Impact of afforestation on earthworm populations in Iceland

Bjarni D. Sigurdsson and **Bjarni E. Gudleifsson**

Agricultural University of Iceland, Hvanneyri, IS-311 Borgarnes, Iceland.
e-mail: bjarnisig@lbhi.is (corresponding author), beg@lbhi.is

ABSTRACT
Earthworms were collected from different vegetation types in East and West Iceland. The vegetation types in East Iceland were Siberian larch (*Larix sibirica*) forests, native mountain birch (*Betula pubescens*) woodlands and open heathlands. The study areas in West Iceland were Sitka spruce (*Picea sitchensis*), lodgepole pine (*Pinus contorta*) forests, mountain birch woodlands and open heathlands. Four earthworm species (*Dendrobaena octaedra, Dendrodrilus rubidus, Aporrectodea caliginosa, Lumbricus rubellus*) were identified at both study areas and two additional ones in the West Iceland (*Aporrectodea rosea* and *Octolasion cyaneum*). No significant differences were detected in average earthworm species number and biomass between treeless heathlands and forests in East or West Iceland. There were, however, significant differences between the native deciduous forests and the coniferous plantations in West, but not East Iceland. Time since afforestation was found to have a significant effect on both earthworm diversity and density and should always be included in future studies. All earthworm parameters were positively related to soil N and amount of monocots, but negatively related to soil C/N ratio, tree LAI and tree height. Soil pH had no significant influence on any of the earthworm parameters. The most noteworthy finding was that earthworms were generally found in similar biomass and species richness in the exotic coniferous plantations in Iceland compared to the treeless heathlands, even if earthworm species composition showed strong changes. The findings apply to the first 50 years after establishment of coniferous trees, but an unexpected, large increase in earthworm biomass and species richness in the oldest thinned Siberian larch forests in East Iceland make any generalisation about future trends uncertain. Further earthworm studies in the oldest coniferous forests in Iceland are therefore still needed.

Key words: chronosequence, C/N-ratio, exotic forests, pH, soil fauna, vegetation type

YFIRLIT
Áhrif skógræktar á tegundafjölda, þéttleika og lífmassa ánamaðka á Íslandi
Ánamöðkum var safnað í mismunandi gróðurlendum á Austur- og Vesturlandi í verkefninu SkógVist. Á Austurlandi voru rannsakaðir rússalerki- og birkiskógar, auk beitts mólendis. Á Vesturlandi voru það sitkagreni-, stafafuru- og birkiskógar og beitt mólendi. Fjórar ánamaðkategundir fundust í báðum landshlutum (mosa-, grá-, garð- og svarðáni) og tvær til viðbótar á Vesturlandi (blá- og rauðáni). Ekki reyndist vera neinn marktækur munur á tegundafjölda, þéttleika eða lífmassa ánamaðka á milli skóglauss mólendis og ræktaðra barrskóga eða birkiskóga á Austur- og Vesturlandi. Á Vesturlandi var tegundafjöldi, þéttleiki og lífmassi

ánamaðka marktækt lægri í greni- og furuskógunum miðað við birkiskógana, en á Austurlandi var lífmassi ánamaðka marktækt hærri í (gömlum) lerkiskógum. Ánamaðkar sýndu jákvætt samband með nitri í jarðvegi og magni einkímblöðunga í botngróðri, en neikvætt samband við kolefnis/nitur hlutfall í jarðvegi, laufflatarmálsstuðul og yfirhæð skóga. Sýrustig jarðvegs hafði engin markæk áhrif á ánamaðkasamfélagið. Það vekur athygli hversu hár tegundafjöldi og lífmassi ánamaðka var í íslenskum barrskógum, eða síst minni en í mólendi, þrátt fyrir að tegundasamsetning þeirra breyttist mikið. Niðurstöðurnar sýna hvað gerist fyrstu 50 árin eftir að barrskógar eru gróðursettir, en þær miklu breytingar sem komu fram á ánamaðkasamfélaginu í elstu lerkiskógunum gera allar spár erfiðar um hvað gerist í framhaldinu. Þörf er því á frekari ánamaðkarannsóknum í elstu barrskógum landsins.

INTRODUCTION

Earthworms are among the most important soil organisms due to their size and ability to promote decomposition, nutrient cycling and soil formation (Lavelle & Spain 2005). They decrease the soil bulk density and incorporate litter and humus materials into deeper horizons of the soil profile, thereby affecting the whole food web and the aboveground plant community (Frelich et al. 2006). The species diversity in earthworm communities generally ranges from 1 to 15 species, but most commonly from 3 to 6 species (Edwards & Bohlen 1996).

Some confusion exists as to the number of earthworm species living in Iceland. Backlund (1949) compiled the Icelandic earthworm fauna from existing samples. If, as suggested by Rundgren (2007), *Dendrobaena rubida* (Savigny), *D. subrubicunda* (Eisen) and *Bimastus tenuis* (Eisen) are considered part of the *D. rubidus*-complex the following nine species were listed in Iceland by Backlund: *Aporrectodea caliginosa* (Savigny), *Aporrectodea rosea* (Savigny), *Dendrobaena octaedra* (Savigny), *Dendrodrilus rubidus* (Savigny), *Eisenia fetida* (Savigny), *Eiseniella tetraedra* (Savigny), *Lumbricus rubellus* Hoffmeister, *Lumbricus terrestris* Linnaeus and *Octolaceum cyaneum* (Savigny). Later Lindroth et al. (1973) identified *Lumbricus castaneus* (Savigny) and Guðleifsson & Ólafsson (1981) *Aporrectodea longa* (Ude). The species number of earthworms in Iceland is therefore presently regarded as eleven. These are the same species as referred to in Þorvaldsson & Sigurðardóttir (1998). Rundgren (2007) pointed out that the existence of *E. fetida* needs to be confirmed. However, it is known that this species has been imported for use in vermiculture in Iceland.

The occurrence of earthworms in Iceland has mainly been studied in hayfields where 4-6 species have been identified (Bengtson et al. 1975, Guðleifsson & Ólafsson 1981, Sigurðardóttir & Þorvaldsson 1994). Bengtson et al. 1975 identified a total of 8 species in Iceland, of which 3 were found in birch woodlands (*Dendrobaena octaedra, Dendrodrilus rubidus, L. rubellus*) and two more in planted forests (*A. caliginosa and O. cyaneum*). At present there exists no systematic survey of woodland and forest living earthworms in Iceland, and the present study is the first study dedicated to a systematic comparison of earthworm densities in planted forests with other vegetation types in Iceland.

The dispersal of earthworms is slow, usually only spreading up to 5 -10 meters year^{-1} (Edwards & Bohlen 1996). Their occurrence is also strongly influenced by soil characteristics such as moisture, temperature, pH, soil air, organic matter and the C/N ratio (Edwards & Bohlen 1996). Because earthworms demand good soil conditions they are considered valuable indicators of soil quality (Doube & Schmidt 1997). As the optimum temperature for growth of most earthworm species is 10-15 °C (Edwards & Bohlen 1996), soil temperature might be a limiting factor in Iceland where the topsoil temperature in grassland only reaches 10-14 °C in the warmest lowland regions. However, during winter the topsoil temperature in Iceland rarely drops below -2°C (Sturludóttir & Guðmundsson

2011), which earthworms are expected to tolerate. On the other hand most Icelandic soils usually have a high moisture and organic matter content and a fairly high pH because of their basaltic origin (Arnalds 2004), factors which are considered favourable for earthworms (Yli-Olli & Huhta 2000, Ammer et al. 2006).

Outside Iceland, the number of earthworms is generally higher in deciduous forest soils than in coniferous forest soils and deciduous forest soils have a higher earthworm species diversity than soils in coniferous forests (Dymond et al. 1997, González et al. 2003, Ammer et al. 2006). Coniferous forests and heathlands are therefore considered species-poor communities whereas deciduous woodlands and permanent pastures are species-rich communities (Edwards & Bohlen 1996).

Iceland is almost completely lacking in forests, only 1.5% of the country being covered by natural mountain birch and 0.3% by planted conifers (Traustason & Snorrason 2008). Extensive afforestation is going on and more is planned in the future. It is of interest to see the ecological impact of this type of land use change. The present study was part of a larger research project entitled "ICEWOODS", where the biological and environmental impact of afforestation in Iceland was studied (Sigurdsson et al. 2005, Elmarsdottir et al. 2007, Elmarsdóttir et al. 2011).

The main goal of the present study was to investigate the effect of afforestation with exotic coniferous tree species (larch, spruce and pine) on earthworm communities. This was done by comparing coniferous plantations of different age to native mountain birch woodlands and natural open heathlands. Based on results from abroad (Muys et al.1992, Edwards & Bohlen 1996), it was expected that earthworm communities would be less diverse and abundant in the coniferous plantations than in the two native ecosystem types. Additional goals were to compare earthworm communities in heathlands and mountain birch woodlands in two different locations in Iceland, and to relate the observed differences in earthworm communities in different vegetation types and locations to differences in soil characteristics and ecosystem structure.

MATERIALS AND METHODS

Site description

Two study areas were selected for the project, one in the eastern part of Iceland and the other in the western part (Figure 1). The study area in the east was located at Fljótsdalshérað (65°06'N, 14°46'W) at an elevation of 60–90 m a.s.l. The western study area was located in Skorradalur (64°30'N, 21°27'W) at an elevation of 60–200 m, and one additional study area (B_W2) was located at the adjacent Litla–Skarð in Norðurárdalur (64°44'N, 21°37'W), at 120–140 m a.s.l.

Within each of the two study areas eight or eleven vegetation types were investigated in eastern and western Iceland, respectively (Table 1 and Table 2). At both study areas the vegetation types consisted of open heathlands

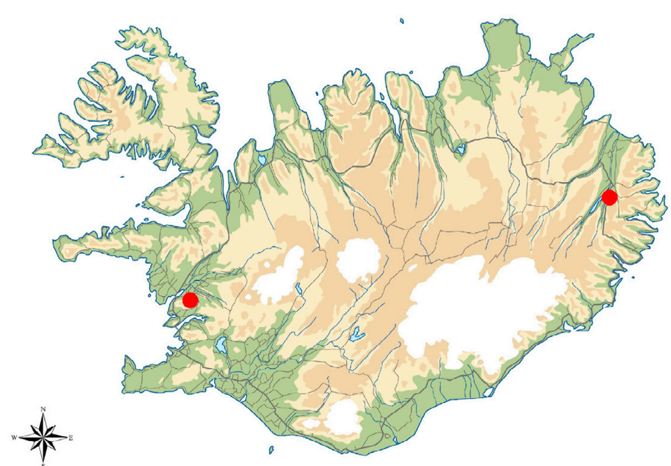

Figure 1. Location of the main study areas in Iceland. Map: Inga Dagmar Karlsdóttir.

used for sheep grazing (Table 2), native mountain birch woodlands (*Betula pubescens* Ehrh. ssp. *czerepanovii*) and exotic coniferous forest plantations of different ages, which had been established on former heathlands (Table 1 and Table 2). The dominant heathland vegetation was *Calluna vulgaris* L. (16%) in eastern Iceland, but *Empetrum nigrum* L. (21%) in western Iceland (Elmarsdottir et al. 2007).

In eastern Iceland the coniferous tree species was Siberian larch (*Larix sibirica* Ledeb.) but in western Iceland the coniferous plantations were of lodgepole pine (*Pinus contorta* Douglas) and Sitka spruce (*Picea sitchensis* (Bong.) Carr.; Table 1 and Table 2). These three tree species have been used in 70% of all afforestation with exotic tree species in Iceland during the 20th century (Pétursson 1999), which was why they were chosen for the present study. Since Siberian larch has mostly been used in East and North Iceland, in contrast to Sitka spruce in West and South Iceland, two main study areas were needed.

All investigated vegetation types at both study areas were located on valley slopes, which were steeper in the Skorradalur study area. The bedrock in both areas is upper Tertiary basalt (Johannesson & Saemundsson 1998) and the soil type is Brown Andosol, which is the most common vegetated upland soil type in Iceland (Arnalds 2004). The soil pH was around 6 in both study areas (Table 1). One vegetation type with spruce in the western study area (S2, Table 2) was, however, situated on a small rhyolite bedrock intrusion, resulting in a lower soil pH (Table 1) but with similar vegetation as the other spruce plantations (Table 2).

Table 1. Soil characteristics of the study sites in eastern and western Iceland. N = soil nitrogen concentration (%), C = soil carbon concentration (%), C/N = soil carbon:nitrogen ratio. Data from Sigurdsson et al. (2005), Elmarsdottir et al. (2007) and Elmarsdóttir et al. (2011).

Vegetation type	Name	Size	Stand age	Soil (0-10 cm)			
		ha	years	pH	N	C	C/N
Eastern Iceland							
Heathland	H_E	7.4	-	6.7	0.41	6.4	15.6
Birch woodland	B_E1	5.1	18	6.0	0.37	7.5	20.3
-	B_E2	6.1	Old growth	5.5	0.42	9.6	22.8
Larch plantation	L1	4.6	12	6.5	0.31	5.1	16.6
-	L2	7.2	18	6.7	0.23	4.1	17.7
-	L3	9.5	19	6.4	0.31	5.1	16.6
-	L4	3.2	36	5.9	0.37	6.8	18.4
-	L5	7.3	50	6.1	0.33	6.9	20.8
Western Iceland							
Heathland	H_W	9.0	-	6.3	0.37	5.6	15.0
Birch woodland	B_W1	9.2	Old growth	6.0	0.73	10.3	14.1
-	B_W2	4.8	Old growth	5.7	0.70	12.7	18.2
-	B_W3	13.6	Old growth	5.9	0.85	12.9	15.2
Spruce plantation	S1	7.8	9	6.1	0.74	10.1	13.6
-	S2*	1.2	34	5.2	0.91	18.2	20.0
-	S3	3.2	43	5.6	0.77	13.4	17.4
-	S4	4.1	43	5.4	0.94	16.3	17.3
Pine plantation	P1	9.9	14	6.0	0.54	8.2	15.2
-	P2	3.4	39	5.9	0.43	6.6	15.4
-	P3	1.8	46	5.5	0.63	11.6	18.4

*This site was found close to a small rhyolite bedrock intrusion (Johannesson & Saemundsson 1998), which led to lower soil pH.

Even though the two study areas are 350 km apart they have similar climatic conditions. Both have a mean annual temperature of 2.7 °C and the mean temperature of the coldest month (January) is -2.4 and -1.6 °C for the eastern and western study areas, respectively. The mean temperature of the warmest month is also similar, 10.2 and 9.7 °C for the eastern and western areas, respectively. The mean annual precipitation is, however, different, or 738 mm in the eastern study area and 1425 mm in the western (Elmarsdottir et al. 2007). The western study area also had somewhat higher total nitrogen (N) content in the mineral soil and a lower carbon to nitrogen ratio (Table 1). Further description of the study areas, the sampling of soil and flora, the analytical methods used and the experimental design are given in Sigurdsson et al. (2005), Elmarsdottir et al. (2007) and Elmarsdóttir et al. (2011).

Earthworm sampling methods

Earthworm collections were carried out twice at each study area, in early and late summer. At the eastern study area collection was undertaken from 11-13 June and 12-14 August 2003. At the western study area the collection was from 18-21 June and 18-22 August 2004. Three samples were taken along five randomly distributed 50 m long transects in each vegetation type, which was on average 6.2 ha in size (Table 2). Thus 15 soil samples (33x33 cm wide, down to 40 cm depth) were taken at each vegetation type, but the unit of replication was the transect (n=5). Earthworms were collected from the samples by handsorting on site and

Table 2. Vegetation characteristics of the study sites in eastern and western Iceland. Gveg = ground vegetation (g DM m^{-2}), LAI = Leaf Area Index of trees (m^2 m^{-2}), Hd = Dominant tree height (m). Additional parameters are "Monoc" and "fMonoc", "fDicots", "fMoss" and "fFerns", which stand for amount (g DM m^{-2}) and relative amount of monocots, dicots, mosses and ferns in the ground vegetation, respectively. Data from Sigurdsson et al. (2005), Elmarsdottir et al. (2007) and Elmarsdóttir et al. (2011).

Vegetation type	Name	Gveg	LAI	Hd	Monoc	Relative amount in understory			
						fMonoc	fDicots	fMoss	fFerns
Eastern Iceland									
Heathland	H_E	549	0.0	0	15.3	0.03	0.28	0.69	0.00
Birch woodland	B_E1	393	1.0	3.3	3.3	0.01	0.74	0.22	0.02
-	B_E2	282	1.7	7.8	22.3	0.09	0.46	0.43	0.01
Larch plantation	L1	687	0.8	3.8	26.4	0.04	0.38	0.57	0.02
-	L2	122	2.1	6.5	16.7	0.17	0.67	0.09	0.07
-	L3	202	1.8	6.8	62.7	0.38	0.23	0.32	0.07
-	L4	105	3.0	10.4	65.3	0.39	0.31	0.04	0.25
-	L5	737	2.0	14.7	113.2	0.15	0.21	0.59	0.05
Western Iceland									
Heathland	H_W	523	0.0	0	39.1	0.07	0.62	0.30	0.00
Birch woodland	B_W1	431	1.4	2.3	185.6	0.39	0.09	0.51	0.00
-	B_W2	639	1.3	2.4	46.9	0.09	0.48	0.42	0.01
-	B_W3	423	1.2	4.6	152.4	0.37	0.31	0.32	0.01
Spruce plantation	S1	714	0.1	1.5	100.3	0.18	0.46	0.33	0.03
-	S2	283	2.1	6.9	26.8	0.16	0.07	0.75	0.02
-	S3	309	3.4	8.8	5.9	0.05	0.07	0.86	0.02
-	S4	73	4.2	14.3	139.0	0.19	0.41	0.40	0.01
Pine plantation	P1	591	1.5	3.2	37.3	0.14	0.42	0.37	0.06
-	P2	136	3.7	8.8	13.9	0.03	0.30	0.67	0.00
-	P3	150	4.1	11.7	5.2	0.05	0.04	0.89	0.03

stored in 70% isopropanol at 4 °C for later identification, length measurement and dry weight determination. Biomass was determined after drying at 70 °C for 24 hours. Species identification and nomenclature were based on Stöp-Bowitz (1969) and Sims & Gerard (1985).

Data analysis

After ensuring that the data met the requirements of normality and equal variance (Proc UNIVARIATE; SAS 9.2 software, SAS Institute Inc., Cary, NC, USA), paired t-tests (Proc TTEST) were used to compare the number of earthworm species, earthworm density and biomass from the June and August sampling. One-Way Analysis of Variance (Proc GLM) was used to compare how earthworm parameters varied with location in Iceland (study area) and vegetation type, and when significant, pairwise post hoc comparisons were tested by LSD tests. The relationship between the earthworm parameters and plantation age and various environmental parameters was studied with regression analysis (Proc rec) and Spearman's correlation matrix (Proc CORR), respectively.

RESULTS

Time of earthworm sampling

When the analysis was done separately for the two study areas, the numbers of species were not significantly different between spring and autumn (paired t-test; P=0.48 and 0.95 for eastern and western Iceland, respectively; data not shown) and neither earthworm community density nor earthworm biomass was significantly affected by sampling time (paired t-test P=0.07 and P=0.63, respectively; data not shown). Therefore all further analyses of the data were done on average numbers of the two sampling times for each transect.

Environmental variables

Soil pH had no significant impact on earthworm species diversity, community density or earthworm biomass (Table 3). In addition, neither of the earthworm parameters had a significant relationship with pH when the study areas were analysed separately (data not shown). It should be noted that the pH values and organic C concentrations are generally high in the Icelandic Andic soils, or on average 6.2 and 6.4% in the eastern and 5.8 and 11.4% in the western study area, respectively (Table 1).

When calculated across both study areas, earthworm parameters significantly increased with increasing total N in the top 10 cm of the soil while they were strongly negatively correlated with the C/N ratio of the soil (Table 3). The negative relationship with the C/N ratio was also maintained when calculated separately for the eastern and western study areas, while the relationship to total N became insignificant (data not shown). The positive relationship to total N was therefore mostly explained by the difference between the eastern and western study areas, while the relationship between earthworm variables and C/N ratio was both found at the site and regional level.

Across both study areas, earthworm species diversity and abundance were strongly positively related to the total amount of ground vegetation in heathland, woodland and forests and the total amount of grasses and sedges ("Gveg" and "Monoc" in Table 3). This positive relationship was also significant when calculated separately for the western and eastern study areas (data not shown).

Some significant relationships between earthworm species number, community density and relative amount of ground vegetation classes were found (Table 3). Earthworm species richness was negatively correlated to the relative contribution of ferns (fFerns) in the ground vegetation. Similarly, earthworm biomass was negatively related to the relative contribution of dicots (dwarf bushes and flowers, fDicots) and positively related to the relative contribution of moss (fMoss, Table 3).

A regression analysis on data from all forested sites from both study areas revealed a significant negative relationship between earthworm species diversity and community

Table 3. Spearman's correlation coefficients (*r*) for correlations between earthworm parameters (species number, population density (individuals m^{-2}), biomass (g DM m^{-2}) and different soil and vegetation parameters, see Table 1 and 2). Significant relationships are marked in bold. Significance level of r values: *** (P<0.001), ** (P = 0.001-0.009) and *(P<0.05-0.01). "ns" stands for non- significant relationship (P>0.10) and (ns) (P = 0.05-0.09).

Variable	Species no.		Density		Biomass	
	r	P-val.	r	P-val.	r	P-val.
Soil parameters						
pH	-0.13	ns	-0.06	ns	-0.17	ns
N	**+0.43**	***	**+0.36**	***	**+0.42**	***
C/N	**-0.32**	**	**-0.32**	**	**-0.32**	**
Vegetation parameters						
Gveg	**+0.39**	***	**+0.42**	***	**+0.36**	***
Monoc	**+0.36**	***	**+0.45**	***	**+0.39**	***
fMonoc.	+0.14	ns	+0.22	(ns)	+0.18	(ns)
fDicots	-0.11	ns	-0.12	ns	**-0.23**	*
fMoss	+0.15	ns	+0.11	ns	**+0.21**	*
fFerns	**-0.21**	*	-0.20	(ns)	-0.19	(ns)
LAI♦	-0.15	ns	**-0.21**	*	-0.04	ns
Hd♦	**-0.23**	*	**-0.22**	*	-0.08	ns

♦ Excluding heathlands.

density and dominant tree height, but this relationship was not valid for earthworm biomass (Hd, Table 3). Earthworm density, similarly, was negatively related to the overstory leaf area index (LAI) but not species diversity or biomass (Table 3).

Earthworm species

In total, six earthworm species were found in the study, four in the eastern study area and two additional species in the western study area (Figure 2). The relative abundance of species was more different between the two parts of the country than between vegetation types (Figure 2). The earthworm species *D. octaedra* dominated the earthworm communities both in the treeless heathlands and in the native mountain birch woodlands in eastern Iceland, but it was among the rarest species in the same vegetation types in western Iceland. There, *A.*

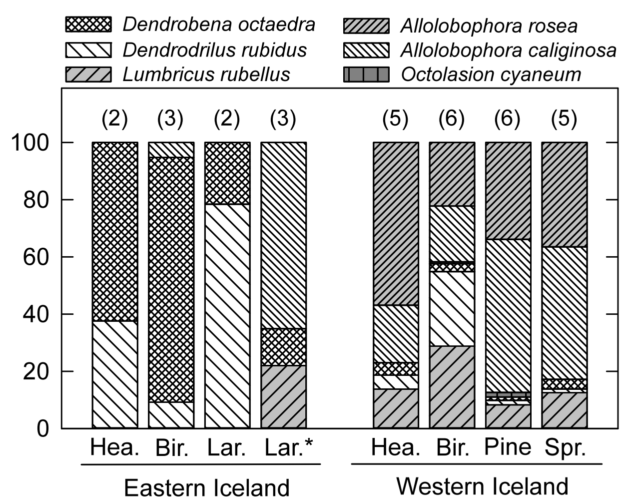

Figure 2. Mean relative abundance of different earthworm species in treeless heathlands (Hea.), native mountain birch woodlands (Bir.) and exotic Siberian larch (Lar.), lodgepole pine (Pine) and Sitka spruce (Spr.) plantations in eastern and western Iceland. The oldest age-class of Siberian larch is shown separately (Lar.*). Numbers above the bars indicate total number of earthworm species found in each vegetation type.

rosea instead dominated the treeless heathland soils, while the birch woodlands harboured *L. rubellus*, *Dendrodrilus rubidus*, *A. rosea* and *A. caliginosa* in similar proportions (Figure 2).

The afforestation with coniferous tree species had a clear effect on the relative earthworm species composition (Figure 2). The Siberian larch forests in eastern Iceland that have been converted from heathlands had a shift in species dominance towards *Dendrodrilus rubidus*, and *D. octaedra* was relatively common. In contrast, patterns of relative species abundance were very different in the oldest thinned age-class in the Siberian larch forest, with *A. caliginosa* dominating the community (81.1 out of 124.6 earthworms m^{-2} in that vegetation type). There, *L. rubellus* was the second most common species, but it was not found elsewhere in eastern Iceland. In western Iceland, afforestation with Sitka spruce and lodgepole pine also shifted earthworm composition towards *A. caliginosa* dominance from *A. rosea* in the treeless heathlands, but both *A. rosea* and *L. rubellus* remained relatively common. This shift towards a dominance of *A. caliginosa* was in accordance with the observed changes in the oldest age-class in the Siberian larch forest in eastern Iceland. The other earthworm species found in treeless heathlands and mountain birch woodlands in western Iceland were also found in the coniferous stands in low numbers (Figure 2).

The average number of earthworm species differed between study areas (Figure 3; Table 4). In eastern Iceland, there were significantly more species found in Siberian larch forests when the oldest larch age-class was included (Figure 3), but when it was excluded no significant differences were found between different vegetation types (Table 4). In western Iceland, the native mountain birch woodland harboured significantly more species than the other exotic forest types, while there was no significant difference in species numbers between the heathland and any of the forest types (Figure 3; Table 4).

Table 4. Relative changes in number of species per transect, population density and earthworm biomass in different study areas (East and West Iceland) and different vegetation types within each area. *** (P<0.001), ** (P = 0.001-0.009) and *(P<0.05-0.01). "ns" stands for non- significant relationship (P>0.05). Bold formatting indicates significant difference derived from a post-ANOVA LSD test (P<0.05).

Factor	Differences	Test	Spp number		Pop. density		Biomass	
			%	P	%	P	%	P
Study area		ANOVA		<.001		<.001		<.001
Heath♦	W / E Iceland	LSD	**+110**	**	**+336**	*	**+1318**	*
Birch♦	W / E Iceland	LSD	**+150**	***	**+619**	***	**+1783**	***
Veg. type♦		ANOVA		0.89		0.07		0.04
E. Icel.	Birch / Heath	LSD	0	ns	-5	ns	+9	ns
	Larch◊ / Heath	LSD	-20	ns	-15	ns	0	ns
	Larch◊ / Birch	LSD	-20	ns	-11	ns	-8	ns
	Larch / Heath	LSD	+10	ns	+247	ns	+1015	ns
	Larch / Birch	LSD	+10	ns	+323	ns	**+912**	*
Veg. type♦	ANOVA			<.001		0.001		0.03
W.-Icel.	Birch / Heath	LSD	+19	ns	+57	ns	+44	ns
	Pine / Heath	LSD	-33	ns	-26	ns	-19	ns
	Spruce / Heath	LSD	-14	ns	-12	ns	-13	ns
	Pine / Birch	LSD	**-44**	***	**-53**	**	-43	ns
	Spruce / Birch	LSD	**-28**	**	**-44**	**	**-43**	*
	Spruce / Pine	LSD	+29	ns	+19	ns	+8	ns

♦ = Averages for June and August sampling; ◊ = Excluding the oldest age-class for larch in eastern Iceland (see Table 1 and Figure 4).

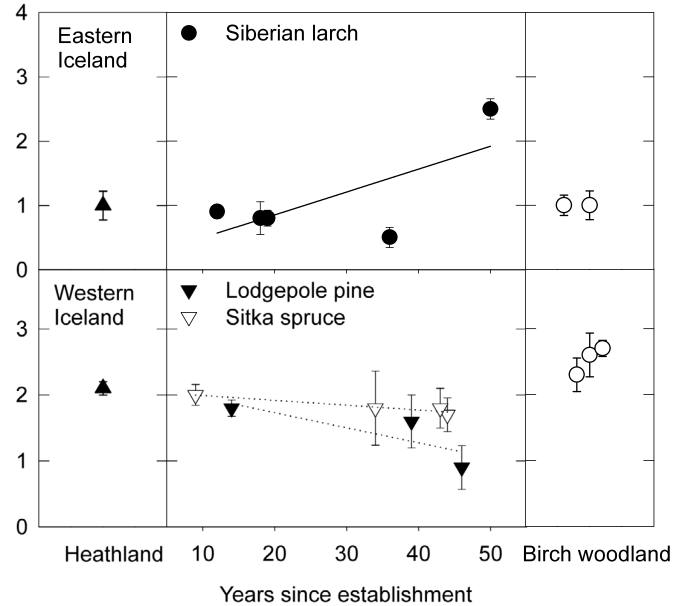

Figure 3. Average number (June and August) of earthworm species per transect in heathlands (far left panels), ca. 50 years after afforestation of heathlands (centre panels) and in mountain birch woodlands (far right panels). Standard Error indicates the diversity between 5 transects per site. Whole lines indicate significant regression analysis of change with time, while dotted lines are not significant. Statistical results of regression analyses are presented in Table 5 and ANOVA analyses between study sites and vegetation types in Table 4.

Earthworm community density

Earthworm density and biomass were both significantly higher in the western study area than in the eastern one for treeless heathland and mountain birch woodland soils (ca. 4-7 times and 14-19 times, respectively; Figure 4; Table 4). The differences in earthworm biomass were relatively greater than differences in community density between study areas due to a higher density of larger earthworm species in western study area, such as *L. rubellus*, *A. caliginosa* and *A. rosea* (Figure 2).

In eastern Iceland, Siberian larch had a significantly higher earthworm biomass than mountain birch woodlands, but not heathlands (Table 4). When, however, the oldest age-class of Siberian larch was excluded there were no significant differences in earthworm density and biomass between vegetation types (Table 4). In West Iceland both community densities and earthworm biomass were significantly higher in the native mountain birch woodlands than in the exotic coniferous plantations (on average 53% and 44% for density and 43% and 43% for biomass of lodgepole pine and Sitka spruce, respectively), but heathland was not significantly different from any forest type in either earthworm densities or biomass (Figure 4; Table 4).

Age of stand

A regression analysis on time since afforestation and earthworm parameters revealed a significant increase in earthworm species with time for all the forest types put together (Table 5). When the same analysis was done separately for West Iceland, the observed (not significant) trend was that the number of earthworm species decreased with increasing age of Sitka spruce and lodgepole pine (Figure 3; Table 5). In East Iceland the average number of earthworm species, however, increased significantly with time since start of afforestation (Figure 3; Table 5). When the oldest age-class of Siberian larch (L5) was excluded from the analysis, this increasing trend disappeared, both for larch alone and for all forest types put together (Table 5). The apparent positive impact of stand age on earthworm species richness was therefore mainly due to the oldest Siberian larch vegetation type.

Earthworm biomass was affected in the same way as average earthworm species numbers (Table 5; data not shown in figure). It did not change significantly with time since

Table 5. Regression analysis between years since establishment and mean number of earthworm species (spp transect^{-1}), community density (individuals m^{-2}) and earthworm biomass (g DM m^{-2}) in different coniferous forest types. Significant linear relationships with age are indicated by *** (P<0.001), ** (P = 0.001-0.009) and *(P<0.05-0.01). "ns" stands for non- significant relationship (P>0.10) and (ns) (P = 0.05-0.09).

Species	No. of transects	R^2	Regression		P-level
			intercept	slope	
Mean number of earthworm species					
Siberian larch	25	0.40	**0.138**	**+0.036**	***
Siberian larch♦	20	0.16	1.107	-0.017	ns
Lodgepole pine	15	0.19	2.185	-0.023	ns
Sitka spruce	20	0.02	2.064	-0.007	ns
All spp◊	60	0.09	**0.560**	**+0.013**	*
All spp◊,♦	55	0.02	0.908	-0.004	ns
Community density					
Siberian larch	25	0.59	**-34.085**	**+2.187**	***
Siberian larch♦	20	0.26	**11.079**	**-0.257**	*
Lodgepole pine	15	0.24	47.321	-0.791	(ns)
Sitka spruce	20	0.37	**50.958**	**-0.797**	**
All spp◊	60	0.13	**-1.474**	**+0.047**	*
All spp◊,♦	55	0.22	**1.496**	**-0.022**	**
Earthworm biomass					
Siberian larch	25	0.62	**-2.283**	**+0.130**	***
Siberian larch♦	20	0.20	0.216	-0.005	(ns)
Lodgepole pine	15	0.07	2.073	-0.005	ns
Sitka spruce	20	0.09	2.090	-0.022	ns
All spp◊	60	0.17	**-8.849**	**+0.466**	**
All spp◊,♦	55	0.04	1.136	-0.009	ns

♦ When the oldest age-class of Siberian larch was excluded; ◊ When vegetation types from both study areas were compared, relative changes from heathland were used instead of measured values to make different areas comparable.

afforestation for Sitka spruce, lodgepole pine or Siberian larch when L5 was excluded, but increased significantly when L5 was included, both for the Siberian larch alone and for relative changes in earthworm biomass of all conifers together.

The community density of earthworms responded most strongly to time since afforestation (Figure 4). The community density increased significantly with age, when all coniferous forests were compared together (+4.7% per year since afforestation), while it decreased significantly with age (-2.2% per year since afforestation) when the oldest age class of Siberian larch (L5) was not included (Table 5). In East Iceland the age-related trend in earthworm community density was significantly negative during the first 40 years after afforestation (excluding L5), but significantly positive when thinned older Siberian larch forest was included (including L5). When the analysis on community density was done only for West Iceland, the negative effect of time since afforestation was significant for Sitka spruce but not for lodgepole pine (Figure 4; Table 5).

DISCUSSION

Time of sampling

Depending on the literature source, the activity of earthworms is either reported highest in spring or in autumn (Nyström 1975, Edwards & Bohlen 1996, Whalen 2004). Therefore sampling in this project was done both in June and August. Despite the lack of significant differences in earthworm parameters between both sampling occasions, the authors would like to recommend an autumn sampling, especially if the main goal of a future study is to identify earthworm species richness in Iceland. The individuals tend to be larger in the autumn, which greatly helps with species identification.

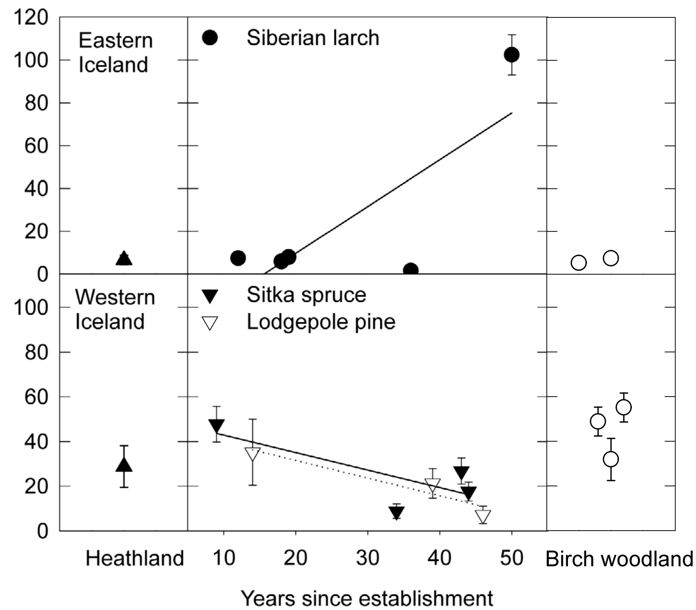

Figure 4. Average population density (June and August) of earthworms (individuals m^{-2}) heathlands (far left panels), ca. 50 years after afforestation of heathlands (centre panels) and in mountain birch woodlands (far right panels). Standard Error indicates the diversity between 5 transects per site. Whole lines indicate significant regression analysis of change with time, but dotted lines are not significant. Statistical results of regression analyses are presented in Table 5 and ANOVA analyses between study sites and vegetation types in Table 4.

Soil acidity

Edwards & Bohlen (1996) present three ecological groups of earthworms; epigeic (surface species), anecic (soil species) and endogeic (subsoil species) All species identified in the present study were epigeic, living close to the soil surface, except the anecic species *O. cyaneum*. Epigeic earthworm species are relatively tolerant to low pH but they will avoid a pH lower than 4.5 (Dominguez 2004). The optimum soil pH seems to be species dependent; *Lumbricus* species are, for example, attracted to a higher pH than *Allolobophora* species (Edwards & Bohlen 1996). No clear relationship between earthworm diversity or abundance and soil pH was detected in the present study. This was probably due to the relatively high and therefore favourable pH (5.2-6.7) in all the soils.

Coniferous versus broadleaved forests

Earthworms are generally reported as less abundant in coniferous forests than in broadleaved forests (Dymond et al. 1997, Gonzáles et al. 2003, Smith et al. 2008). This has been related to poorer litter quality, lower pH and more compact soil structure in the coniferous forests (Curry 2004). Such differences in soil pH or more compact soils between birch woodlands and coniferous stands were not detected in the present study (Table 1, Sigurdsson, unpubl. data on soil bulk density). However, there was a large reduction in understory vegetation in spruce, pine and the younger larch stands, compared to heathlands, which should have added to the known differences in litter quality between conifers and broadleaf trees (Chapin 2002). In the present study, both average earthworm species numbers and community densities were somewhat lower for lodgepole pine and Sitka spruce than for birch in western Iceland, with the lowest number found in pine. In Finland, Scots pine stands (*Pinus sylvestris* L.) also tend to contain lower earthworm densities than Norway spruce (*Picea abies* [L.] Karst.) forests (Terhivuo & Valovirta 1978). It was, however, noteworthy that neither earthworm species richness nor community density changed significantly for larch in eastern Iceland compared to birch woodlands. Only one study has previously collected earthworms in native mountain birch woodlands and planted conifers in Iceland (Bengtson et al. 1975). In that study the number of earthworm species and density were similar in the two forest types and the biomass was even higher in the larch plantation. It is therefore apparent that the difference in earthworm densities is dependent on more factors than tree species alone.

Afforestation

It has been stated that coniferous afforestation of treeless areas is usually accompanied by a marked impoverishment of the earthworm fauna (cf. Curry 2004). The present study does not support these claims under Icelandic conditions. Hence, the effects of afforestation may not be as straightforward as described by, for example, Peterken (2001). One factor that clearly needs to be taken into consideration is time since afforestation, which in the present study was found to have a significant effect on both earthworm diversity and density.

One of the most important results in the present study was the fact that earthworm communities had similar biomass and species richness in the exotic coniferous forests in Iceland compared to heathlands. This was in contrast to results from other studies that generally report only few earthworm species and low earthworm biomass in coniferous forests compared to other vegetation types (Smith et al. 2008, Gonzáles et al. 2003, Dymond et al. 1997). High biomass of earthworms in exotic coniferous plantations in Iceland may have ecological implications for other organisms. It may partly explain why bird densities are similar in both the native mountain birch woodlands and exotic coniferous forests in Iceland (Nielsen 2003, Nielsen et al. 2007).

Soil N and C/N ratio

The number, density and biomass of earthworms were higher in the western than in the eastern study area. Some of the regional differences in earthworm diversity and abundance in the present study seem to have been related to differences in soil fertility as can be seen by the positive relationship between earthworms and total soil N. More fertile soils are generally observed to harbour greater numbers of earthworms than less fertile soils (cf. Terhivuo & Valovirta 1978). Also, the higher precipitation and soil organic matter content in the western study area might contribute to higher earthworm populations. Higher earthworm abundance and biomass in fertile Icelandic hayfields than in nutrient poor hayfields support the comparison of earthworm abundance and abundance in the more fertile West Iceland study sites in the present study (Gudleifsson & Ólafsson 1981, Sigurðardóttir & Þorvaldsson 1994).

Earthworms ingest organic matter with a relatively wide range of C/N ratios and convert it to earthworm tissue of a lower C/N ratio (Bohlen et al. 2004a, 2004b). In the present study earthworm diversity and abundance were strongly negatively related to the C/N ratio in the top 10 cm of soil. Muys et al. (1992) report a similar negative relationship between earthworm diversity or abundance and the C/N ratio for a range of different vegetation types. The soil C/N ratio tends to increase as the dominant vegetation changes from treeless lands to forests (Chapin 2002). This was also the case in the present study.

Ground vegetation

The strong positive relationship of earthworm parameters to the amount of ground vegetation, and more specifically to the amount of monocots is noteworthy. The amount of ground vegetation and the relative amounts of monocots tend to be higher in young forests when compared to grazed heathlands (see Sigurdsson et al. 2005). Also, a high relative dominance of horsetails (*Equsetum* spp.) is a typical successional stage of all native and exotic forest types in Iceland before self-thinning (unmanaged mountain birch) or organized thinning (exotic plantations) has taken place (Sigurdsson et al. 2005). The negative relationship between earthworm species richness and the relative amount of horsetails is therefore likely caused by the lower plant diversity in forest stands at this successional stage.

Vigorous ground vegetation commonly appears in 40-50 year old thinned Siberian larch stands in eastern Iceland (Sigurðardóttir 2000). In the present study this change was accompanied by a drastic increase in earthworm densities. This raised an interesting question as to the cause of this finding. Was the accelerated nutrient turnover by the increased earthworm activity the key behind the lush ground vegetation in older larch forests? Another explanation might be that earthworms benefit from the enhanced understory production following thinning of this relatively shade-intolerant tree species. Further studies are needed on this issue.

Earthworm species

A total of six species of earthworms were identified in the study, four in the eastern study area and six in the western study site, indicating more favourable conditions in the western study area (see later discussion). The species identified in eastern Iceland were *D. octaedra*, *Dendrodrilus rubidus*, *A. caliginosa* and *L. rubellus*. In addition, *A. rosea* and *O. cyaneum* were found in western Iceland. Apart from *A. rosea* these are the same species as found by Bengtson et al. (1975) in Icelandic mountain birch woodlands. In eastern Iceland two and three species were detected in open heathland and mountain birch woodlands, respectively, compared to five and six species in the same ecosystems in western Iceland. This is a comparable number of earthworm species as that reported from natural deciduous birch forests in Finland, for example, where Räti & Huhta (2004) found up to eight earthworm species. All the above mentioned species, except *A. caliginosa*, were also found in Scots pine stands in Germany (Ammer et al. 2006), but *A. caligninosa* has been reported only to occur in non-forested habitats in Finland (Terhivuo & Valovirta 1978). In Iceland, in contrast, *A. caligninosa*, is found in forest soils (Bengtson et al. 1975 and the present study). Such apparent differences in habitat selection between Iceland and the Eurasian continent are also known for other taxa, e.g. in the distribution of the plant *Armeria maritima* (Mill.) Willd., which is a strictly coastal plant in most of Europe but is found from the coasts to the highest mountains in Iceland. Such habitat shifts have been explained by a lack of key competition species in Iceland (Nielsen 2003).

Earthworm community changes

The observed reductions in *D. octadea* in heathlands in the eastern study area, towards a dominance of *Dendrodrilus rubidus* in middle aged Siberian larch forests, was in contrast to findings in southern Sweden (Rundgren 1994) and in the USA (Gonzáles et al. 2003), where *D. octaedra* was the only earthworm species found in coniferous forests. In Finland, however, *Dendrodrilus rubidus* has been reported to be the secondmost common earthworm species in coniferous forest soils after *D. octaedra* (Terhivuo & Valovirta 1978). Both *A. caliginosa* and *A. rosea* became dominant in Sitka spruce and lodgepole pine forests in the western study area, which again does not conform well with Scandinavian findings. *A. rosea* is relatively uncommon in Finnish forests, and is only found in South Finland in the richest soils and more often in mixed forests than coniferous ones (Terhivuo & Valovirta 1978).

Age of stand

The regression analysis showed an increase in average earthworm species numbers per vegetation type with time since afforestation. Since the positive age-trend only became significant because of large shifts in the oldest vegetation type of Siberian larch, this result has to be interpreted with caution. What can be safely concluded from the present study is that earthworm species diversity (average number of species) was not affected by afforestation of heathlands with exotic coniferous trees during the first 40 years or so following afforestation of heathlands. Further studies on older afforestation areas (>45 years) are necessary to safely conclude whether the long-term trend is positive, as was indicated here, or negative, as the insignificant trends in Sitka spruce and lodgepole pine could indicate.

The earthworm community densities were much more responsive to time since afforestation than average species numbers or biomass. The earthworm community in the afforested vegetation types seemed to follow a similar negative trajectory during the first 40 years or so after establishment, during which the forests move from an establishment phase into the (dark) thicket phase (also termed stem exclusion phase) in the forest succession (Smith et al. 1997, Kimmins 2004). During this stage, ground vegetation is reduced and horsetail becomes the dominant species (Sigurdsson et al. 2005). However, what happens in the earthworm community after thinning has taken place is highly uncertain.

Future changes

Based on the results of the present study, it could be hypothesized that the earthworm populations in the two different coniferous forest types, i.e. the shade intolerant deciduous Siberian larch and the shade tolerant and evergreen Sitka spruce and lodgepole pine, may follow different trajectories as they become older. The shade intolerant Siberian larch has a lower LAI than spruce and pine, which allows more light to penetrate the canopy, leading to lush ground vegetation after thinning (Sigurdsson et al. 2005). In fact, in the present study the oldest age-class of Siberian larch had the largest biomass of ground vegetation. The latter could result in a more favourable habitat for earthworms, and together with the relatively high soil pH of the volcanic soils, could lead to a large increase in earthworm densities in older Siberian larch forests. A modelling study, predicting the 200 year development of soil pH in Siberian larch forests in Iceland, supports the prediction that soil pH will remain high well into the future (Haraldsson et al. 2007). However this is not expected to happen in the denser and darker Sitka spruce and lodgepole pine stands, where a higher normal tree spacing and higher LAI after thinning may not allow as much ground vegetation (James 1955).

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