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

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ABSTRACT

Degradation of ecosystems and introductions of invasive species pose a threat to global biodiversity. Ecosystem restoration and revegetation actions are important for amending habitat loss and for the protection of species of plants and animals. Iceland has the highest rate of soil erosion and desertification in Northern Europe and counteractions to erosion and revegetation measures have taken place for over a century. We studied the effect of revegetation on the density and composition of birds and invertebrate abundance in 26 survey areas comparing: a) unvegetated eroded areas, b) native heathlands restored on eroded land, and c) revegetation by the introduced and exotic Nootka lupin (*Lupinus nootkatensis*) on eroded land. Birds were counted on transects and invertebrates sampled with a sweep net. Both revegetation methods greatly increased the abundance of birds. The highest total numbers of invertebrates and birds were recorded on land revegetated with Nootka lupin. On average 31 birds km^{-2} were recorded on barren land, 337 on heathland and 627 in Nootka lupin. Bird species composition differed between the two revegetation methods. Restored heathland provided habitat for waders of internationally decreasing populations, whereas Nootka lupin stands harboured more common bird species. Golden Plover (*Pluvialis apricaria*) and Dunlin (*Calidris alpina*) were most common on restored heathland, while Snipe (*Gallinago gallinago*) and Meadow Pipit (*Anthus pratensis*) were most common in Nootka lupine. The abundance of birds was positively correlated with that of invertebrates. The abundance of different bird species differed by successional stage in each habitat. The study showed the generally positive effects of revegetation on animal biodiversity and also how different revegetation methods produce different trajectories of ecosystem development.

Keywords: birds, ecological restoration, invasive species, invertebrates, Nootka lupin, waders.

YFIRLIT

Þéttleiki og samfélög fugla á svæðum sem hafa verið grædd upp með framandi eða innlendum plöntutegundum

Hnignun vistkerfa og dreifing ágengra tegunda ógna líffræðilegum fjölbreytileika á heimsvísu. Vistheimt og landgræðsla eru mikilvægar aðgerðir til að endurheimta töpuð vistkerfi. Hvergi í Norður-Evrópu hefur jarðvegseyðing og eyðimerkurmyndun verið hraðari en á Íslandi. Í þessari rannsókn voru könnuð áhrif mismunandi landgræðsluaðgerða á þéttleika og tegundasamsetningu fugla og á fjölda smádýra. Rannsóknirnar voru gerðar á 26 stöðum á landinu. Á hverjum stað voru borin saman; a) óuppgrætt svæði, b) endurheimt mólendi og c) land sem hafði verið grætt upp með alaskalúpínu (Lupinus nootkatensis). Á óuppgræddu landi var að meðaltali 31 fugl á km^2, 337 á endurheimtu mólendi og 627 á landi sem hafði verið grætt upp með lúpínu. Þéttleiki fugla hafði jákvæða fylgni við fjölda smádýra. Tegundasamsetning fugla var ólík eftir uppgræðsluaðferðum. Í endurheimtu mólendi var mest um vaðfugla af tegundum sem er að hnigna á heimsvísu, en í lúpínu var meira um algengari tegundir. Heiðlóa og lóuþræll voru algengustu tegundirnar í endurheimtu mólendi, en hrossagaukur og þúfutittlingur í lúpínu. Þéttleiki sumra fuglategunda virtist vera háður framvindustigi landgræðslusvæða. Þessi rannsókn sýnir að landgræðsla eykur líffræðilega fjölbreytni dýrategunda, en mismunandi landgræðsluaðgerðir leiða til mismunandi þróunar vistkerfanna.

INTRODUCTION

Habitat loss is the greatest cause of diminishing global biodiversity, followed by the expansion of invasive species (Schmitz et al. 1997). The Convention of Biological Diversity (CBD 2013) has announced a strategic plan for biodiversity 2011-2020, aiming to slow down the rate of natural habitat loss by 50% and restore at least 15 % of degraded ecosystems by 2020, as well as controlling or eradicating invasive species, and preventing their introduction and establishment (CBD 2013).

Birds and bird groups can be good indicators for judging environmental health (Doxa et al. 2010, Gregory & Strien 2010) as they are near the top of the food chain and reflect productivity patterns at lower trophic levels (Klvanova et al. 2009, Doxa et al. 2010) and at large spatial scales. Therefore birds are one of the best animal groups for evaluating the success of ecological restoration (DaSilva & Vickery 2002) and are used as biodiversity indicators in various environmental schemes by some national governments and by the European Union (Klvanova et al. 2009, Gregory & Strien 2010).

Exotic plant species invading low herbaceous vegetation have various effects on existing bird communities. While invasions of grass species into established grassland communities have been shown to alter the relative population sizes of terrestrial invertebrate groups without affecting the existing passerine bird community (Kennedy et al. 2009), other studies have shown effects on bird community composition through changes in vegetation structure and subsequent decline in habitat quality (Scheiman et al. 2003, Fleishman et al. 2003). This is particularly true for specialist bird species (Ma et al. 2012) and those foraging on or near the ground (Flanders et al 2006). However, where invasive species are established they can provide valuable habitat for birds (McCusker 2010, Fischer et al. 2012) and where little is left of native vegetation, invasive plant species can have a boosting effect on productivity and biodiversity (Kaiser-Bunbury et al. 2010). So studying highly degraded ecosystems revegetated with introduced species, as an alternative to natural revegetation, can give important information on the effect revegetation actions can have on native plant and animal communities (Kaiser-Bunbury et al. 2010).

Iceland has undergone severe loss of vegetated habitats since its settlement in the late 9th century (Arnalds 2011). Currently, over 40,000 km^2 consist of barren land with limited plant production, compared to an estimated 5,000-15,000 km^2 at the time of settlement (Arnalds 2011). Significant efforts to restore eroded land in Iceland started in 1907 (Crofts 2011). The most common method is protection from livestock grazing, often combined with other methods, the most common being top dressing with fertilizers and spreading of a mixture of grass seeds (Halldorsson et al. 2011a). All these methods lead eventually to the restoration of local native vegetation, mostly heathland (Aradottir et al. 2013). In addition, the introduced (from N America) nitrogen-fixating Nootka lupin (*Lupinus nootkatensis* Donn ex Sims, hereafter referred to as lupin) has been extensively used for revegetation in Iceland (Halldorsson et al. 2011a). The lupin is an economical and effective tool for revegetating barren land where other methods are uneconomical or logistically difficult (IINH & SCS 2010), even if its use has increasingly been questioned in recent years (IINH & SCS 2010, Petursdottir et al. 2012). It has been shown to disperse over native heathland (Magnusson et al. 2001) and has been recognized as an invasive species in Iceland (Magnusson 2010) and potentially invasive in Finland (NOBANIS 2013). A recent estimate of the total distribution of lupin in Iceland suggests that it covers at least 314 km^2 (IINH 2016). Lupin has been widely used by the Soil Conservation Service of Iceland (SCS), and presently the total area of lupin stands established by this institute is estimated to be ca 100 km^2 or 0.1% of Iceland's surface (Thorsson, personal communication). Other parties have also distributed the lupin and it has expanded extensively in some places where livestock grazing is limited (Thoroddsen et al. 2009, IINH & SCS, 2010). In Iceland, the lupin forms large patches with few coexisting plant species during its first successional stages, showing different growth performance depending on annual precipation and temperature (Magnusson et al. 2003). In inland North and East Iceland, where annual precipitation is 500-800 mm, lupin mostly grows tall along the edge of the establishing patches, but within the patches the plants are low and less competitive against other plant species (Magnusson et al. 2001). In South and West Iceland, (annual precipitation 900-3400 mm), lupin plants tend to be relatively tall within dense uniform fields (Magnusson et al. 2003). Secondary succession, where the lupin is generally replaced with grasslands after some decades, has been shown to occur, but the succession rate is variable between parts of Iceland and seems related to variation in annual precipitation across the country (Magnusson et al. 2001, 2003).

The variation in growth form and successional trajectories may have a different effect on invertebrate fauna, bird abundance and species composition. Icelandic studies on soil fauna and birds have revealed an increase in animal abundance in lupin stands compared to eroded land and an increasing animal density with increasing time from the establishment of a lupin stand (Sigurdardottir 2002, Oddsdottir et al. 2008, Gunnarsson & Indridadottir 2009). This is also true for soil invertebrate fauna after grass seeding (Friðriksson et al. 1977) or where ecosystem N stocks increase during primary succession (Ilieva-Makulec et al. 2014). However, few systematic surveys have compared the potential differences in bird species composition and density between eroded areas restored with native plant species or areas that have undergone natural secondary succession (passive restoration) in contrast to those that have been revegetated with the introduced lupin.

The avifauna of Iceland is characterized by relatively large populations of few species, but includes a large proportion (10-40%) of the global populations of ten wader (Charidrii) species (Gunnarsson et al. 2006, Johannesdottir et al. 2014, Gunnarsson et al. 2015). Populations of waders in the world are proportionately small compared to many other groups and in addition nearly half of them are currently in decline, mainly due to habitat loss and degradation (International Wader Study Group 2003, MacKinnon et al. 2012). Heathland is an important breeding ground for waders in Iceland (Gunnarsson et al. 2006, Magnusson et al. 2009, Johannesdottir et al. 2014). The present coverage of heathland in Iceland is estimated to be ca. 30,000 km^2 (Arnalds 2011). In total ca. 5,700 km^2 of eroded areas are in the process of being restored in Iceland (Crofts 2011), of which a minimum of 1,500 km^2 is restored heathland (Halldorsson et al 2011b), primarily in lowland areas.

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

METHODS

Study sites

Iceland (63-66°N) is a volcanic island of about 103,000 km^2 in the North-Atlantic Ocean. The climate is oceanic with a variable annual precipitation of 500-3400 mm (Vedurstofa

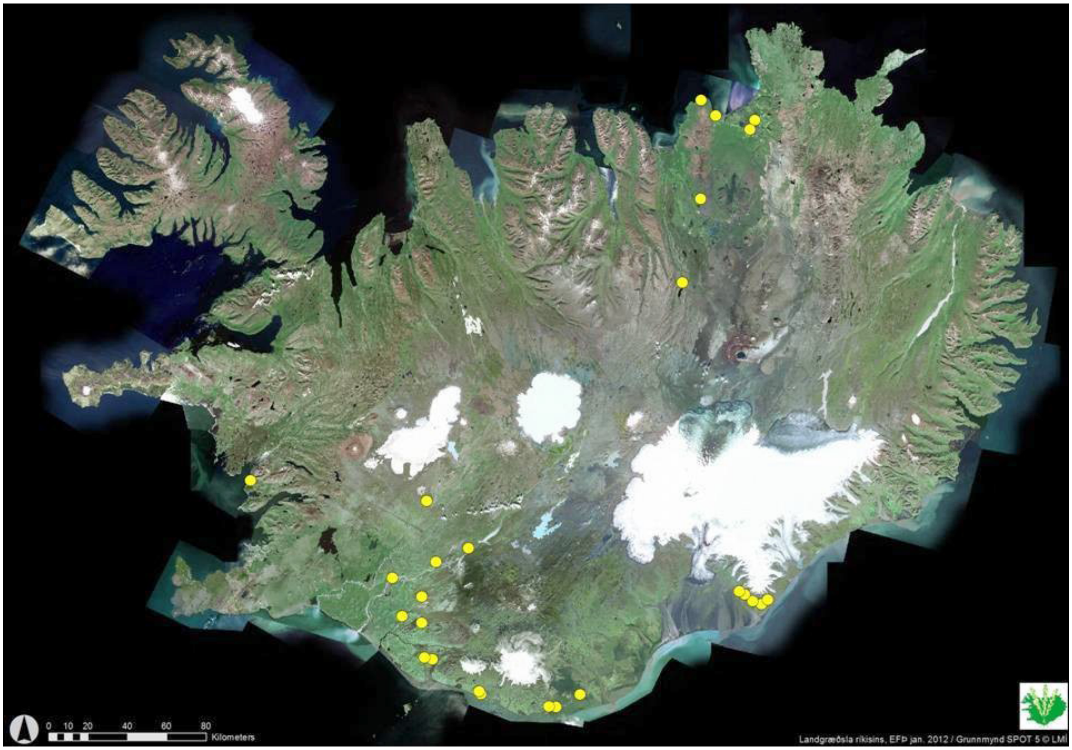

Figure 1. Filled yellow circles show the position of study plots where birds were counted and invertebrates sampled. Each circle shows the approximate location of three habitat types studied as a cluster.

Islands 2013). The soil consists mainly of Histic, Gleyic and Brown Andosols (>50%) and Virtisols (30%) (Arnalds 2008) which correspond to Histic-, Gleyic, Silandic and Vitric Andosols using the FAO/WRB classification.

Bird and invertebrate surveys were carried out in different regions of Iceland (Figure 1), from the 29th of May to the 14th of August 2011. The survey areas formed 26 clusters, each consisting of three habitat types: i) Barren land that had

Table 1. Description of habitat types.

Type	Description	Common plant species
Barren land	Barren or very sparsely vegetated land on sand or gravel.	*Agrostis vivealis, Festuca rubra, Phleum pratensis, Thymus praecox*
Heathland	Dry young heathland, on previous sand or gravel, re-vegetated by fertilisation and sowing of grass seeds or by self regeneration. Cover of native species, varying from biological crust with sparse grasses, rushes and sedges, moss and lichen to a homogeneous coverage of grasses and/or moss with sparse small shrubs. Often subject to grazing.	Mosses, lichens, grasses, rushes, sedges, sparse low *Empetrum nigrum*, *Vaccinum* spp. and *Salix* ssp.
Nootka lupin	Fields consisting of varying ages and densities of *Lupinus nootkatensis*. With bare patches or native grasses amongst lupin plants at earlier succession stages or when lupins are retreating.	Nootka lupin *Lupinus nootkatensis*

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

been eroded during the past few centuries and where secondary succession is still in its early stages due to physical or biological pressures. ii) Heathland restored on formerly barren land sometime during the past 50 years, either with passive methods that enhance the secondary succession, such as management of grazing and river regulation, or intial fertilization that may have included seeding with grass species. iii) Areas covered by the exotic N-fixating Nootka lupin, where barren land has been revegetated by active methods in the past 40 years. All three habitat types within each cluster were within 5 km of each other, at similar heights above sea level, and with similar climate and other physical conditions, apart from the difference in vegetation and soil properties caused by revegetation actions (Table 1, Figure 2).

Survey methods

Habitats within each cluster were usually visited during the same day (77% of clusters), or during subsequent days (23% of clusters), depending on weather conditions. The habitat types were surveyed in a random order each day, to eliminate possible systematic effects of diurnal rhythms in animal behavior. Date, time of day, wind speed, air temperature and cloud coverage were recorded and the plant successional stages of heathland and Nootka lupin were given a grade on a scale of 0 to 3 and 0 to 4, respectively (Table 2).

Bird surveys were carried out from 29th May to 25th June 2011, which is the period of highest breeding activity of the most common terrestrial bird species in sub-arctic and arctic conditions (Meltofte 2001, Gunnarsson 2006). One to two sets of habitat clusters were surveyed per day, either before noon or between four and eleven p.m., which are the periods when most terrestrial bird species show a peak in detectability (Bibby et al. 2000). To obtain site-specific density

Table 2. Description of succession stages which heathland and lupin habitats were classified as. Heathland has three stages, lupin four.

Succession class	Heathland	Nootka lupin
1	Soil organic crust with sparse grasses	Sparse low lupin plants on barren land
2	Shallow mat of low vegetation or a dominating cover of moss and lichen	Tall lupin with barren land between plants
3	Homogeneous coverage of grasses, rushes and sedges, moss and forbs with sparse low growing shrubs.	Tall dense lupin with little coexisting flora.
4	NA	Tall lupin starting to retreat with often with grass between plants.

estimates, birds were recorded on transects (Bibby et al. 2000) using a 50 m inner belt which was suitable for the sizes of the survey patches and the species surveyed (Gunnarsson & Indridadottir 2009). The mean transect length was 0.74 km (SE 0.12 km) and was often restricted by the size of homogeneous habitat patches (Table 3). All birds were recorded, at the distance perpendicular to the transect line, from where they were first seen, and their behaviour noted. Birds outside the transect and those overflying were recorded but excluded from further analysis. Binoculars (Leica Ultravid 8x32, Leica, Germany) were used together with a rangefinder (icaddie G-543, Magadoro Ltd., Neatherlands) to verify the observer's ability to accurately evaluate distances. The unit calculated was individual birds, of each species, per km^2.

Insects were sampled directly following the bird counts, at each transect, with a sweep net at three random points placed along the transect. The net, diameter 39 cm and mesh size 0.3 mm, was swept over the surface at each survey point with ten, nonoverlapping, 2 m long strokes. The number of caught diptera, moths and spiders (>3 mm) was counted and the animals then released. These groups made up nearly the entire invertebrate catch (>95%). We used the average invertebrate number of the three catches per area as a measurement of invertebrate abundance per site.

Data and statistical analyses

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

We carried out a Principal Components Analysis (PCA) with the nine most commonly occurring species to assess differences in species composition between the three habitat types. The difference in species composition between habitats was estimated by comparing the mean factor scores between habitats with ANOVA and Tukey post-hoc tests. The difference in invertebrate abundance between habitats was assessed with a generalized linear model (negative binomial with log link function in SPSS 20) (IBM 2012) and the overall relationship between bird and invertebrate abundance with a Spearman correlation. We then explored the effect of successional stage within lupin (four stages, Table 2) and heathland (three stages, Table 2) on bird density. Models of the effects of succession stage on bird densities in lupin and on heathland were comparable to the overall models (quasi-poisson generalized linear models) but were only suitable for species which occurred on more than 50% of transects, due to sample size restrictions.

RESULTS

The effect of revegetation on bird density

Overall a total distance of 59 km of transects was walked and 1511 birds of 19 species were detected (Table 3). A low density of birds was generally recorded on barren land and both revegetation methods increased bird density greatly from the unvegetated state (Table 3) with an average density of 31 birds km^{-2} on barren land, 337 birds km^{-2} on heathland and 627 birds km^{-2} in Nootka lupin. Of the nine most commonly occurring species, none was most abundant on barren land (Table 4). Golden Plover and Dunlin were significantly most abundant on heathland and Snipe, Redshank (*Tringa totanus*) and Meadow Pipit most abundant in lupin (Table 4).

Table 3. Mean bird density (individuals/km^2 with SE) and proportional occurrence of species on 26 transects in three habitat types. Species are listed in taxonomic order. Species with a mean density of over 10 individuals/km^2 and the occurrence of a species which were found on 50% or more of the transects are indicated in bold letters.

	Barren land		Heathland		Lupin	
	Density (SE)	**Prop. Occur-rence**	**Density (SE)**	**Prop. Occur-rence**	**Density (SE)**	**Prop. Occur-rence**
Greylag Goose *Anser anser*	0.0 (0.0)	-	0.0 (0.0)	-	>0.0 (0.0)	0.08
Mallard *Anas platyrhynchos*	0.0 (0.0)	-	0.9 (0.9)	0.04	1.6 (1.6)	0.04
Ptarmigan *Lagopus mutus*	0.0 (0.0)	-	1.3 (1.3)	0.08	0.0 (0.0)	-
Oystercatcher *Haematopus ostralegus*	1.5 (1.5)	0.08	2.7 (1.9)	0.19	4.4 (4.4)	0.08
Ringed Plover *Charadrius hiaticula*	**11.3 (5.7)**	0.23	**18.8 (6.7)**	0.35	3.6 (2.7)	0.12
Golden Plover *Pluvialis apricaria*	2.8 (2.0)	0.12	**74.2 (34.1)**	**0.77**	9.8 (3.4)	0.42
Dunlin *Calidris alpina*	4.4 (3.1)	0.15	**72.4 (23.1)**	**0.65**	**22.1 (7.6)**	0.35
Redshank *Tringa totanus*	>0.0 (0.0)	0.04	1.8 (1.8)	0.12	**53.1 (25.6)**	0.27
Black-tailed Godwit *Limosa limosa*	0.0 (0.0)	-	0.0 (0.0)	-	**11.8 (8.4)**	0.15
Whimbrel *Numenius phaeopus*	0.9 (9.9)	0.08	**26.4 (6.1)**	**0.73**	**29.9 (11.1)**	0.46
Snipe *Gallinago gallinago*	2.8 (2.2)	0.08	**12.0 (5.3)**	0.46	**96.6 (22.2)**	**0.77**
Great Skua *Catharacta skua*	>0.0 (0.0)	0.08	**10.7 (7.4)**	0.15	0.0 (0.0)	-
Arctic Skua *Stercorarius parasiticus*	3.8 (3.8)	0.08	5.4 (3.1)	0.27	1.1 (1.1)	0.12
Lesser Black-backed Gull *Larus fuscus*	0.0 (0.0)	-	0.0 (0.0)	-	3.1 (3.1)	0.04
Meadow Pipit *Anthus pratensis*	2.4 (1.7)	0.12	**83.4 (25.9)**	**0.81**	**337.2 (43.5)**	**0.96**
White Wagtail *Motacilla alba*	1.1 (1.1)	0.04	**14.8 (7.6)**	0.23	7.1 (4.0)	0.12
Wheatear *Oenanthe oenanthe*	0.0 (0.0)	-	1.2 (1.2)	0.04	0.0 (0.0)	-
Redwing *Turdus iliacus*	0.0 (0.0)	-	0.6 (0.6)	0.08	**45.3 (21.5)**	0.38
Snow Bunting *Plectrophenax nivalis*	1.5 (1.5)	0.04	**10.8 (7.9)**	0.08	0.0 (0.0)	-
Total birds	31		337		627	
No. of species detected	12		16		15	
Total transect length (Km)	17		27		15	

Table 4. Poisson Generalized linear models (adjusted for overdispersion, quasi-poisson) comparing density of the most common 9 species between three habitats. Estimates of Lupin and Unvegetated are relative to heatland (intercept model).

Species	Habitat	Estimate	SE	t	P
	Intercept	4.3067	0.286	15.044	<0.0001
Golden Plover	Lupin	-2.0196	0.836	-2.415	0.0182
	Unvegetated	-3.2743	1.499	-2.184	0.0321
	Intercept	2.9322	0.360	8.135	<0.0001
Ringed Plover	Lupin	-1.6470	0.897	-1.837	0.0702
	Unvegetated	-0.5033	0.587	-0.857	0.3941
	Intercept	2.4849	0.505	4.918	<0.0001
Snipe	Lupin	2.0854	0.536	3.892	0.0002
	Unvegetated	-1.4663	1.167	-1.257	0.2127
	Intercept	3.2728	0.285	11.496	<0.0001
Whimbrel	Lupin	0.1233	0.391	0.315	0.7533
	Unvegetated	-3.3528	1.548	-2.166	0.0335
	Intercept	0.5921	1.615	0.367	0.7149
Redshank	Lupin	3.3790	1.642	2.058	0.0431
	Unvegetated	-15.8946	2769.72	-0.006	0.9954
	Intercept	4.2836	0.237	18.101	<0.0001
Dunlin	Lupin	-1.1908	0.490	-2.430	0.01751
	Unvegetated	-2.8055	0.991	-2.831	0.00595
	Intercept	4.4221	0.244	18.134	<0.0001
Meadow Pipit	Lupin	1.3985	0.272	5.136	<0.0001
	Unvegetated	-3.5693	1.473	-2.423	0.0178
	Intercept	2.6977	0.404	6.682	<0.0001
White Wagtail	Lupin	-0.7464	0.712	-1.048	0.2978
	Unvegetated	-2.6236	1.552	-1.690	0.0952
	Intercept	-0.4855	2.420	-0.201	0.8415
Redwing	Lupin	4.2998	2.436	1.765	0.0817
	Unvegetated	-14.8171	2422.00	-0.006	0.9951

The effect of revegetation on bird diversity

Both revegetation methods had a strong positive effect on all measures of diversity. Overall, 12 species of birds occurred on barren land, 16 on heathland and 15 in lupin (Table 3). There were significantly fewer bird species on average on barren land than on heathland and in lupin stands (ANOVA: $F_{2,.77}$=37.25; P<0.001), but the average number of species did not differ significantly between the two revegetation methods (ANOVA: $F_{4,3}$ = 1.76; P = 0.19; Figure 3).

Species composition was different between habitats (Table 3). On barren land no species occurred on more than 50% of transects. On heathland, four species - Golden Plover, Dunlin, Whimbrel (*Numenius phaeopus*) and Meadow Pipit, occurred on over 50% of transects; in lupin two species, Meadow Pipit and Snipe, had > 50% occurrence (Table 3). A PCA was

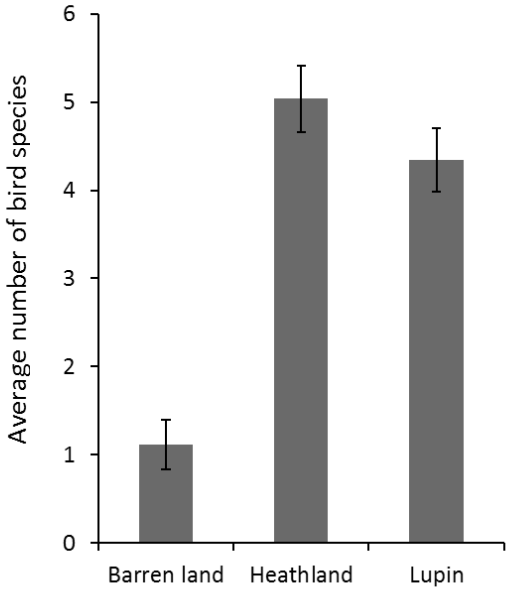

Figure 3. Average number of bird species per transect within three different habitat types. Bars are 1 SE.

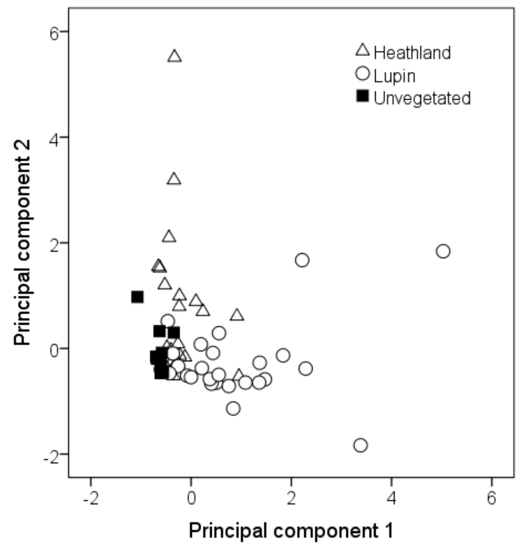

Figure 4. Principal components plot of the first two factors of the 9 most commonly occurring species with habitats overlaid. See table 5 for components scores.

conducted with the 9 most common species (species in Table 5). Four components were extracted from the PCA, where component one explained 27% of the variation in the data and the next three 22%, 17% and 11%, respectively (Table 5). Overall, the species that occurred on barren land were not clearly distributed on any single component, but species which were common in lupin tended to load positively on component one (Meadow Pipit, Snipe and Redshank most strongly) and species more common on heathland loaded positively on component 2 (Dunlin, Golden Plover and Ringed Plover (*Charadrius hiaticula*) most strongly) (Figure 4). Mean factor scores of components 1 and 2 varied significantly between habitat types (ANOVA - Factor 1: $F_{2,77} = 25.67$, $P < 0.0001$; Factor 2: $F_{2,77} = 7.45$, $P = 0.001$). Tukey's post-

Table 5. Species loadings of four components from a Principal Components Analysis. Species with the three highest loadings in component one and two are indicated in bold letters.

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

hoc test (alpha = 0.05) showed that factor 1 was significantly higher in lupin than in other habitats, but factor 2 was higher in heathland than in the others. Mean scores for factors 3 and 4 did not vary significantly between any habitats.

The effect of succession within revegetated areas on bird density

Although sample sizes were small, some variation in density was evident with succession stage (Figure 5, Table 6). In heathland, densities of Golden Plover and Dunlin were highest at intermediate vegetation succession and Whimbrel density increased with advancing vegetation succession. Both Snipe and Meadow Pipit were more common in the most advanced heathland than at earlier successional stages. In lupin both Snipe and Meadow Pipit increased in density as lupin succession advanced. Of the species most common on heathland (Golden Plover and Dunlin), both were relatively rare in

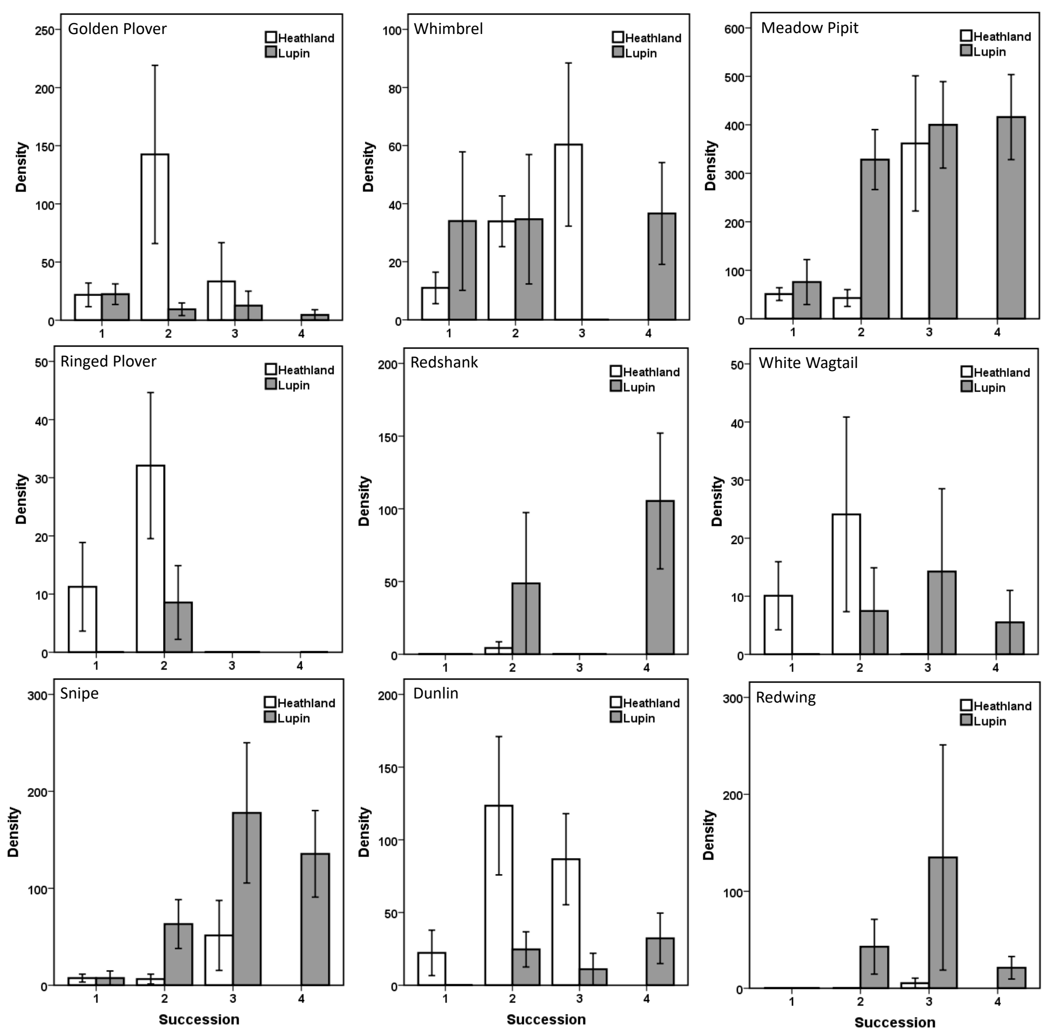

Figure 5. Density (individuals/km^2) of the nine most commonly occurring bird species in relation to vegetation succession on heathland and in lupin. Lupin has four (1-4) defined succession stages whereas heathland has only three (1-3) (Table 2). Note the different scales on the y-axis. Bars are 1 SE.

Table 6. Results of Poisson Generalized linear models (corrected for overdispersion, quasi-poisson) predicting the abundance of individual species at different successional stages in lupin and heathland. Lupin has four succession stages and heathland three (Table 2). Only species which occurred on more than 50% of study plots were analysed (Table 3). Estimates of stages 2-4 are relative to stage 1 (intercept). See figure 5 for direction of relationships.

			LUPIN		
Species	**Succession**	**Estimate**	**SE**	**T**	**P**
Golden Plover	1 (Intercept)	31.061	0.721	4.305	<0.001
	2	-0.869	0.926	-0.938	0.358
	3	-0.580	1.103	-0.526	0.604
	4	-1.602	1.220	-1.313	0.203
Snipe	1 (Intercept)	1.992	2.193	0.909	0.373
	2	2.152	2.227	0.966	0.344
	3	3.188	2.226	1.432	0.166
	4	2.917	2.215	1.317	0.201
Meadow Pipit	1 (Intercept)	43.263	0.739	5.852	<0.0001
	2	14.675	0.762	1.926	0.067
	3	16.651	0.790	2.108	0.047
	4	17.043	0.764	2.231	0.036
			HEATHLAND		
	Succession	**Estimate**	**SE**	**T**	**P**
Golden Plover	1 (Intercept)	3.079	0.945	3.258	0.003
	2	1.880	10.208	1.842	0.078
	3	0.426	17.957	0.238	0.814
Snipe	1 (Intercept)	1.992	0.670	2.972	0.007
	2	-0.141	10.070	-0.141	0.889
	3	1.945	0.840	2.315	0.029
Whimbrel	1 (Intercept)	23.979	0.473	5.064	<0.0001
	2	11.258	0.551	2.043	0.053
	3	17.020	0.623	2.733	0.012
Dunlin	1 (Intercept)	31.023	0.758	4.095	<0.001
	2	17.135	0.829	2.067	0.049
	3	13.597	10.787	1.261	0.220
Meadow Pipit	1 (Intercept)	39.286	0.334	11.775	<0.0001
	2	-0.174	0.506	-0.343	0.734
	3	19.622	0.417	4.705	<0.0001

lupin and of similar density in all its successional stages. Whimbrel was also found at similar density in advancing and retreating lupin (stages 1, 2 and 4), but was absent in the densest lupin patches (stage 3). Other bird species occurred too rarely to make inferences about the effects of succession on their abundance on heathland or in lupin.

The relationship between the abundance of birds and invertebrates

The total invertebrate catch by sweep net was 75, 141 and 594 individuals on barren land, heathland and in lupin, respectively. There was no significant difference between the mean abundance of caught invertebrates on barren land and on heathland, but invertebrate abundance was significantly higher in lupin than in other habitats (GLM, negative binomial with log link function: Test of model effects, Wald Chi-square = 39.90, DF = 2, $P < 0.0001$, deviance/df = 1.64, with pairwise comparsions) (Figure 6). There was a significant positive relationship between the total abundance of birds counted and the total abundance of invertebrates caught by sweep net on all transects when compared across all habitat types, indicating that bird density and invertebrate abundance were both higher on the same sites (Spearman rank correlation with untransformed data: Rho = 0.59 , P<0.001).

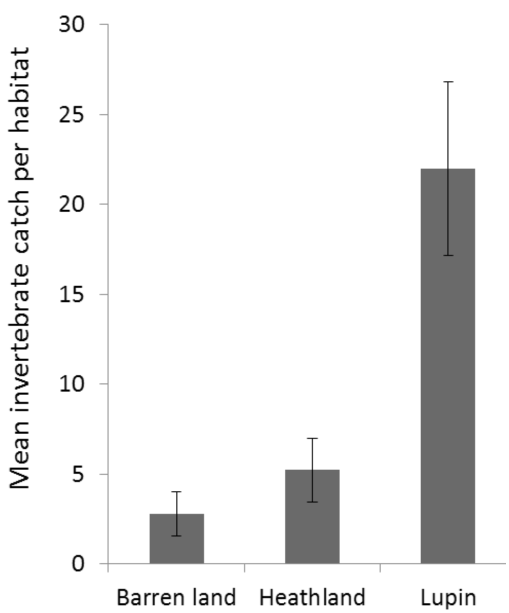

Figure 6. The mean catch of foliar invertebrates by sweep net in barren land, heathland and in lupin. Bars are 1 SE.

There was a positive correlation between the numbers of ground dwelling invertebrates caught in pitfall traps and invertebrates caught by sweep net (Appendix 1).

DISCUSSION

The current study compared and assessed the effects of two revegetation methods of barren land on bird density and diversity in Iceland; revegetation with introduced lupin vs. restoration of native vegetation. Our results showed that bird species responded strongly and positively both to restoration of native heathland vegetation and to revegetating with lupin. Each revegetation method, however, supported different bird communities.

Restored habitats and revegetation efforts have been shown to provide valuable habitat for birds (Kaiser-Bunbury et al. 2010, Williams et al. 2012) even though the assembly of bird species is rarely the same in restored areas as in original or remnant habitats, at least during the first decades (Munro et al. 2011). Studies have shown that restored habitats that have evolved by natural succession in a complete succession series often contain higher bird species diversity and tend to sustain a larger number of rare bird species compared to sites that are reclaimed with methods which "skip" steps of natural succession (Šálek 2012). Our results partly confirmed these findings; although the number of species recorded did not differ between the native heathlands and introduced lupin stands, bird communities in the two habitats were composed of mostly different species. Species which show a preference for open low growing vegetation (Gunnarsson et al. 2006) were common on heathland, whereas species which show a preference for taller swards, forests or shrubland were more common in lupin stands (Jónsson et al. 2006, Nielsen et al. 2007). Early successional areas and shrublands have become scarce in Europe and in North America (Oehler 2003) and avian early successional specialists are subsequently rarer than generalists and woodland birds (Šálek 2012). Iceland is globally an important nesting ground for ten wader species (Gunnarsson et al. 2006, Johannesdottir et al. 2014), which tend to prefer open habitats. This suggests that heathland restoration on barren land in Iceland is of great value for the conservation of these heathland species, which generally have internationally decreasing populations (International Wader Study Group 2003, MacKinnon et al. 2012).

Although the structural complexity of an ecosystem has been shown to have a positive effect on bird species richness (e.g. Munro et al. 2011), populations of rare bird species that favour early successional stages decline with succession stage (Šálek 2012). In our study, bird species responded differently to various successional stages within vegetation types. In the very early stages of heathland succession, which lacked woody shrubs, early successional specialists (Gunnarsson et al. 2006), such as Ringed Plover, Golden Plover and Dunlin, were most abundant. Woody plants and shrubs, became more noticeable in the later stages of heathland succession where Whimbrel, Snipe and Meadow Pipit were increasingly abundant. Lupin stands on the contrary tended to have more structural complexity in earlier and later successional stages (referred to as successional stages 2 and 4 in this study) in the form of mosaics of tall lupin plants/patches with gravel or low vegetation in between plants, compared to their densest stage which was dominated by tall dense lupin (stage 3). There were indications that the densest stage of lupin stands had a negative effect on some bird species such as Whimbrel and Redshank, which were absent in these patches, whereas in scattered lupin stands there appeared to be the necessary structural complexity for the foraging of various bird species of foliar and terrestrial invertebrates. The observed habitat selection of the different species in this study fit well with what is known about the breeding and feeding habits of these species. Meadow Pipit is the only species which feeds largely in flight on foliar arthropods, which were most abundant in the lupin, whereas the heavier wader species take mostly surface dwelling arthropods. Snipe is the only wader species of the ones studied which relies on camouflache and can feed and nest in dense undergrowth such as forests and lupin, whereas the others feed and nest in open habitats or habitats with staggered vegetation where they have good visibility to avoid predators (Green et al. 1990, Gunnarsson et al. 2006, Gunnarsson & Indridadottir 2009).

The observed increase in invertebrate abundance where barren land had been transformed into lupin stands was in accordance with other studies on invertebrate abundance in the same habitat types (Sigurdardottir 2002, Oddsdottir et al. 2008; See also Appendix 1). When compared across all habitat types the total abundance of birds and invertebrates, caught by sweep net, showed a significant positive relationship, indicating that bird density and invertebrate abundance were both higher on the same sites. While revegetation with exotic species can provide important habitat for birds (Munro et al. 2011, this study) restoration of native plant communities has become a priority in the protection of biodiversity (MacMahon & Holl 2001). In the process of restoration of native communities, modification of environmental factors can be necessary to overcome environmental barriers and speed up natural succession. Application of fertilizers, sowing of seeds and providing of safe sites for seedlings are methods used to speed up succession or to turn around the actual degradation and thus aiding the recovery of the degraded land (Elmarsdottir et al. 2003, Petursdottir et al. 2012, Arnalds et al. 2013), especially in Iceland where harsh winds, a short growing season and frequent freeze-thaw cycles causing ice needles all considerably hinder or slow the natural revegetation of barren land.

Although lupin stands in Iceland attract and sustain a high density of some bird species and invertebrates, the future direction of succession of lupin stands is unclear, but at least in some cases grasslands replace the lupin after a few decades (Magnusson et al. 2003). It should also be considered, however, that lupin areas expand with time and they have presently invaded some existing heathlands in Iceland (Magnusson et al. 2003). Where invasive plants invade meadow bird communities, these communities have been shown to greatly decrease in bird species richness (Skórka et al. 2010). When deciding between reclamation of native vegetation and revegetating with an introduced N-fixating plant, it may be important to consider that using lupin might have a lower initial cost but has uncertain ecological trajectories (Petursdottir et al. 2012) and can result in extreme coverage by alien vegetation in the future (Thoroddsen et al. 2009).

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

Our results showed that both lupin sowing and heathland reclamation in Iceland have had a substantial value for the restoration of bird biodiversity but have supported somewhat different species. Whereas lupin stands support a higher density of some bird species, these species are commonly found on a wider range of habitats with a wider global distribution than the species characterising early successional heathland in Iceland.

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