Interacting effects of agriculture and landscape on breeding wader populations

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Abstract

The capacity of different landscapes to sustain viable populations depends on the spatial and temporal availability of key population-specific resources. Heterogeneous landscapes provide a wider range of resources and often sustain higher levels of biodiversity than homogeneous ones. Across the globe, agricultural expansion has resulted in large-scale homogenisation of landscapes with associated declines in many taxa. However, during the early stages of agricultural development, in terms of area and intensity, increased landscape heterogeneity and changes in local productivity through fertilizer inputs can potentially increase resource availability for some species. Agriculture in Iceland is currently neither highly intensive nor extensive, and primarily occurs as hayfields (> 90% of agricultural land) embedded within a mosaic of semi-natural wetlands and heaths. These landscapes support internationally important breeding populations of several wader species but the role of agricultural land in promoting or constraining breeding wader densities is currently unknown. Understanding the relationship between cultivation and wader populations is important as the area of cultivated land is predicted to expand in Iceland in near future, largely through conversion of the remaining semi-natural wetlands. Here we (a) quantify relationships between breeding wader densities in lowland Iceland and the amount of cultivated land and wetland in the surrounding landscape using density estimates from 200 transects in common semi-natural habitats, (b) assess the extent to which cultivated land affects wader densities in these landscapes, and the potential effects of future agricultural expansion at the expense of wetlands on wader populations. Wader densities in semi-natural habitats were consistently greater when surrounding landscapes had more wetland at scales ranging from 500 m to 2500 m, indicating the importance of wetland availability. However, the effects of cultivated land in the surrounding landscape varied with altitude (ranging from 0-200 m); in low-lying coastal areas, wader numbers decline with increasing amounts of cultivated land (and the lowest densities (<1 km2) occur in areas dominated with cultivated land) the inverse occurs at higher altitudes (>100 m a.s.l., where lowest densities occur in areas without cultivated land). This suggests that additional resources provided by cultivated land may be more important in the less fertile uplands. Further agricultural conversion of wetlands in low-lying areas of Iceland is likely to be detrimental for breeding waders, but such effects may be less apparent at higher altitudes.

1. Introduction

Landscapes vary in their ability to sustain viable populations of species through the different resources that they provide, with more heterogeneous landscapes typically providing more diverse resources (Roth, 1976; Benton et al., 2003; Tscharntke et al., 2005). Habitat heterogeneity influences species diversity and density, and ecosystem function (Roth, 1976; Pickett and Cadenasso, 1995; Christensen, 1997). Landscape and habitat heterogeneity can stem, for example, from variability in vegetation structure, composition, density and biomass which are partly driven by the underlying productivity of ecosystems (Pickett and Cadenasso, 1995; Forman, 2014; Gunnarsson et al., 2015) and also by anthropogenic actions, such as agriculture. Agricultural land has become one of the largest terrestrial biomes, occupying ~40% of all land on the planet (Foley et al., 2005). The expansion and intensification of agriculture has altered landscapes and the associated homogenisation of landscapes has greatly influenced species abundance and diversity (Donald et al., 2001; Foley et al., 2005). Populations of numerous species, particularly specialist species, have declined as agriculture has expanded, while generalist species have often thrived in agricultural habitats (Wright et al., 2012).

The relationship between agricultural intensification and biodiversity supported within a landscape can follow a unimodal trajectory, with the onset of agricultural development initially increasing heterogeneity and fertiliser inputs increasing local productivity, but ongoing increases in agricultural intensification eventually resulting in landscape homogenisation with associated reductions in resource availability and biodiversity (Fig. 1) (Flowerdew, 1997; Sotherton and Self, 1999; Donald et al., 2001). The processes and mechanisms that drive the relationship between agriculture and biodiversity will vary between farming systems but a key factor is typically the change in habitat heterogeneity (Benton et al., 2003). The effect of increases in agricultural area on landscape heterogeneity can be mediated by the underlying habitat structure and fertility. For example, in nutritionally impoverished areas, the input of synthetic fertilisers to cultivated fields may boost local productivity and thus be beneficial for some species (Gunnarsson et al., 2015; Jóhannesdóttir et al., 2017a). Information on the relative impacts of agriculture in different landscapes is therefore key to understand and ultimately predict the consequences of further agricultural expansion and intensification for the maintenance of biodiversity in such landscapes.

There is great variation in the extent to which agriculture has developed across regions and countries, and in the impact of this development on the environment (Alexandratos and Bruinsma, 2012). In areas suitable for cultivation, agriculture is often very intense and many taxa have declined in abundance (Robinson and Sutherland, 2002; Benton et al., 2003; Pe'er et al., 2014). However, in more marginal areas for production and in less developed countries, agriculture is often less intensive and widespread, and has less impact on the environment and can even benefit biodiversity (Loos et al., 2014; Sutcliffe et al., 2015). In Iceland, agricultural development started late and only grew beyond domestic subsistence at the beginning of the 20th Century (Júlíusson and Ísberg, 2005). Icelandic agriculture is restricted by the northern location of the country, just south of the Arctic Circle, and agriculture does not dominate the landscape, as only 7% of the area below 200 m a.s.l. (the area which is suitable for agriculture) is currently used for cultivation (National Land Survey of Iceland, 2013; Snorrason et al., 2015). However, it has been estimated that up to 63% of this land could be used for cultivation (FAI, 2010). Icelandic lowlands currently comprise a fine-scale mosaic of open semi-natural habitats and cultivated fields (primarily for silage production), making the landscape highly heterogeneous (Jóhannesdóttir et al., 2017a). For example, Iceland has over one million wetland patches smaller than one hectare, which together comprise 30% of the 9000 km^2 of inland wetlands (50% are >5 ha), and inland wetlands cover about 20% of all vegetated surfaces of Iceland (Arnalds et al., 2016). These wetlands are of high value for biodiversity and they support several internationally important breeding bird populations (Einarsson et al., 2002; Gunnarsson et al., 2006; Jóhannesdóttir et al., 2014). Icelandic landscapes are particularly important for several wader species, such as Snipe (*Gallinago gallinago*), Black-tailed Godwit (*Limosa limosa*), Dunlin (*Calidris alpina*), Redshank (*Tringa totanus*), Whimbrel (*Numenius phaeopus*) and Golden Plover (*Pluvialis apricaria*), for which global populations are generally declining (International Wader Study Group, 2003; Piersma et al., 2016; Pearce-Higgins et al., 2017), and for which Iceland supports an estimated 3 - 34% (3, 7, 10, 12, 27 and 34%, respectively) of global populations (Delany and Scott, 2004; Thorup, 2004).

However, wetlands in Iceland have undergone extensive drainage in recent decades, and an estimated 47% of inland wetlands have now been affected by drainage (Arnalds et al., 2016). This drainage was primarily undertaken to create potentially suitable agriculture land, both for cultivation and grazing, and many drainage ditches are currently not associated with cultivated land. Today approximately half the cultivated land in Iceland is on drained wetland soils (Snorrason et al., 2015). Furthermore, a recent study showed 63% of farmers intend to increase their area of cultivated land in the coming years in Iceland (Jóhannesdóttir et al., 2017b). This expansion is likely to increase drainage of wetlands, with potentially serious impacts on the breeding bird populations as a consequence of the resulting habitat loss and reductions in landscape heterogeneity.

Frequent volcanic events and aeolian redistribution of dust from desert surfaces in Iceland result in intense deposition of basaltic volcanic materials. The amount is geographically variable depending on distance from the Mid-Atlantic ridge (where most volcanic activity and main dust release areas occur), which runs from south-west to north-east Iceland (Arnalds, 2015). This deposition strongly influences soil fertility (due to the resulting higher pH and favourable nutrient availability). This gradient of aeolian deposition has been shown to influence the distribution of breeding birds, with densities in wetland areas, in particular, being greater in areas of higher aeolian deposition (Gunnarsson et al., 2015). This gradient and the abundant remaining semi-natural land and high densities of breeding waders (Jóhannesdóttir et al., 2014) offer a rare opportunity to quantify the influence of cultivated land on bird distribution and abundance in semi-natural habitats, and how these vary in areas of differing underlying productivity. Expansion of agriculture inevitably means loss of other habitats and, in Iceland, wetlands have historically been the most common habitat converted for production. In this study, we make use of existing variation in extent of agriculture in lowland Iceland, and of the underlying productivity gradient, to examine how densities of internationally important breeding wader populations on semi-natural habitats vary in relation to the amount of agriculture and wetland in the surrounding landscape, and how this varies across an altitudinal gradient that reflects variation in underlying productivity as a consequence of historical aeolian dust deposition.

2. Methods

This study was undertaken in South-Iceland, an island in the North-Atlantic Ocean located between 63° and 66° North on the mid Atlantic ridge. Agriculture in Iceland, which is mostly based on livestock rearing and fodder production for their winter food (silage), is still of relatively low intensity and large patches of semi-natural habitats (e.g. wetlands, bogs, heathland and river-plains) are present in most agricultural areas (Fig. 2).

2.1 Survey locations and bird censuses

Single surveys of breeding birds were carried out at 200 transects in the lowlands of South Iceland, in areas below 200 m a.s.l. (Fig. 2). The area is one of the most important agricultural regions in Iceland, providing 36% of annual agricultural GDP in the year 2010 (FAI, 2010) and about 10% of land below 400 m a.s.l. in the area is cultivated land (Wald, 2012). Icelandic agriculture is almost entirely livestock-based (pastoral), and primarily comprises hayfields that are used for grazing and fodder production (silage for winter feed) for livestock farmed for meat and dairy production. Arable production is small-scale and mostly comprises barley grown for fodder on the farm where it is grown, although most grain fodder is imported (Helgadóttir et al., 2013). The concentration of cultivated land around individual farms throughout lowland Iceland means that agricultural habitats are very evenly spread throughout the region (Jóhannesdóttir et al., 2017a).

Land cover data for this study were extracted from the Icelandic Farmland Database, which uses satellite images with extensive ground truth verification to classify the surface of

Iceland into 12 different classes (Arnalds and Barkarson, 2003; Gísladóttir et al., 2014). The classification represents variables that reflect productivity; mostly vegetation cover, soil and drainage and is well suited for landscape analyses of biodiversity (Jóhannesdóttir et al., 2014). Survey sites within the five most common vegetated habitats (40 each of wetland (saturated), semi-wetland (damp), grassland, rich heathland, poor heathland, Fig. 2) were selected by a stratified random method, employing ArcGis 10.1 GIS software. The selected sites had to cover at least 20 ha of a single habitat type and to be at least 0.5 km apart, and the altitudinal variation within transects was very small (< 20 m, Fig. S1). In addition, for practical reasons of access, survey sites were selected so that they were not more than 2 km from roads and tracks (Jóhannesdóttir et al., 2014). Previous studies have shown that the distribution of habitat types in lowland Iceland varies little with respect to distance from roads and tracks (Gunnarsson et al., 2006).

Breeding bird surveys were conducted in 2011 and 2012, from the middle of May until the end of June, a period which encompasses incubation and early parts of chick rearing for the species involved. The date on which each site was visited was random to avoid any systematic bias in the counts (e.g. adults being more obvious when chicks have hatched). Only adult birds were counted. Counts were performed during periods of greatest bird activity, in the morning from 06:00 to 13:00 and in the afternoon from 17:00 to 22:00 (Davíðsdóttir, 2010). Surveys were only conducted during suitable weather conditions (wind speed lower than 6 m/s and in dry weather) to avoid conditions of low bird detectability (Bibby et al., 2000). At each survey site, birds were counted along a line transect, and every bird within 100 m on each side of the observer was recorded (Bibby et al., 2000). The placement and direction of transect line was designed to minimise any influence of adjacent habitats, i.e. in the middle of the habitat patch and in the direction that had the widest habitat coverage. The length of transects was often restricted by the habitat patch size. Average length of the transects was 511 m (sd = 69.4 m, range 216-685 m), and their total length was 101 km (Jóhannesdóttir et al., 2014).

The amount of agriculture and wetland habitat in the landscape surrounding each survey transect was calculated for four different sized buffers (500, 1000, 1500 and 2500 m radius – buffer sizes were selected arbitrarily as the size of area used by the species has not been clearly identified) centred on each transect, and habitat data were extracted from the Icelandic Farmland database.

2.2 Data analysis

Models were constructed at two levels: first, a multispecies model was used to explore landscape drivers of the overall abundance of all wader species combined; second, individual models were used to explore species-specific responses to landscape variables. For the multispecies model we used a generalized linear mixed model (GLMM) with a Poisson error distribution and a log-link function to analyse the variation in the total number of waders on each transect, with transect area (natural log-scale) as an offset. Separate models were run for each buffer, with the amount of cultivated land and wetland within the buffer, altitude of transect and interactions between altitude and area of cultivated land, and altitude and wetland area as fixed factors, including species as a random factor to control for differences in community composition at each site. All waders which commonly occurred both at higher and lower elevations were included in the analysis. The least common species included was Redshank which occurred 112 times. For the single-species models, which were constructed for the six most common wader species (Golden Plover, Dunlin, Snipe, Whimbrel, Black-tailed Godwit and Redshank), generalized linear models (GLMs) with a Poisson error distribution and log-link function were constructed with the same fixed effects and with transect area (natural log-scale) as an offset, but with no random effects. Altitude was included in the models as a surrogate of landscape composition which is related to fertility and changes gradually from the coast to inland. Areas closer to the coast are flatter, have more grassland, cultivated land and semi-wetlands (which tend to be drained wetlands) whereas inland areas have more heathland and less vegetated land (Fig. S2; Jóhannesdóttir et al., 2014; Gunnarsson et al., 2015; Arnalds et al., 2016). For data presentation, altitude was split into above and below 50 m a.s.l. (Fig. 2) as there is a compositional change in the landscape at approximately that altitude where it changes from flat coastal plains to higher altitude inlands. Density predictions are only presented for species which showed significant relationships, and density is predicted across the range of altitudes (25, 50 and 100 m). For simplicity models are only presented for the 1000 m buffer, as models from different buffer sizes all showed similar patterns (see Table S1 for results for all buffers). We tested for spatial autocorrelation in the model residuals using Moran's I correlograms. Transects lying within a lag distance were defined as neighbours using a binary weighing matrix for each distance class using the ncf package (Bjornstad, 2016). Significant Moran's I ($p<0.05$) at shorter pair-wise distance intervals up to 160 Distance units was taken as an indication of important spatial autocorrelation in nearby transects and as an indication of violating the independence of data points in our GLM models. All statistical analyses were performed in R 2.15.2 (R Development Core Team, 2008).

3. Results

3.1 Landscape structure

The habitat composition around each of the 200 survey locations was similar for buffers ranging from 500 m to 2500 m radius (Fig. S2). Areas around survey locations below 50 m a.s.l. had slightly less heathland and more semi-natural wetland and grassland than areas above 50 m, but the overall habitat composition varied little with each buffer (Fig. S2). The correlograms revealed significant positive autocorrelation at one or more of the three shortest lag distance intervals for model residuals using different buffer distances for only Snipe, Dunlin and Redshank. The remaining species and all wader combined showed spatial autocorrelation at occasional (but inconsistent) intermediate or larger distance intervals (Figs. S3-S6).

3.2 Factors influencing combined breeding wader species density

There was substantial variation in the density of all the six most common wader species recorded on the transects, ranging from 0 to 284 birds/km^2 (Fig. 3).

The effect of the amount of cultivated land in the landscape on overall wader densities varied significantly depending on altitude (Table 1); wader density declined with increasing area of cultivated land below 50 m but increased with area of cultivated land above 50 m (Fig. 4). Wader density also varied significantly with altitude, with higher densities occurring at lower altitudes (Fig. 4), and wader densities were higher in landscapes containing larger amounts of wetland in all buffer sizes. The effect of amount of wetland also differed with altitude but only at the smallest buffer size (500 m), and this interaction was much weaker than the altitudinal variation in the effect of area of cultivated land (Table S1).

3.3 Factors influencing density of wader species

Densities of three wader species (Golden Plover, Dunlin and Whimbrel) declined significantly with increasing area of cultivated land within the 1000 m buffer at lower altitudes but increased at higher altitudes (Table 2, Fig. 5). Densities of Dunlin and Black-tailed Godwit increased with area of wetland in the surrounding 1000 m but density of Redshank decreased (Table 2, Fig. 6), while Golden Plover density were unrelated to wetland area (Table 2). The effects of wetland area on densities of Snipe and Whimbrel varied with altitude but the direction of the relationship varied between them; Whimbrel densities increased with wetland area at higher altitudes but decreased at lower altitudes, while Snipe densities increased more rapidly with wetland area at lower altitudes (Fig. 6).

4. Discussion

Our studies indicate that changes in the amount of cultivated land, which is likely to expand, and wetland, which is likely to be lost, have the potential to greatly impact wader densities on semi-natural land in Iceland, but that the direction and relative impact of these effects may vary depending on altitude and associated underlying productivity of the land. Overall, wader densities are higher in landscapes with larger amounts of wetland and lower in landscapes with larger amounts of cultivated land, but the latter effect only occurs at low (coastal) altitudes. At higher altitudes (~100 – 200 m a.s.l), where heathlands are more common than wetland, grassland and cultivated land, wader densities increase with increasing area of cultivated land.

4.1 Species-specific response to different landscapes

The contrasting responses to the amount of cultivated land at different altitudes were apparent in three species (Golden Plover, Dunlin and Whimbrel); all of which declined in abundance with increasing amounts of cultivated land at low altitudes, but increased in abundance at higher altitudes. These three species primarily breed in drier heath habitats, while the other species (Snipe, Black-tailed Godwit and Redshank) are more commonly found breeding in wetter habitats (Jóhannesdóttir et al., 2014). Expansion of agriculture into areas of semi-natural habitat is ongoing in Iceland (Jóhannesdóttir et al., 2017b) and, at higher altitudes, such increases may provide areas of relatively high productivity (as a result of fertiliser applications and nutrient release by wetland drainage) and may increase foraging opportunities for adults feeding off territory (as a result of ploughing and associated increases in availability of soil invertebrates), which may allow greater breeding densities of Golden Plover, Dunlin and Whimbrel to be supported. Such use of cultivated fields as foraging habitats by breeding waders in upland landscapes has been reported elsewhere (Pearce-Higgins and Yalden, 2003).

While cultivated habitats at higher altitudes may provide additional resources for the breeding waders in these areas, such relationships are likely to have tipping points (e.g. Fig.1). If, as intended by farmers (Jóhannesdóttir et al., 2017b), agricultural expansion continues at the expense of natural wetlands, then these internationally important breeding populations will likely decline, in both coastal and upland areas.

4.2 Differences in underlying productivity and habitat composition

The altitudinal variation in the influence of amount of cultivated land on breeding wader densities is likely to reflect altitudinal variation in the underlying productivity of the land. We have previously shown (Jóhannesdóttir et al., 2017a) that the relative importance of cultivated land for breeding waders in lowland Iceland varies regionally, with larger numbers of waders using cultivated land in the West than in the North and the South of the country. This difference was linked to an underlying gradient of soil fertility which varies across Iceland, due to volcanic activity being mostly restricted to the divergent tectonic plate boundary that crosses Iceland on a SW-NE axis along the North-Atlantic ridge (Arnalds, 2015;

Gunnarsson et al., 2015). As a consequence, areas in the South and North receive larger quantities of volcanic dust than areas in the west (Arnalds, 2015).

This variation in soil fertility also occurs along altitudinal gradients, and influences the type and extent of semi-natural habitats. At coastal altitudes, more fertile and wetter habitats, such as grasslands and wetlands, dominate the landscape (~75%) but, at higher altitudes, heathland, forests and unvegetated land which are less suitable for breeding waders comprise ~60% of the area within the buffers (Fig. S2). Thus the dominant habitats above 50 m a.s.l. are generally dryer and less fertile, which is likely to make cultivated land relatively more beneficial as a wader foraging habitat than at lower altitudes, where more fertile habitats are abundant (O´Connell et al., 1996).

4.3 Conservation implications

Changes in Icelandic landscapes are to be expected in the coming years as most farmers intend to increase their area of cultivated land (Jóhannesdóttir et al., 2017b). This expansion will inevitably impact the internationally important breeding wader populations of Iceland, but the level of such impact will also depend on where the expansion will occur. The results presented here highlight that increases in the area of cultivated land at lower altitudes is more likely to negatively impact wader density than at higher altitudes in these regions, and that the important next steps will be to identify the landscape structures and scales of management that can continue to support high densities of breeding waders.

This information should be considered in land management, as it highlights that the implications of land use changes for biodiversity can be highly context-dependent. Given the international importance of the breeding wader populations that occur in Iceland, there is an urgent need to develop national land management policies to prevent the unintended loss of these species, which landowners value and wish to preserve (Jóhannesdóttir et al., 2017b). It also highlights the key importance of maintaining the complex and heterogeneous landscapes of lowland Iceland, and collaboration with stakeholders will be crucial in identifying management strategies that allow these landscapes and their breeding species to persist. Other potential threats to Icelandic wader populations have been identified, for example afforestation of lowland areas (Pritchard and Galbraith, 2016) and spread of invasive species (Davíðsdóttir et al., 2016). However, more information about the nature and spatial extent of threats is needed before robust assumptions can be made about cumulative impacts or interaction of threats. Results presented here demonstrate how waders are affected by landscape and habitats on scales which are well beyond their territory and emphasis the need to address conservation at different spatial scales. This applies to different types of land use, but agriculture is especially important and its impact is likely to be context dependant (Douglas et al., 2014; Buchanan et al., 2017; Franks et al., 2017).

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Table 1 - Results of a generalized linear mixed model (GLMM) of the variation in the total number of individuals of the six most common wader species (Golden Plover, Dunlin, Snipe, Whimbrel, Black-tailed Godwit and Redshank) on 200 survey locations, in relation to amount of cultivated land and wetland (within the surrounding 1000 m), and the altitude of the survey location. Transect area was included as an offset and species as a random effect. Significant factors are shown in bold.

Fixed effect	Est.	z	p
Intercept	-10.98	-47.12	**<0.001**
Cultivated land	6.32e-2	2.66	**0.008**
Wetland	1.14e-1	4.93	**<0.001**
Altitude	-1.17e-1	-4.79	**<0.001**
Cultivated * Altitude	2.14e-1	8.73	**<0.001**
Wetland * Altitude	-4.92e-4	-0.02	0.988

Table 2 – Results of generalized linear models (GLMs) on the variation in numbers of the six most common wader species in relation to amount of cultivated land and wetland (within the surrounding 1000 m) and the altitude of the survey transects. Transect area was included as an offset. Significant factors are shown in bold.

Fixed effect	**Golden Plover**			**Dunlin**			**Whimbrel**		
	Est.	z	p	Est.	z	p	Est.	z	p
Intercept	-10.54	-54.42	**<0.001**	-10.25	-52.13	**<0.001**	-9.34	-62.18	**<0.001**
Cultivated land	-1.07e-6	-3.92	**<0.001**	-1.13e-6	-4.28	**<0.001**	-.1.13e-6	-5.69	**<0.001**
Wetland	-5.02e-7	-1.23	0.217	1.33e-6	4.44	**<0.001**	-1.31e-6	-4.22	**<0.001**
Altitude	2.51e-4	0.14	0.893	-1.51e-2	-5.69	**<0.001**	-1.9e-2	-9.30	**<0.001**
Cultivated * Altitude	1.14e-8	3.88	**<0.001**	1.97e-8	5.45	**<0.001**	2.25e-8	8.57	**<0.001**
Wetland * Altitude	1.59e-9	0.33	0.742	-6.35e-9	-1.84	0.066	1.85e-8	5.30	**<0.001**

Fixed effect	**Black-tailed Godwit**			**Redshank**			**Snipe**		
	Est.	z	p	Est.	z	p	Est.	z	p
Intercept	-11.77	-42.77	**<0.001**	-10.92	-34.551	**<0.001**	-10.61	-60.03	**<0.001**
Cultivated land	2.71e-7	0.93	0.353	-4.9e-7	-1.231	0.218	-2.06e-7	-0.96	0.338
Wetland	1.19e-6	2.53	**0.012**	-1.67e-6	-2.229	**0.026**	9.81e-7	3.17	**0.002**
Altitude	-2.35e-3	-0.77	0.441	-1.67e-2	-3.78	**<0.001**	-2.43e-3	-1.27	0.206
Cultivated * Altitude	2.95e-9	0.73	0.468	1.02e-8	1.61	0.107	4.89e-9	1.70	0.089
Wetland * Altitude	-5.41e-9	-1.05	0.293	1.5-e8	1.659	0.097	-8.07e-9	-2.31	**0.021**

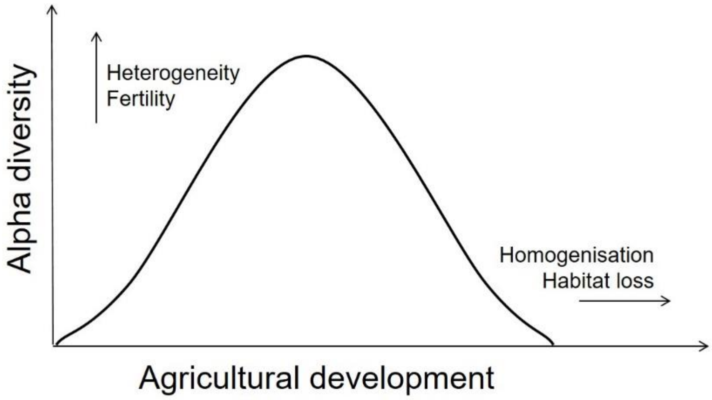

Figure 1 –The potential relationship between agricultural development and alpha diversity. Initially, agricultural development may increase habitat and resource heterogeneity in the landscape and soil fertility may increase in some conditions, with potentially positive effects on alpha diversity. However, as agricultural intensity and extent increase, homogenisation and habitat loss can drive declines in alpha diversity.

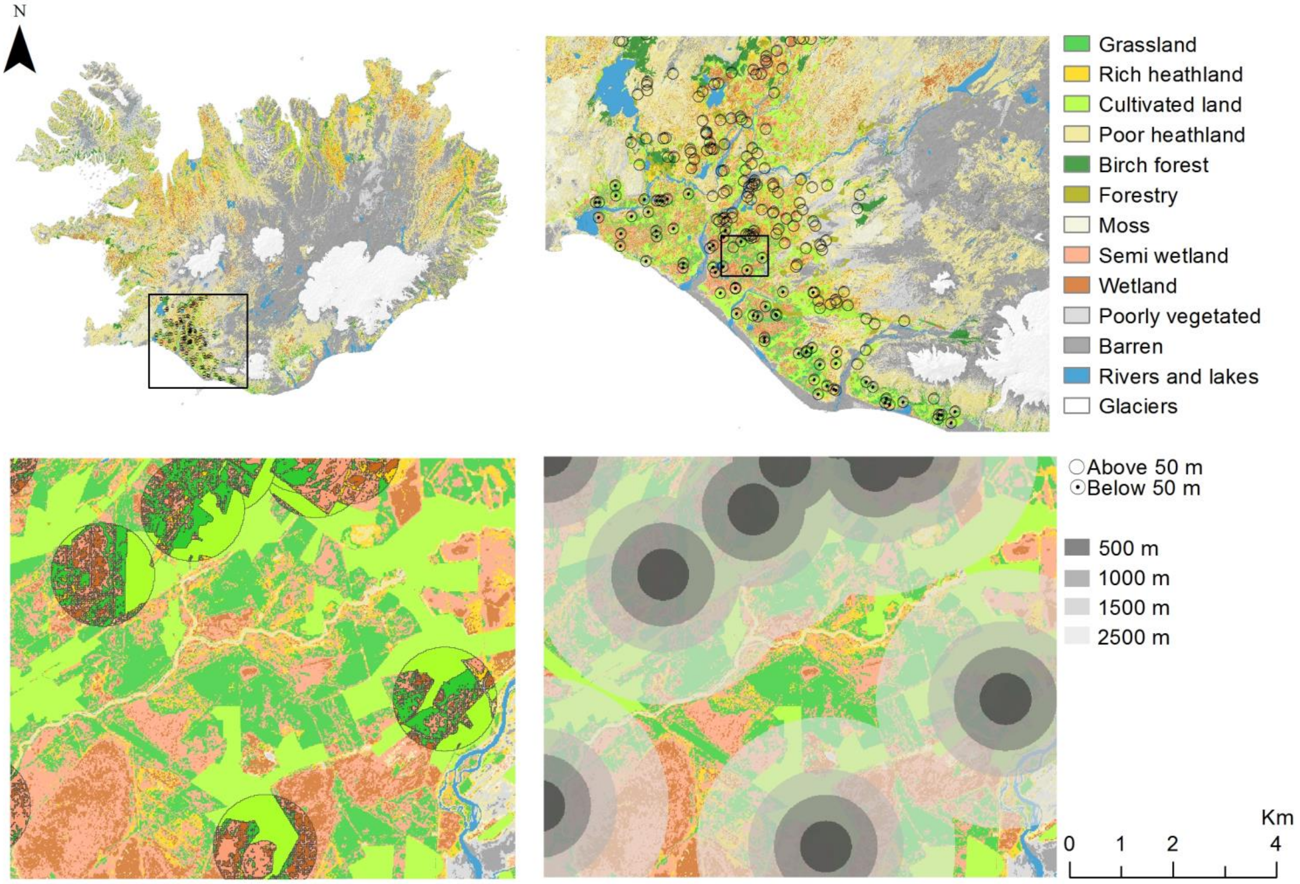

Figure 2 - The location of the 200 bird survey transects (top left), and their distribution above and below 50 m a.s.l (top right). The two lower images display the area within the rectangle in the top right panel, and portray the fine-scale mosaic of habitats in the southern lowlands (lower left, circles are 1000 m buffers around survey locations) and the four different buffers (500, 1000, 1500 and 2500 m radius) within which areas of agriculture and wetland were calculated (lower right).

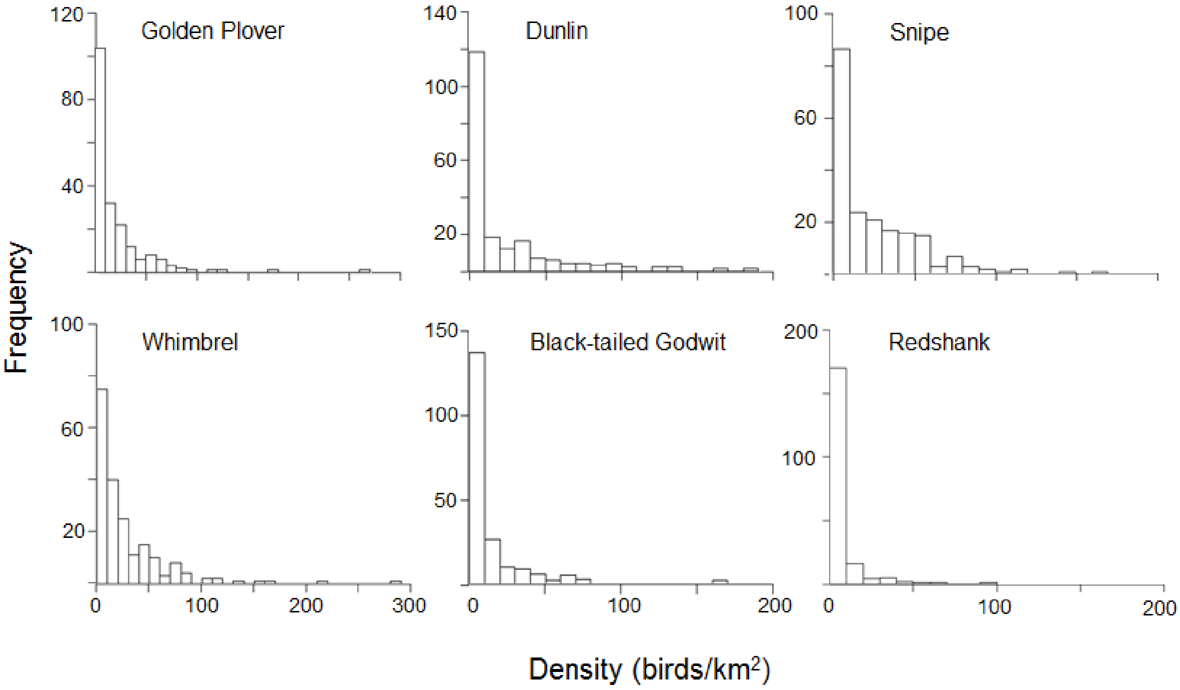

Figure 3 - Frequency distributions of the density of the six most common wader species in the lowlands of South-Iceland on the 200 transects (note variable y axis).

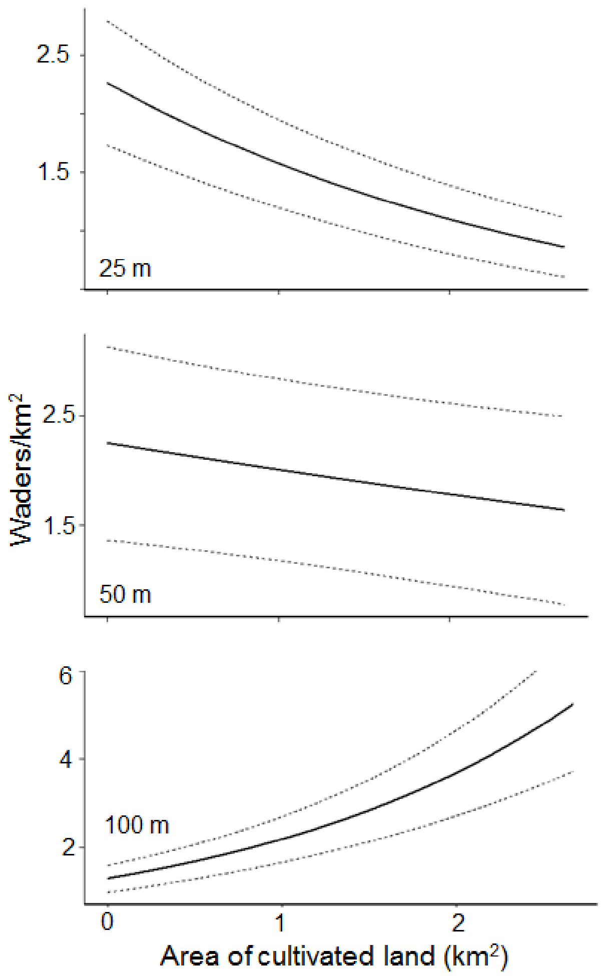

Figure 4 - Predicted wader densities (from the GLMM in Table 1) in relation to the area of cultivated land within the surrounding 1000 m radius buffer (size 3.13 km^2) at three different altitudes (dotted lines = SE).

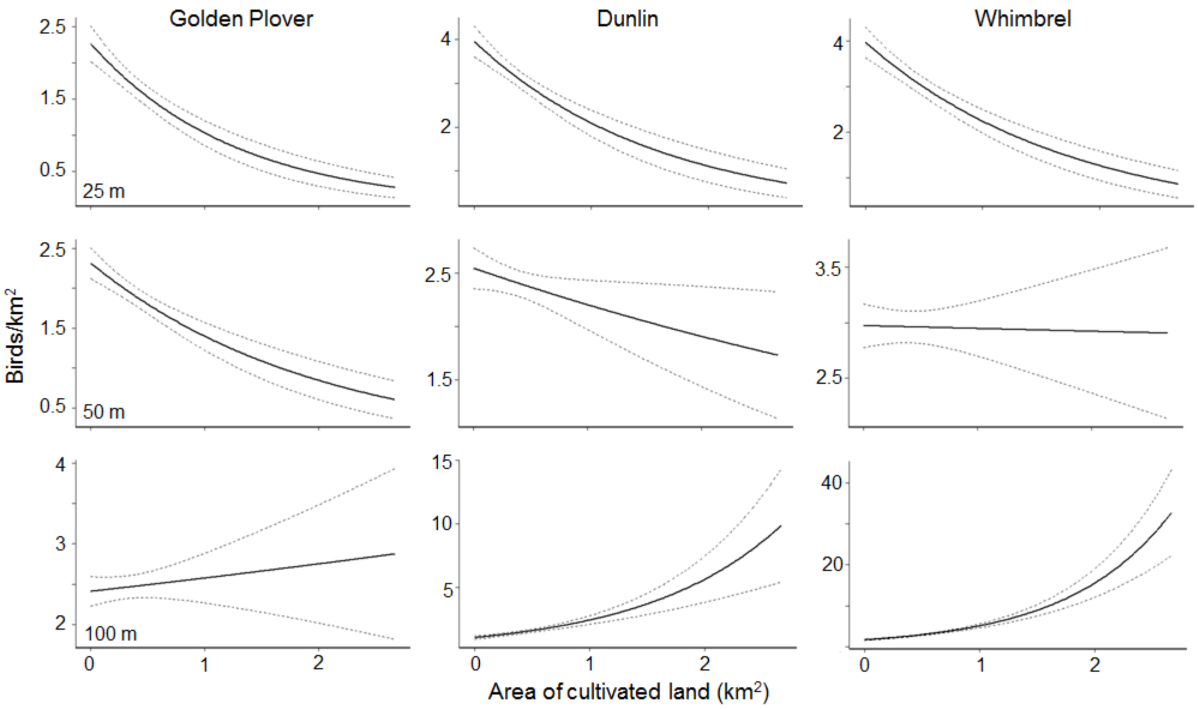

Figure 5 – Predicted wader densities (from the GLMs in Table 2) for three species with significant effects of the interaction cultivated land area and altitude within the surrounding 1000 m at three different altitudes (dotted lines = SE).

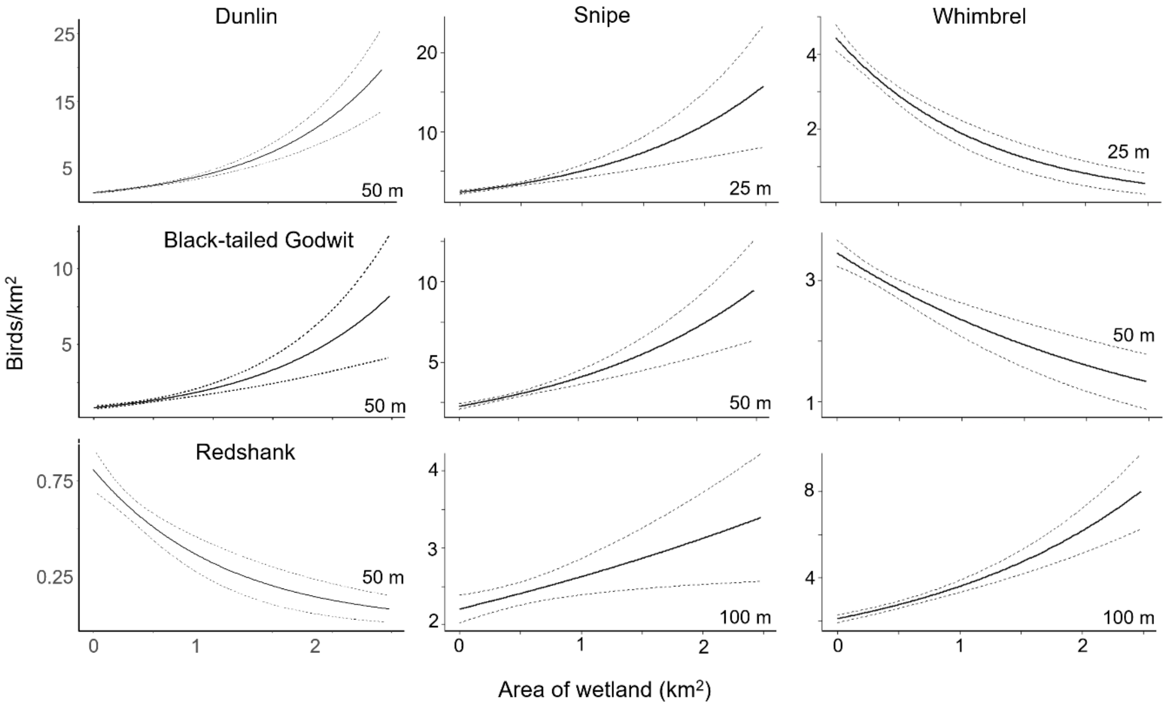

Figure 6 – Predicted wader densities (from the GLMs in Table 2) for the three species (Dunlin, Black-tailed Godwit and Redshank) which density varied with the amount of wetland in the surrounding 1000 m and the two species (Snipe and Whimbrel) for which effects on density of wetland area within the surrounding 1000 m vary significantly with altitude (dotted lines = SE).