	16.13	1.8758 ± 0.2740	6.53
Moss	17.33	1.6482 ± 0.3037	5.20
Grassland	20.4	1.811 ± 0.3515	6.12
Heathland	19.06	1.7635 ± 0.7741	5.83
Wetland	16.27	1.689 ± 0.2103	5.41
Tall vegetation	20.15	1.9232 ± 0.4446	6.84

3.3. Bird and invertebrate relationships

Bird density (birds/km^2) and invertebrate biomass (mg/trap/day) were not correlated at the sample level as variation within habitats was high (n= 31), but the average bird density correlated strongly with the average biomass at the habitat level (Pearson r_4= 0.925, P=0.008, Figure 13).

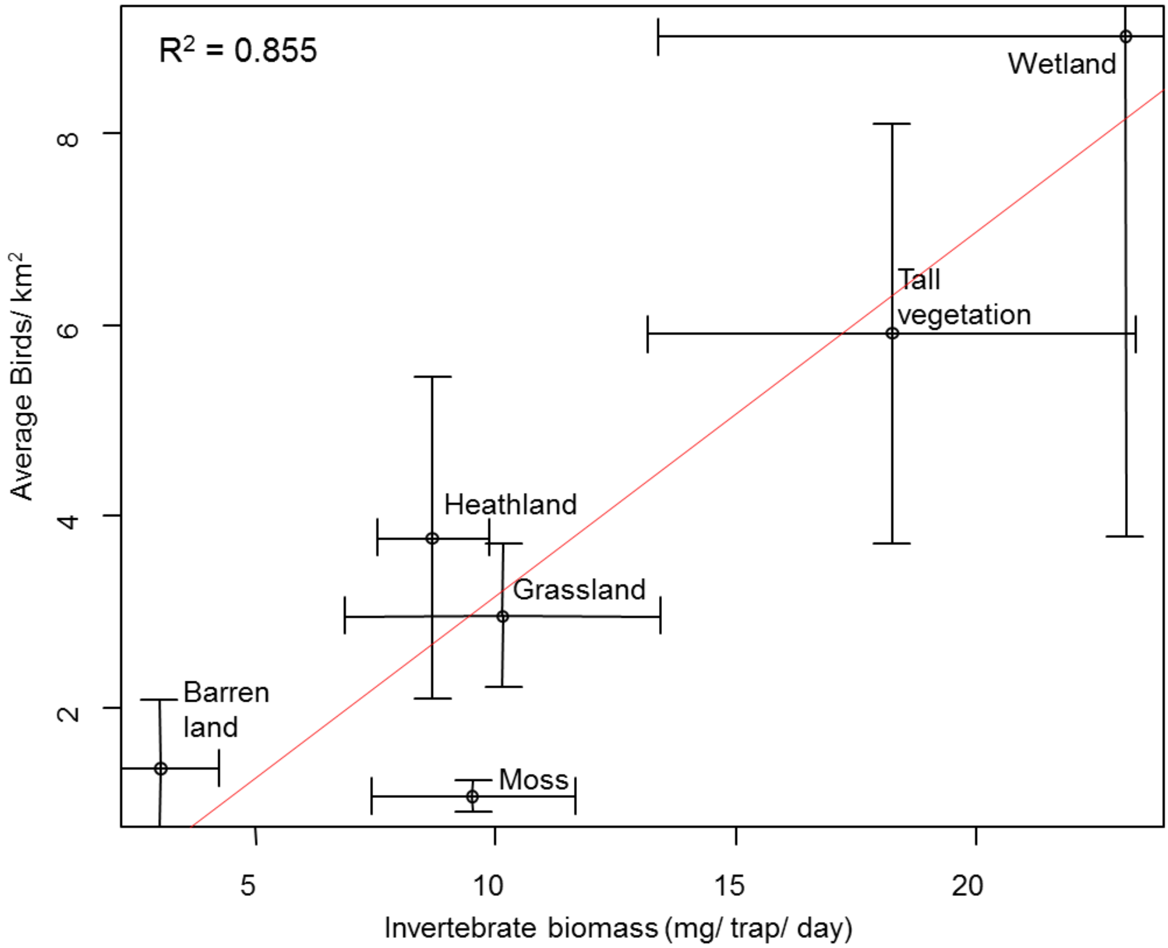

Figure 13. Relationship between mean invertebrate biomass and mean bird density (± X and Y SE) in each of the six habitats in Hekluskógar 2011-2012. n= 6.

When comparing bird and invertebrate diversity (Shannon entropy index), the main difference was the gradual increase in bird diversity with increasing succession but invertebrate diversity showed little difference between habitats (Figure 14).

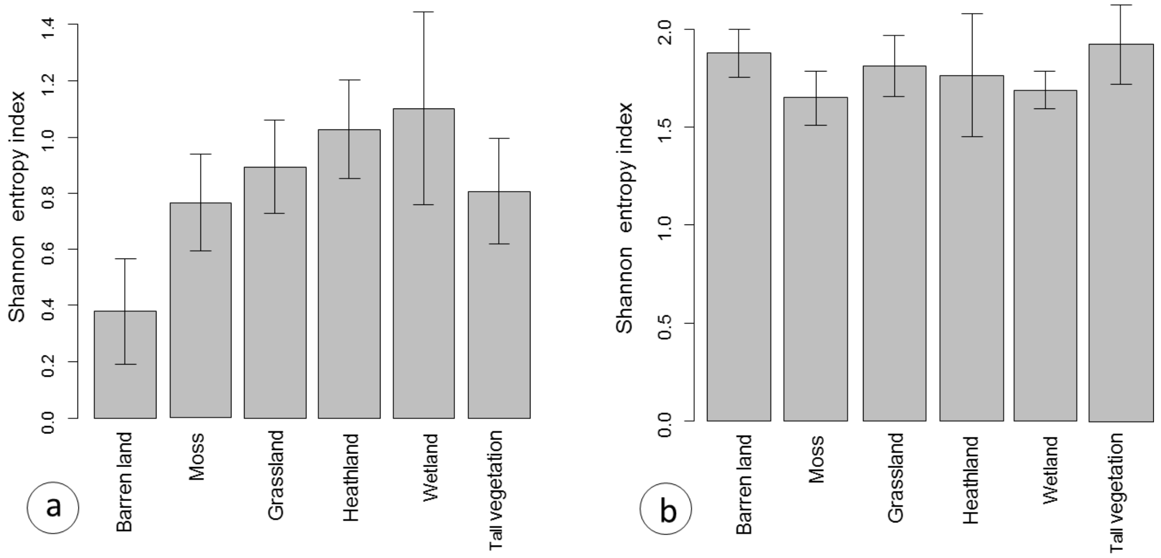

Figure 14. a) Average bird and b) invertebrate diversity using Shannon entropy index (± SE) of each of the six habitats in Heklukógar 2011-2012.

When considering the three-way relationship between vegetation cover, bird density and invertebrate catch, a Detrended Correspondance Analysis (DCA) showed that all habitats overlap, except for tall vegetation (Figure 15). The variables diagnostic of tall vegetation are Snipe and Meadow pipit, bushes and Earthworms.

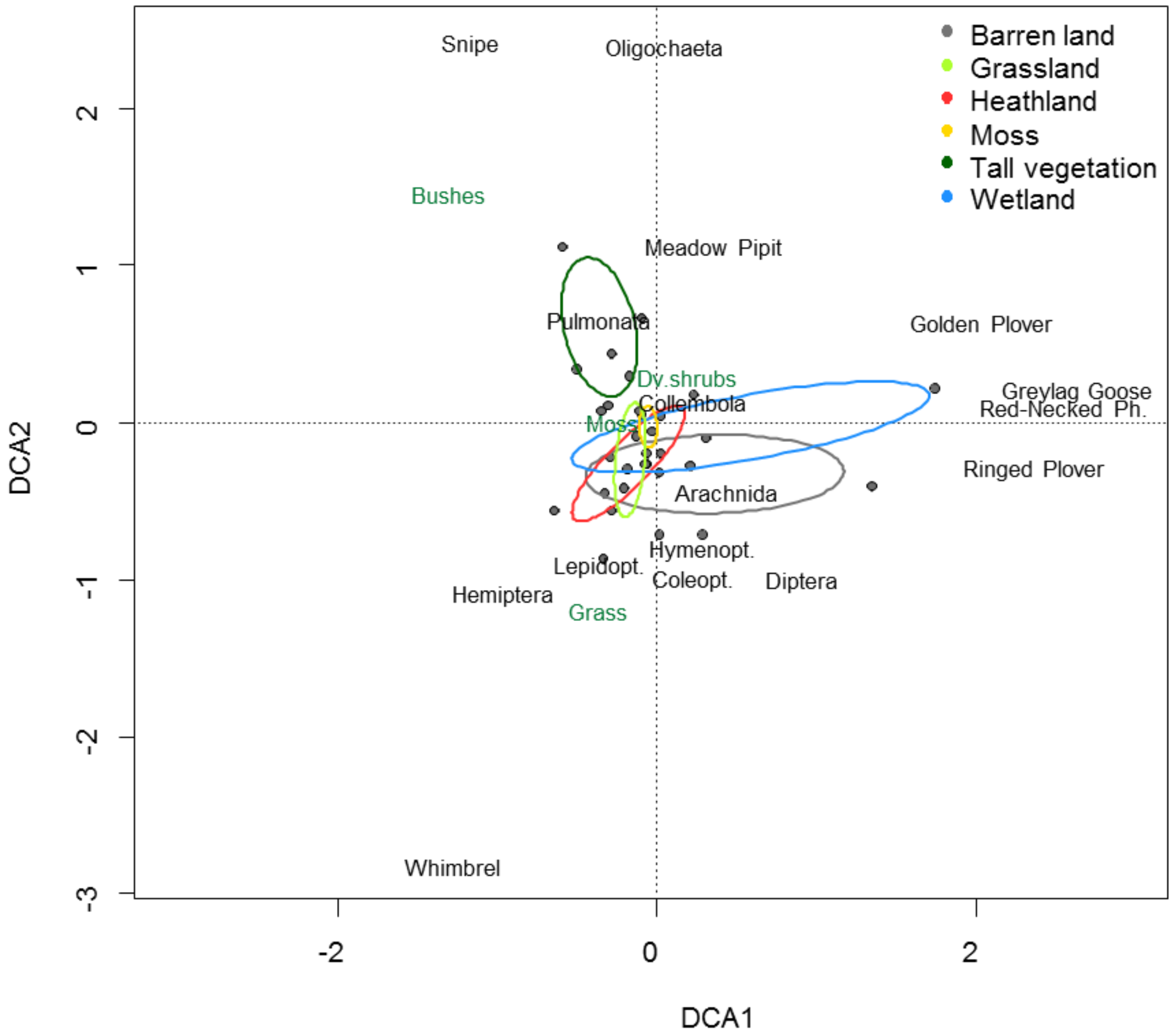

Figure 15. The first two components of a Detrended Correspondence Analysis (DCA) for invertebrates and birds in the six habitats (shown as ellipses around sites (grey dots)) with vegetation cover as environmental factors.

4 Discussions

This study compared biodiversity of birds and invertebrates on different habitats in a large area in South Iceland, which has been under pressure from erosion, volcanic activity and human impact for centuries and where vegetation restoration action is on-going. The aim was to investigate the relationship of bird and invertebrate biodiversity to habitats which are on a gradient of succession and to provide a baseline for future studies of the impact of volcanic eruptions and revegetation efforts in the study area. Six different habitat types were studied and birds and invertebrates sampled in a stratified random manner. For both birds and invertebrates, measures included density and diversity. In addition, predictors of bird occurrence and invertebrate biomass were calculated.

Both bird and invertebrate density increased with increasing vegetation and subsequent refuge from erosive forces, confirming other studies (e.g. Davíðsdóttir, 2013; Tómas G. Gunnarsson & Indriðadóttir, 2009; Halldórsson & Oddsdóttir, 2007; Jóhannesdóttir, 2013; Milcu, Partsch, Langel, & Scheu, 2006; Mills, Dunning Jr, & Bates, 1991; Ólafsson & Ingimarsdóttir, 2007). Furthermore, bird diversity and predicted occurrence increased with succession as did invertebrate biomass. Biodiversity decreases with land degradation (Aradóttir, 2007b) so consequently, biodiversity generally increases with succession (Jóhannesdóttir, 2013) especially in the early phases (Walker & del Moral, 2003). The only measure which showed little relationship with succession was invertebrate diversity.

4.1. Bird and invertebrate density in relation to succession

Barren land is likely to suffer the most erosion. It sustains life supporting factors like nutrients, water and shelter poorly. In this study, barren land had the lowest densities of birds, confirming other studies from Iceland which have shown that unvegetated land has the lowest densities of birds (Davíðsdóttir, 2013; Tómas. G. Gunnarsson et al., 2006; Tómas G. Gunnarsson & Indriðadóttir, 2009). Barren land had also the lowest density of invertebrates (as in e.g. Oddsdóttir et al., 2008), for all groups but True flies. Flies are significantly more frequently found in barren land than in the other habitats and the PCA showed that True flies were least likely to occur in traps in areas of high vegetation cover. This could be the result of a bias of the pitfall traps in catching different taxa. Pitfall traps on the ground that catch high number of flying insects could have some unknown attraction for them (Greenslade & Greenslade, 1971), e.g. as active or passive shelter. In addition, pitfall traps are more likely to catch larger invertebrates, for smaller animals can more readily escape from the traps (Lang, 2000).

Mosses are primary colonizers on barren land. In harsh conditions, like in Hekluskógar, mosses have been found to facilitate vascular plant growth. They have a high thermal insulation and water-holding capacities (Longton, 1997) and serve as seed traps (Groeneveld, Masse, & Rochefort, 2007) but they can also have a negative influence on seedling survival (Jeschke & Kiehl, 2008; Jónsdóttir, 2009). In this study, very few birds were seen on moss or similar density as on barren land but other studies in Iceland has shown higher density on moss (e.g. S. H. Magnússon et al. (2009).

Invertebrates were on the other hand more abundant in mossy areas. Mites are often associated with mosses (Gerson, 1969) which were the most abundant invertebrates found in there.

Soil fauna density has been found to be significantly correlated with vascular plant cover (Oddsdóttir et al., 2008) and here the highest invertebrate abundance in this study was in grassland. The most abundant invertebrates were leafhoppers and aphids, which are very small but are nevertheless eaten by shorebird chicks (Schekkerman & Beintema, 2007). Mites were also commonly found in grassland, but they are often the most abundant invertebrate species in temperate grasslands, especially on surfaces with accumulation of organic matter (Curry, 1994). Wasps were commonly found in grasslands. All the wasps in the study are parasites on either vegetation (saw wasps) or on other invertebrates. They are therefore obliged to vegetated habitats with prey species like aphids and caterpillars (Halldórsson, Sigurðsson, & Ólafsson, 2002). It is therefore not surprising that the most abundance of Hymenopterans, True Bugs and Moths are in the same habitat (Tables 9 and 10). Some parasitic wasps prey on beetles too, which are also common in grassy areas (Fouts, 1948). Of birds, Whimbrel was most commonly found in heath- and grasslands. Feeding mostly on large surface invertebrates, they are not bound to wetlands and nest equally on dry and wet areas (Garðarsson, 1998). In grasslands sheep were grazing on few study plots. Shorebirds often utilize the same habitats as livestock, maybe because of insects that feed on dung or merely because low-intensity grazing stops the vegetation from growing tall Grazing can thus improve conditions for shorebirds, through increased visibility and lower transport costs for their self-feeding chicks (Székely, Karsai, & Kovács, 1993). Some other shorebirds, such as Black-tailed Godwits and Redshanks prefer uncut and ungrazed grass for their broods (Schekkerman & Beintema, 2007).

Invertebrate biomass was not highest were the highest invertebrate density was, in grassland. The biomass was highest in wetland and tall vegetation and showed a significant relationship with bird density (Figure 13) when comparing means. The habitat that deviated furthest from the trend line was moss, but as earlier mentioned, moss was different from other habitats for its abundance of invertebrates but few birds. Otherwise, the relationship between mean bird abundance and invertebrate biomass was relatively strong. Invertebrates form the majority of the diet of the most abundant bird species in the study but birds and invertebrates also share favourable conditions, which relate to primary productivity and cover. Variation in invertebrate biomass is somewhat driven by the size of dominant groups in each habitat but food item size can be an important driver of bird abundance (e.g. in van de Kam, Ens, Piersma, & Zwarts, 2004).

In this study, heathland was in intermediate group in bird and invertebrate density. Bird density in heathland was though a little higher than in grassland, but that is reversed from Jóhannesdóttir (2013) who studied lowland habitats exclusively and invertebrate density is also higher in grassland than in heathland.

Golden plovers were most abundant in wetland, as well as the total bird density which is in accordance to a study done on Icelandic highland ecosystems (S. H. Magnússon et al., 2009). The shorebirds, which are a dominating group of terrestrial birds in Iceland, generally breed in highest densities in wetlands (Tómas. G. Gunnarsson et al., 2006; Jóhannesdóttir, 2013). Chicks depend on invertebrates emerging from the water (Schekkerman & Beintema, 2007) and adults feed on invertebrates in shallow water. Some passerines, like Meadow pipit, have also shown a preference for wetlands(Tómas G.

Gunnarsson et al., 2007). Springtails were the most frequently caught invertebrates in wetland, although they were found in all habitats.

Passerines, e.g. Meadow pipit and Redwing (*Turdus iliacus*) preferred tall vegetation. Most shorebirds avoid forested areas (Tómas. G. Gunnarsson et al., 2006; Sutherland et al., 2012), especially dense forests, but sparsely forested areas and early succession stages of other taller vegetation like the Nootka Lupin can be preferred by Common snipe (Davíðsdóttir, 2013; Elmarsdóttir et al., 2011). The occurrence of shorebirds and Meadow pipit was significantly and positively correlated with the total vegetation cover (Figure 7). There were a few samples where vegetation cover was high but without birds and vice versa: little vegetation and many birds. An observation of the data points which did not fit the relationship showed that other environmental factors, like precipitation, temperature, time of day and wind velocity could influence the birds detected although they did not have any one factor in common. It is therefore likely that an interaction of these factors influences bird detectability and that both true and false absences/presences occurred.

Of invertebrates in tall vegetation, Arachnids were most common in this study, followed by Springtails, which is in accordance to Oddsdóttir et al. (2008). Earthworms were more often found in Tall vegetation than other habitats. Earthworm density is often linked directly to plant primary production which is in turn affected by plant species richness (Milcu et al., 2006; Spehn, Joshi, Schmid, Alphei, & Körner, 2000).

4.2. Diversity of birds and invertebrates in relation to succession

In this study, barren land had the lowest diversity of birds. Heathland and wetland had the highest bird species richness but tall vegetation only medium diversity. Other studies have shown that in the first stages of reclamation, species richness increases. This is caused by new colonising species added to those that were before in the area and have the ability to adapt to the new circumstances (Marquiss, 2007).

Invertebrates had the highest diversity in tall vegetation and the lowest in moss and wetland. Other studies show a relationship of invertebrate diversity with vegetation diversity (Crisp, Dickinson, & Gibbs, 1998) but the latter was not measured in this study. The Shannon diversity index was second highest in barren land although it had the fewest average families caught. This bias could be caused by the fact that mites, a group with high densities, were not identified into families like many other invertebrate groups. Identification of mites is very difficult and time consuming (Halldórsson et al., 2002).

The diversity of organisms is affected by the environment but in turn affects ecosystem resilience (Elmqvist et al., 2003). For example, plant cover has not only a physical effect on soil stabilization, i.e. as wind-breakers and anchors, but plant diversity seems to have a positive effect on stabilizing soil. This is due to diverse below-ground growth forms consisting of both fine and coarse root systems (Pohl et al., 2009).

Active land reclamation, as opposed to spontaneous succession, greatly enhances reclamation success of barren land (Whisenant, 1999). Fertilization and addition of seeds or plants trigger the succession on such areas (Grétarsdóttir et al., 2004), increasing niches for invertebrates (Oddsdóttir et al., 2008) and vertebrates (Tómas G. Gunnarsson & Indriðadóttir, 2009). This reduces water run-off too (Whisenant, 1999) creating wetland oases. The water added to the habitats seems to be a very important factor in determining animal density and diversity in Hekluskógar. For instance, the bird PCA was not able to correlate known wetland birds (Golden plover, Red-necked phalarope and Greylag goose) to any vegetation type and species of wet and dry habitats grouped together.

4.3. Survey issues

The approach and sampling scheme of this study was large scale. This has both positive and negative effects when trading off gain and resources such as generality of results and fieldwork effort. The negative effects are mainly that, when the area is large and variable in terms of several external factors, the variation in measured variables within habitats is high and the statistical certainty will be lower. On the positive side, a study at this spatial scale captures the inherent large scale variation which is necessary for any generalization of results to larger areas and habitat types and is as such a good basis for any more local studies. When setting out baseline studies to estimate the effects of future environmental change, like of restoration and volcanism, it is also better to spread the study plots out to increase the probabilities of successfully estimating impact.

The spring of 2011 was unusual in terms of weather and volcanism, as opposed to average temperatures in 2012. In early May 2011 the temperatures were far above average but at the end of the month a very cold period turned the unusual amount of precipitation into snow. The temperatures dropped down to -14°C in the highlands (Icelandic Met Office, 2011). In addition, a volcanic eruption began in Grímsvötn (about 125 km east of Mt. Hekla) on May 21, 2011. This eruption lasted one week or until May 28 (Thorlacius, 2011). More ash than in the eruption of Eyjafjallajökull 2010 was blown out into the atmosphere and the first two days, heavy ash fall occurred south west of the volcano (Björnsson & Arason, 2011) and onto the Hekluskógar study area. Arthropods (i.e. invertebrates with exoskeleton) are desiccated by ash, as it abrasives the cuticle and clogs the spiracles (Marske, Ivie, & Hilton, 2007). It is therefore expected that the ash may have had some influence on invertebrates in the area. The effects of ash on vertebrates is mainly in the form of lower invertebrate food supply (Marske, 2004). These unusual conditions are likely to be one of the factors which contributed to the variation in measured variables. But the high correlations between bird and invertebrate numbers on the plots from 2011 which were repeated in 2012 suggest that temporally more stable factors, like the effect of habitat type, do override the annual effect.

4.4. General conclusions

This study was undertaken to gain further understanding of the effects of vegetation succession and erosion on terrestrial animal diversity in Iceland and to be a yardstick on which to estimate the future effects of volcanism and vegetation reclamation in the Hekluskógar area. It demonstrates the current relationship of birds and invertebrates to habitats on a successional gradient. Areas, where plant succession is more advanced, have generally more animal density and diversity. Looking at the succession from one habitat to another, it is clear that most are quite similar, possibly due to the short time for which they have evolved. Barren land supports the lowest animal density and diversity on average but wetland the most, indicating that it is not necessarily vegetation cover that is the most important factor influencing animal biodiversity and density. Other factors that contribute to within-habitat heterogeneity, e.g. the presence of water in an otherwise desert area are very important drivers of animal abundance and diversity.

5 References

Andersen, A. N., Fisher, A., Hoffman, B. D., & Read, J. L. (2004). Use of terrestrial invertebrates for biodiversity monitoring in Australian rangelands, with particular reference to ants. *Australian Ecology, 29,* 87-92.

Aradóttir, Á. L. (2007a). Restoration of birch and willow woodland on eroded areas. In G. Halldórsson, E. S. Oddsdóttir & Ó. Eggertsson (Eds.), *Effects of afforestation on ecosystems, landscape and rural development, Proceedings of the AFFORNORD conference, Reykholt, Iceland, June 18-22, 2005* (Vol. 2007:508, pp. 67-74). Copenhagen: Nordic Council of Ministers.

Aradóttir, Á. L. (2007b). *The Role of Ecological Restoration and Sustainable Land Management for Biodiversity* Paper presented at the International Forum Celebrating the Centenary of Conservation and Restoration of Soil and Vegetation in Iceland, Selfoss, Iceland.

Aradóttir, Á. L., & Arnalds, Ó. (2001). Ecosystem degradation and restoration of birch woodlands in Iceland. In F. E. Wielgolaski (Ed.), *Nordic mountain birch ecosystems* (pp. 293-306).

Aradóttir, Á. L., Arnalds, Ó., & Archer, S. (1992). Hnignun gróðurs og jarðvegs. In Andrés Arnalds (Ed.), *Græðum Ísland. Landgræðslan 1991-1992*: Landgræðsla ríkisins.

Arnalds, A., & Runólfsson, S. (2007). *Iceland's Century of Conservation and Restoration of Soils and Vegetation.* Paper presented at the International Forum Celebrating the Centenary of Conservation and Restoration of Soil and Vegetation in Iceland, Selfoss, Iceland.

Arnalds, Ó. (2004). Volcanic soils of Iceland. *Catena, 56,* 3-20.

Arnalds, Ó., Þórarinsdóttir, E. F., Metúsalemsson, S., Jónsson, Á., Grétarsson, E., & Árnason, A. (1997). Jarðvegsrof á Íslandi: Soil Conservation Service of Iceland and the Agricultural research institute.

Bagnold, R. A. (1988). *The Physics of Sediment Transport by Wind and Water: A Collection of Hallmark Papers*: The American Society of Civil Engineers.

Bibby, C. J., Burgess, N. D., & Hill, D. A. (1992). *Bird Census Teqniques*. London: Academic Press Limited.

Björnsson, H., & Arason, ó. (Producer). (2011, 29.4.2013). Grímsvötn 2011: Eldgosið frá veðurfræðilegu sjónarhorni. [Powerpoint slides] Retrieved from http://vedur.org/wp-content/uploads/2011/07/Grimsvotn2011VFRV2.pdf

Breshears, D. D., Whicker, J. J., Zou, C. B., Field, J. P., & Allen, C. D. (2009). A conceptual framework for dryland aeolian sediment transport along the grassland–forest continuum: Effects of woody plant canopy cover and disturbance. *Geomorphology, 105*(1-2), 28-38.

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L., & Thomas, L. (2001). *Introduction to Distance Sampling. Estimating abundance of biological populations*. New York: Oxford University Press.

Butchart, S. H. M., Walpole, M., Collen, B., Strien, A. v., Scharlemann, J. P. W., Almond, R. E. A., . . . Watson, R. (2010). Global Biodiversity: Indicators of Recent Declines. *Science, 328*, 1164-1168.

Chew, S. C. (2001). *World Ecological Degradation: Accumulation, Urbanization, and Deforestation, 3000bc-ad2000*. England: Rowman & Littlefield Publishers, Inc. .

Christensen, N. L., & Muller, C. H. (1975). Effects of Fire on Factors Controlling Plant Growth in Adenostoma Chaparral. *Ecological Monographs, 45*(1), 29-55.

Collins, P. T. (1992). Length-Biomass Relationships for Terrestrial Gastropoda and Oligochaeta. *American Midland Naturalist, 128*(2), 404-406.

Connell, J. H., & Slatyer, R. O. (1977). Mechanisms of succession in natural communities and their role in community stability and orgainzation. *The American Naturalist, 111*(982), 1119-1144.

Convention on Biological Diversity. (2002). Strategic Plan for the Convention on Biological Diversity. *COP 6 Decision VI/26* Retrieved 1.5.2013, from http://www.cbd.int/decision/cop/default.shtml?id=7200

Costa, M. H., Botta, A., & Cardille, J. A. (2003). Effects of large-scale changes in land cover on the discharge of the Tocantins River, Southeastern Amazonia. *journal of Hydrology, 283*, 206-217.

Crisp, P. N., Dickinson, K. J. M., & Gibbs, G. W. (1998). Does native invertebrate diversity reflect native plant diversity? A case study from New Zealand and implications for conservation. *Biological Conservation, 83*(2), 209-220.

Curry, J. P. (1994). *Grassland Invertebrates: Ecology, Influence on Soil Fertility and Effects on Plant Growth*. London: Chapman & Hall.

Dale, V. H., Delgado-Acevedo, J., & MacMahon, J. (2005). Effects of modern volcanic eruptions on vegetation. In J. Martí & G. Ernst (Eds.), *Volcanoes and the environment* (pp. 227-249). Cambridge: Cambridge University Press.

Davíðsdóttir, B. (2013). *The effect of vegetation reclamation on birds and invertebrates. A comparative study of barren land, restored heathland and land revegetated by Nootka lupin.* Master's thesis, Agricultural University of Iceland.

Deyn, G. B. D., Raaijmakers, C. E., Zoomer, H. R., Berg, M. P., Ruiter, P. C. d., Verhoef, H. A., . . . Putten, W. H. v. d. (2003). Soil invertebrate fauna enhances grassland succession and diversity. *Nature, 422*, 711-713.

Einarsson, E. (2005). Flóra og gróður Íslands *íslandsatlas*. Reykjavik: Edda útgáfa hf. & Fixlanda ehf.

Elmarsdóttir, Á., Sigurðsson, B. D., Oddsdóttir, E. S., Fjellberg, A., Guðleifsson, B. E., Magnússon, B. ó., . . . Nielsen, Ó. K. (2011). Áhrif skógræktar á tegundaauðgi. *Náttúrufræðingurinn, 81*(2), 69-81.

Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B., & Norberg, J. (2003). Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment, 1*(9), 488-494.

Eswaran, H., & Dumanski, J. (1994). *Land degradation and sustainable agriculture: A global perspective.* Paper presented at the 8th International Soil Conservation Conference, New Dehli, India.

Eswaran, H., Lal, R., & Reich, P. F. (2001). *Land Degradation: An overview.* Paper presented at the Responses to Land Degradation. Proc. 2nd. International Conference on Land Degradation and Desertification, Khon Kaen, Thailand.

Field, J. P., Breshears, D. D., & Whicker, J. J. (2009). Toward a more holistic perspective of soil erosion: Why aeolian research needs to explicitly consider fluvial processes and interactions. *Aeolian Research, 1*, 9-17.

Fouts, R. M. (1948). Parasitic wasps of the genus Trimorus in North America. *Proceedings Of The United States National Museum, 98*, 91-148.

Garðarsson, A. ó. (1998). Íslensk votlendi. In J. S. Ólafsson (Ed.), *Íslensk votlendi - verndun og nýting*: Háskólaútgáfan.

Gathorne-Hardy, F. J., Erlendsson, E., Langdon, P. G., & Edwards, K. J. (2009). Lake sediment evidence for late Holocene climate change and landscape erosion in western Iceland. *Journal of Paleolimnology, 42*, 413-426.

Gerson, U. (1969). Moss-Arthropod Associations. *The Bryologist, 72*(4), 495-5000.

Giller, K. E., Beare, M. H., Lavelle, P., Izac, A.-M. N., & Swift, M. J. (1997). Agricultural intensification, soil biodiversity and agroecosystem function. *Applied Soil Ecology, 6*, 3-16.

Gray, D. H., & Sortir, R. B. (1996). *Biotechnical and soil bioengineering slope stabilization: a practical guide for erosion control*: John Wiley & Sons Inc.

Greenslade, P., & Greenslade, P. J. M. (1971). The use of baits and preservatives in pitfall traps. *Australian Journal of Entomology, 10*, 253-260.

Gregory, R. (2006). Birds as biodiversity indicators for Europe. *Significance*, 106-110.

Greipsson, S., & Davy, A. J. (1994). *Leymus arenarius*. Characteristics and uses of a dune-building grass. *Icelandic Agricultural Sciences, 8*, 41-50.

Grétarsdóttir, J., Aradóttir, Á. L., Vandvik, V., Heegaard, E., & Birks, H. J. B. (2004). Long-Term Effects of Reclamation Treatments on Plant Succession in Iceland. *Restoration Ecology, 12*(2), 268-278.

Groeneveld, E. V. G., Masse, A., & Rochefort, L. (2007). *Polytrichum strictum* as a Nurse-Plant in Peatland Restoration. *Restoration Ecology, 15*(4), 709-719.

Guðmundsson, A. T. (2001). *Íslenskar eldstöðvar*: Vaka Helgafell.

Gunnarsson, T. G., Appleton, G. F., Gíslason, H., Garðarsson, A. ó., Atkinson, P. W., & Gill, J. A. (2007). Búsvæðaval og stofnstærð þúfutittlings á láglendi. *Bliki, 28*, 19-24.

Gunnarsson, T. G., Gill, J. A., Appleton, G. F., Gíslason, H., Garðarsson, A. ó., Watkinson, A. R., & Sutherland, W. J. (2006). Large-scale habitat associations of birds in lowland Iceland: Implications for conservation. *Biological Conservation, 128*, 265-275.

Gunnarsson, T. G., & Indriðadóttir, G. H. (2009). Effects of sandplain revegetation on avian abundance and diversity at Skogasandur and Myrdalssandur, South-Iceland *Conservation Evidence 6*, 98-104.

Halldórsson, G., Aradóttir, Á. L., Fosaa, A. M., Hagen, D., Nilsson, C., Raulund-Rasmussen, K., . . . Tolvanen, A. (2012). *ReNo. Restoration of damaged ecosystems in the Nordic countries*: Nordic Council of Ministers.

Halldórsson, G., & Oddsdóttir, E. S. (2007). ICEWOODS: The effects of afforestation on the abundance of soil fauna in Iceland. In G. Halldórsson, E. S. Oddsdóttir & Ó. Eggertsson (Eds.), *Effects of afforestation on ecosystems, landscape and rural development, Proceedings of the AFFORNORD conference, Reykholt, Iceland, June 18-22, 2005* (Vol. 2007:508, pp. 147-151). Copenhagen: Nordic Council of Ministers.

Halldórsson, G., Sigurðsson, O., & Ólafsson, E. (2002). *Dulin veröld: smádýr á Íslandi*: Mál og Mynd ehf.

Hallsdóttir, B. S., Wöll, C., Guðmundsson, J., Snorrason, A., & Þórsson, J. (2013). Emissions of greenhouse gases in Iceland from 1990 to 2011 *National Inventory Report 2013*: Environmental Agency of Iceland.

Holechek, J. L., Gomez, H., Molinar, F., & Galt, D. (1999). Grazing Studies: What We've Learned. *Rangelands, 21*(2), 12-16.

Hooke, J., & Sandercock, P. (2012). Use of vegetation to combat desertification and land degradation: Recommendations and guidelines for spatial strategies in Mediterranean lands. *Landscape and Urban Planning, 107*, 389-400.

Icelandic Met Office. (2011). Tíðarfar í maí 2011 Retrieved 29.4.2013, from http://www.vedur.is/um-vi/frettir/2011/nr/2194 & http://www.vedur.is/um-vi/frettir/nr/2507

Jeschke, M., & Kiehl, K. (2008). Effects of a dense moss layer on germination and establishment of vascular plants in newly created calcareous grasslands. *Flora, 203*, 557-566.

Johnson, D. L., & Lewis, L. A. (2007). *Land Degradation: Creation and Destruction* (2 ed.). UK: Rowman & Littlefield Publishers, Inc.

Jost, L. (2006). Entropy and diversity. *Oikos, 113*(2), 363-375.

Jóhannesdóttir, L. (2013). *Comparing biodiversity of birds in different habitats in South Iceland.* Master´s thesis, Agricultural University of Iceland.

Jónsdóttir, J. B. (2009). *Gróðurframvinda í Skaftáreldahrauni og áhrif hraungambra (Racomitrium lanuginosum) á landnám háplantna.* Master´s thesis, Háskóli Íslands.

Jónsson, o. H. (2001). *Biological Diversity in Iceland, National Report to the Convention on Biological Diversity*. Reykjavík.

Klipple, G. E., & Bement, R. E. (1961). Light Grazing—Is it Economically Feasible as a Range-Improvement Practice. *Journal of Range Management, 14*(2), 57-62.

Kristinsson, H. (1974). Lichen Colonization in Surtsey 1971-1973 *Surtsey Research Progress Report VII* (pp. 9-16). Reykjavik: The Surtsey Research Society.

Kristinsson, H. (1995). Post-settlement history of Icelandic forests. *Búvísindi 9*, 31-35.

Lang, A. (2000). The pitfalls of pitfalls: a comparison of pitfall trap catches and absolute density estimates of epigeal invertebrate predators in arable land. *Journal of Pest Science, 73*, 99-106.

Larsen, F. W., Bladt, J., Balmford, A., & Rahbek, C. (2012). Birds as biodiversity surrogates: will supplementing birds with other taxa improve effectiveness? *Journal of Applied Ecology, 49*, 349-356.

Longton, R. E. (1997). The role of bryophytes and lichens in polar ecosystems. In S. J. Woodin & M. Marquiss (Eds.), *Ecology of Arctic Environments: 13th Special Symposium of the British Ecological Society*: The British Ecological Society & Blackwell Science Ltd.

Magnússon, B. (2006). NOBANIS – Invasive Alien Species Fact Sheet – Lupinus nootkatensis: Online Database of the North European and Baltic Network on Invasive Alien Species – NOBANIS

Magnússon, B., Magnússon, S. H., & Friðriksson, s. (2009). Developments in plant colonization and succession on Surtsey during 1999–2008 *Surtey Research* (Vol. 12, pp. 57-76).

Magnússon, S., & Friðriksson, S. (1974). Moss Vegetation on Surtsey in 1971 and 1972 *Surtsey Research Progress Report VII* (pp. 45-57). Reykjavik: The Surtsey Research Society.

Magnússon, S. H., Magnússon, B. ó., Ólafsson, E., Guðjónsson, G., Guðmundsson, G. A., Kristinsson, H., . . . Ottósson, J. G. (2009). Vistgerðir á miðhálendi Íslands. Flokkun, lýsing og verndargildi (pp. 175). Reykjavík: Náttúrufræðistofnun Íslands.

Magnússon, S. H., & Svavarsdóttir, K. (2007). Effects of sheep grazing protection on succession in sparsely vegetated areas in Iceland. *Fjölrit Náttúrufræðistofnun, 49*, 67 pp.

Majer, J. D. (1997). Invertebrates assist the restoration process: an Australian perspective. In K. M. Urbanska, N. N. R. Webb & P. J. Edwards (Eds.), *Restoration Ecology And Sustainable Development*. United Kingdom: Cambridge University Press.

Marquiss, M. (2007). AFFORNORD- 'Summing up' of ecosystem biodiversity sessions. The effect of afforestation on ecosystem biodiversity. In G. Halldórsson, E. S. Oddsdóttir & Ó. Eggertsson (Eds.), *Effects of afforestation on ecosystems, landscape and rural development, Proceedings of the AFFORNORD conference, Reykholt, Iceland, June 18-22, 2005* (Vol. 2007:508, pp. 167-169). Copenhagen: Nordic Council of Ministers.

Marske, K. A. (2004). *Effects of volcanic ash on the insect food of the Montserrat Oriole Icterus oberi Lawrence 1880.* Mastersritgerð, Montana State University, Bozeman.

Marske, K. A., Ivie, M. A., & Hilton, G. M. (2007). Effects of Volcanic Ash on the Forest Canopy Insects of Montserrat, West Indies. *Environmental Entomology 36*, 817-825.

Matson, P. A., Parton, W. J., Power, A. G., & Swift, M. J. (1997). Agricultural Intensification and Ecosystem Properties. *Science, 277*, 504-509.

Matthews, J. A. (1992). *The ecology of recently-deglaciated terrain: a geoecological approach to glacier forelands and primary succession*. Cambridge: Cambridge University Press.

McGovern, T. H., Vésteinsson, O., Fririksson, A., Church, M. J., Lawson, I. T., Simpson, I. A., . . . Dunbar, E. (2007). Landscapes of settlement in northern Iceland : historical ecology of human impact and climate fluctuation on the millennial scale. *American anthropologist, 109*(1), 27-51.

Meyer, W. B., & Turner, B. L. (1992). Human Population Growth and Global Land-Use/Cover Change. *Annual Review of Ecology and Systematics, 23*, 39-61.

Milcu, A., Partsch, S., Langel, R., & Scheu, S. (2006). The response of decomposers (earthworms, springtails and microorganisms) to variations in species and functional group diversity of plants. *Oikos, 112*, 513-524.

Millennium Ecosystem Assessment. (2005). Ecosystems and Human Well-being: Synthesis. Washington, D.C: World Resources Institute.

Mills, G. S., Dunning Jr, J. B., & Bates, J. M. (1991). The Relationship between Breeding Bird Density and Vegetation Volume. *The Wilson Bulletin, 103*(3), 468-479.

Ministry for the Environment, & the Icelandic Institute of Natural History. (2001). Biological Diversity in Iceland, National Report to the Convention on Biological Diversity.

Morgan, R. P. C. (2005). *Soil Erosion and Conservation* (3 ed.): Blackwell Publishing.

National Land Survey of Iceland. (2013a). Ísland í tölum (e. Iceland in numbers), 2013, from http://www.lmi.is/island-i-tolum/

National Land survey of Iceland. (2013b). Kortasjá IS 50V Retrieved 11.4.2013, from http://atlas.lmi.is/is50v/

Nemergut, D. R., Anderson, S. P., Cleveland, C. C., Martin, A. P., Miller, A. E., Seimon, A., & Schmidt, S. K. (2007). Microbial Community Succession in an Unvegetated, Recently Deglaciated Soil. *Microbial Ecology, 53*, 110-122.

Normann, D., Harris, R. J., & Newson, S. E. (2012). Producing regional estimates of population size for common and widespread breeding birds from national monitoring data. *Bird Study, 59*, 10-21.

Norris, K., Brindley, E., Cook, T., Babbs, S., Brown, C. F., & Yaxley, R. (1998). Is the density of redshank *Tringa totanus* nesting on saltmarshes in Great Britain declining due to changes in grazing management? *Journal of Applied Ecology, 35*, 621-634.

Nytjaland. (2013). Flokkun gróðurs Retrieved 16.2.2013, from http://nytjaland.is/landbunadur/wgrala.nsf/key2/grodurflokkar-flokkunarkerfi.html

Oddsdóttir, E. S., Svavarsdóttir, K., & Halldórsson, G. (2008). The influence of land reclamation and afforestation on soil arthropods in Iceland. *Icelandic Agricultural Sciences, 21*, 3-13.

Oldeman, L. R. (1992). Global Extent of Soil Degradation *ISRIC Bi-Annual Report 1991-1992* (pp. 19-36). AJ Wageningen.

Ólafsson, E., & Ingimarsdóttir, M. (2007). ICEWOODS: Changes in communities of ground living invertebrates following afforestation. In G. Halldórsson, E. S. Oddsdóttir & Ó. Eggertsson (Eds.), *Effects of afforestation on ecosystems, landscape and rural development, Proceedings of the AFFORNORD conference, Reykholt, Iceland, June 18-22, 2005* (Vol. 2007:508, pp. 171-176). Copenhagen: Nordic Council of Ministers.

Ólafur Arnalds, Gísladóttir, F. Ó., & Sigurjónsson, H. (2001). Sandy deserts of Iceland: an overview. *Journal of Arid Environments, 47*, 359-371.

Óskarsson, H. (2011). Hekluskógar. In Á. L. Aradóttir & G. Halldórsson (Eds.), *Vistheimt á Íslandi*: Agricultural University of Iceland & Soil Conservation Service of Iceland.

Óskarsson, H., Arnalds, Ó., Guðmundsson, J., & Guðbergsson, G. (2004). Organic carbon in Icelandic Andosols: geographical variation and impact of erosion. *Catena, 56*, 225-238.

Pohl, M., Alig, D., Körner, C., & Rixen, C. (2009). Higher plant diversity enhances soil stability in disturbed alpine ecosystems. *Plant Soil, 324*, 91-102.

R Development Core Team. (2008) (Version 2.15.0). Retrieved from http://www.r-project.org/

Raven, P. H., Evert, R. F., & Eichhorn, S. E. (1999). *Biology of Plants* (6 ed.): W.H. Freeman and Company /Worth Publishers.

Ravi, S., Breshears, D. D., Huxman, T. E., & D'Odorico, P. (2010). Land degradation in drylands: Interactions among hydrologic–aeolian erosion and vegetation dynamics. *Geomorphology, 116*, 236-245.

Reynolds, J. F., Maestre, F. T., Kemp, P. R., Stafford-Smith, D. M., & Lambin, E. (2007). Natural and Human Dimensions of Land Degradation in Drylands: Causes and Consequences. In J. G. Canadell, D. E. Pataki & L. F. Pitelka (Eds.), *Terrestrial Ecosystems in a Changing World* (pp. 247-257).

Sadler, J. P. (1999). Biodiversity on oceanic islands: a palaeoecological assessment. *Journal of Biogeography, 26*(1), 75-87.

Sample, B. E., Cooper, R. J., Greer, R. D., & Whitmore, R. C. (1993). Estimation of Insect Biomass by Length and Width. *American Midland Naturalist, 129*(2), 234-240.

Schekkerman, H., & Beintema, A. J. (2007). Abundance of invertebrates and foraging success of Black-tailed Godwit *Limosa limosa* chicks in relation to agricultural grassland management. *Ardea, 95*(1), 39-54.

Scherr, S. J., & Yadav, S. (1996). Land Degradation in the Developing World: Implications for Foor, Agriculture, and the Environment to 2020 *Food, Agriculture, and the Environment Discussion Paper 14*. Washington: International Food Policy Research Institute.

Schuh, R. T., & Slater, J. A. (1995). *True Bugs of the World (Hemiptera: Heteroptera) : Classification and Natural History*: Cornell University.

Schwabe, G. H. (1974). Nitrogen fixing blue-green algae as pioneer plants on Surtsey 1968-1973 *Surtsey Research Progress Report VII* (pp. 22-25). Reykjavik: The Surtsey Research Society.

Shariff, A. R., Biondini, M. E., & Grygiel, C. E. (1994). Grazing intensity effects on litter decomposition and soil nitrogen mineralization. *Journal of Range Management, 47*, 444-449.

Sigurðsson, H. (1982). Volcanic Pollution and Climate: The 1783 Laki Eruption. *Eos, 63*(32), 601-602.

Sigurmundsson, F. ó. S. (2011). *Hnignun skóg -og kjarrlendis í Þjórsárdal frá 1587 til 1938 og ástæður hennar*. meistararitgerð, Háskóli Íslands.

Spehn, E. M., Joshi, J., Schmid, B., Alphei, J., & Körner, C. (2000). Plant diversity effects on soil heterotrophic activity in experimental grassland ecosystems. *Plant and Soil, 224*, 217-230.

Streeter, R., Dugmore, A. J., & Vésteinsson, O. (2012). Plague and landscape resilience in premodern Iceland. *PNAS, 109*(10), 3664-3669.

Sutherland, W. J., Alves, J. A., Amano, T., Chang, C. H., Davidson, N. C., Finlayson, C. M., . . . Thompson, D. B. A. (2012). A horizon scanning assessment of current and potential future threats to migratory shorebirds. *Ibis, 154*(4), 663-679.

Székely, T., Karsai, I., & Kovács, S. (1993). Availability of Kentish Plover (Charadrius alexandrinus) prey on a Central Hungarian grassland. *Ornis Hungarica, 3*, 41-48.

Thordarson, T., & Larsen, G. (2006). Volcanism in Iceland in historical time: Volcano types, eruption styles and eruptive history. *Journal of Geodynamics, 43*, 118-152.

Thorlacius, J. M. (2011). Gos í Grímsvötnum Retrieved 29.4.2013, from http://www.vedur.is/skjalftar-og-eldgos/frodleikur/greinar/nr/2179

Tichit, M., Durant, D., & Kernéïs, E. (2005). The role of grazing in creating suitable sward structures for breeding waders in agricultural landscapes. *Livestock Production Science, 96*, 119-128.

Tilman, D. (1994). Community Diversity and Succession: The Roles of Competition, Dispersal, and Habitat Modification. In E. D. Schulze & H. A. Mooney (Eds.), *Biodiversity and ecosystem function*. Germany: Springer Verlag Berlin Heidelberg.

van de Kam, J., Ens, B., Piersma, T., & Zwarts, L. (2004). *Shorebirds. An illustrated behavioral ecology*. Utrecht, The Netherlands: KNNV.

Walker, L. R., & Chapin, F. S. (1987). Interactions among processes controlling successional change. *Oikos, 50*(1), 131-135.

Walker, L. R., & del Moral, R. (2003). *Primary Succession and Ecosystem Rehabilitation*. Cambridge: Cambridge University Press.

Whisenant, S. G. (1999). *Repairing Damaged Wildlands: A Process-Orientated, Landscape-Scale Approach*. Cambrigde: Cambridge University Press.

Woods, L. (1987). Degradation pressures from non-agricultural land uses. In A. H. Chisholm & R. G. Dumsday (Eds.), *Land Degradation: Problems and Policies*: Cambridge University Press.

Yasuoka, J., & Levins, R. (2007). Impact of deforerstation and agricultural development on Anopheline ecology and malaria epidemiology. *American journal of tropical medicine and hygiene, 76*(3), 450-460.

Þorsteinsdóttir, A. B., Eggertsson, B. Ö., Guðmundsson, B., Þorfinnsson, G., Óskarsson, H., Jóhannsson, M. H., & Aradóttir, Á. L. (2006). *Hekluskógar - flokkun lands og tillögur um aðgerðir*. Paper presented at the Fræðaþing landbúnaðarins 2006, Reykjavík.

Þórarinsdóttir, E. F., & Arnalds, Ó. (2012). Wind erosion of volcanic materials in the Hekla area, South Iceland. *Aeolian Research, 4*, 39-50.

Þórarinsson, S. (1961). Uppblástur á Íslandi í ljósi öskulagarannsókna *Ársrit Skógræktarfélags Íslands 1960-1961* (pp. 17-55). Reykjavík: Skógræktarfélag Íslands.

Appendix A

Number of birds counted on transects by total number

	Barren land	Moss	Grassland	Heath	Wetland	Tall vegetation	Total birds
Meadow pipit	6	12	58	67	13	40	**196**
Golden plover	7	15	17	24	24	11	**98**
Whimbrel	5	5	19	51	6	2	**88**
Red-necked Phalarope	0	0	0	6	49	0	**55**
Redwing	1	1	17	0	0	17	**36**
Common snipe	0	0	4	8	9	14	**35**
Greylag Goose	0	0	0	3	31	0	**34**
Ringed plover	9	0	5	3	11	0	**28**
Dunlin	3	1	0	2	15	0	**21**
Black-tailed Godwit	2	0	1	10	3	4	**20**
Black-headed Gull	0	0	0	7	1	11	**19**
Redshank	2	0	9	0	2	1	**14**
Eurasian Wigeon	0	0	0	2	7	0	**9**
White Wagtail	2	0	2	3	1	0	**8**
Mallard	0	0	0	2	4	0	**6**
Arctic Skua	0	0	1	3	0	0	**4**
Arctic Tern	0	2	0	1	1	0	**4**
Northern Wheatear	1	0	1	2	0	0	**4**
Unidentified Ducks	1	0	0	2	1	0	**4**

Pink-footed Goose	2	0	0	0	0	0	**2**
Barrow's Goldeneye	0	0	0	0	2	0	**2**
Snow Bunting	0	0	0	2	0	0	**2**
Whooper Swan	0	0	0	0	2	0	**2**
Oyestercatcher	0	0	0	0	2	0	**2**
Rock Ptarmigan	0	0	0	1	0	0	**1**
Lesser Black-backed Gull	0	0	1	0	0	0	**1**
Tufted Duck	0	0	0	0	1	0	**1**
Great Black-backed Gull	0	0	0	1	0	0	**1**
Total birds in habitat	**41**	**36**	**135**	**200**	**185**	**100**	**697**

Appendix B

Mean catch of invertebrate families per trap per day

	Barren land		Heathland		Wetland		Moss		Tall vegetation		Grassland	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Muscidae	53.5	40.2	9.7	17.4	4.1	4.9	1.7	2.7	9.6	11.6	15.2	20.4
Empididae	0.0	0.0	0.1	0.3	0.1	0.3	0.1	0.2	0.4	1.5	0.0	0.0
Phoridae	0.3	0.6	2.9	5.3	0.4	0.5	0.6	1.1	4.4	6.1	1.6	2.0
Chironomidae	21.8	26.2	0.3	0.7	3.1	6.1	0.2	0.4	2.1	4.3	3.7	10.6
Mycetophilidae	0.1	0.3	1.0	2.2	1.0	1.5	0.1	0.3	0.3	0.5	0.4	0.8
Cecidomyiidae	0.1	0.3	0.0	0.2	0.2	0.5	0.3	0.5	0.1	0.3	0.0	0.0
Sciaridae	1.0	0.8	9.5	8.5	4.8	8.8	20.2	28.4	1.5	1.8	12.5	16.7
Simuliidae	0.3	0.6	0.0	0.0	0.1	0.3	0.1	0.2	0.4	1.3	0.3	1.0
Ceratopo-gonidae	0.0	0.0	0.1	0.4	0.0	0.0	0.0	0.0	2.3	8.2	0.0	0.0
Tipulidae	0.0	0.0	0.0	0.2	0.7	1.1	0.0	0.0	0.4	1.0	0.0	0.0
Bibionidae	0.0	0.0	0.2	0.6	0.0	0.0	0.0	0.0	0.3	0.8	0.2	0.8
Dolicho-podidae	0.0	0.0	0.2	0.9	0.1	0.3	0.1	0.3	0.4	0.6	0.5	0.6
Symphyta	2.3	3.4	3.2	7.1	0.1	0.2	0.2	0.5	0.6	1.4	0.3	0.6
Scelionidae	0.9	1.7	9.8	10.4	6.4	7.0	7.7	8.8	3.8	3.0	25.5	18.1
Ichneumonidae	1.3	1.5	8.4	9.8	4.2	3.8	1.8	2.9	5.1	6.1	6.0	5.8
Mymaridae	0.2	0.5	0.9	1.7	1.3	4.5	0.2	0.5	0.9	2.1	1.5	3.9

Cicadellidae	1.3	1.2	6.2	6.8	6.7	8.3	2.6	2.9	5.6	11.9	86.7	121.6
Aphidoidea	2.8	2.5	4.3	7.4	0.6	1.1	0.2	0.4	14.8	36.3	22.0	33.8
Coccoidea	1.8	2.4	4.2	6.3	0.7	2.1	4.3	6.9	1.9	3.2	3.7	4.3
Orthezidae	0.0	0.0	0.2	0.9	1.7	5.1	0.1	0.2	0.3	1.3	0.0	0.0
Tingidae	0.0	0.0	0.0	0.0	0.0	0.0	6.3	14.0	0.1	0.3	0.0	0.0
Ligaeidae	0.2	0.4	0.0	0.2	0.0	0.0	1.7	4.2	0.0	0.0	0.0	0.0
Saldidae	0.0	0.0	0.0	0.0	3.7	12.7	0.0	0.0	0.1	0.5	0.1	0.3
Unid. Hemiptera	2.2	5.2	1.4	1.8	0.3	0.8	2.3	5.6	0.4	0.6	1.3	1.5
Gnaphosidae	0.3	0.6	1.4	2.2	0.5	1.0	1.6	1.4	3.3	5.8	2.0	2.2
Lycosidae	3.5	3.9	27.8	14.5	18.1	17.9	12.5	6.7	16.6	15.2	23.7	23.3
Linyphidae	3.7	3.0	7.5	6.7	5.6	4.9	2.7	1.7	5.4	4.2	10.8	7.5
Thomisidae	0.3	0.8	0.7	0.9	0.1	0.2	0.5	1.2	0.3	0.6	0.8	0.9
Phalangidae	15.5	10.4	9.5	10.0	1.4	3.8	0.6	1.2	7.7	9.7	3.5	7.9
Acari	47.3	43.4	250.3	220.0	177.1	179.0	167.8	99.7	168.6	272.1	312.9	160.5
Staphylinidae	0.8	1.0	6.3	9.7	1.1	1.7	1.2	2.2	7.2	15.1	9.7	14.0
Carabidae	29.2	42.5	10.6	17.2	11.5	14.7	4.8	4.9	7.8	7.4	16.3	12.5
Elateridae	2.9	6.8	0.6	0.9	5.9	13.8	2.6	4.1	0.8	1.1	3.0	4.5
Coccinellidae	0.3	0.6	0.9	1.5	0.1	0.2	1.6	4.3	0.3	1.0	0.9	1.3
Byrrhidae	0.1	0.2	0.7	1.7	0.5	1.2	0.0	0.0	0.0	0.0	0.1	0.4
Curculionidae	4.8	5.2	1.2	2.0	1.0	1.8	0.2	0.4	0.1	0.3	1.1	1.2

Dytiscidae	0.0	0.0	0.0	0.0	0.1	0.2	0.0	0.0	0.0	0.0	0.0	0.0
Entomobryo-morpha	11.8	10.0	45.3	37.6	170.2	331.3	80.9	85.6	110.3	97.2	79.1	68.8
Smithuridae	27.2	45.3	14.4	22.6	56.0	59.1	28.9	16.2	12.6	19.9	28.5	37.2
Thripidae	0.6	0.7	0.6	0.9	0.1	0.2	0.1	0.3	0.5	0.6	1.9	2.4
Limnephilidae	0.2	0.4	0.7	1.6	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.5
Geometridae	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.1	0.3	0.5	1.1
Noctuidae	0.3	0.8	0.1	0.3	0.1	0.3	0.4	0.6	0.0	0.0	0.3	0.5
Sigmurethra	0.0	0.0	2.0	3.4	11.2	26.6	0.1	0.2	31.9	65.7	2.1	4.2
Lumbricidae	0.0	0.0	0.3	0.6	0.3	0.6	0.2	0.5	0.3	1.0	0.7	1.7
Lithobiomorpha	0.2	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.3