# Interacting effects of agriculture and landscape on breeding wader populations

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**Abstract**

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20  The capacity of different landscapes to sustain viable populations depends on the spatial and

21  temporal availability of key population-specific resources. Heterogeneous landscapes

22  provide a wider range of resources and often sustain higher levels of biodiversity than

23  homogeneous ones. Across the globe, agricultural expansion has resulted in large-scale

24  homogenisation of landscapes with associated declines in many taxa. However, during the

25  early stages of agricultural development, in terms of area and intensity, increased landscape

26  heterogeneity and changes in local productivity through fertilizer inputs can potentially

27  increase resource availability for some species. Agriculture in Iceland is currently neither

28  highly intensive nor extensive, and primarily occurs as hayfields (> 90% of agricultural land)

29  embedded within a mosaic of semi-natural wetlands and heaths. These landscapes support

30  internationally important breeding populations of several wader species but the role of

31  agricultural land in promoting or constraining breeding wader densities is currently

32  unknown. Understanding the relationship between cultivation and wader populations is

33  important as the area of cultivated land is predicted to expand in Iceland in near future,

34  largely through conversion of the remaining semi-natural wetlands. Here we (a) quantify

35  relationships between breeding wader densities in lowland Iceland and the amount of

36  cultivated land and wetland in the surrounding landscape using density estimates from 200

37  transects in common semi-natural habitats, (b) assess the extent to which cultivated land

38  affects wader densities in these landscapes, and the potential effects of future agricultural

39  expansion at the expense of wetlands on wader populations. Wader densities in semi-

40  natural habitats were consistently greater when surrounding landscapes had more wetland

41  at scales ranging from 500 m to 2500 m, indicating the importance of wetland availability.

42  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).

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67    The relationship between agricultural intensification and biodiversity supported within a

68    landscape can follow a unimodal trajectory, with the onset of agricultural development

69    initially increasing heterogeneity and fertiliser inputs increasing local productivity, but

70    ongoing increases in agricultural intensification eventually resulting in landscape

71    homogenisation with associated reductions in resource availability and biodiversity (Fig. 1)

72    (Flowerdew, 1997; Sotherton and Self, 1999; Donald et al., 2001). The processes and

73    mechanisms that drive the relationship between agriculture and biodiversity will vary

74    between farming systems but a key factor is typically the change in habitat heterogeneity

75    (Benton et al., 2003). The effect of increases in agricultural area on landscape heterogeneity

76    can be mediated by the underlying habitat structure and fertility. For example, in

77    nutritionally impoverished areas, the input of synthetic fertilisers to cultivated fields may

78    boost local productivity and thus be beneficial for some species (Gunnarsson et al., 2015;

79    Jóhannesdóttir et al., 2017a). Information on the relative impacts of agriculture in different

80    landscapes is therefore key to understand and ultimately predict the consequences of

81    further agricultural expansion and intensification for the maintenance of biodiversity in such

82    landscapes.

83    There is great variation in the extent to which agriculture has developed across regions and

84    countries, and in the impact of this development on the environment (Alexandratos and

85    Bruinsma, 2012). In areas suitable for cultivation, agriculture is often very intense and many

86    taxa have declined in abundance (Robinson and Sutherland, 2002; Benton et al., 2003; Pe'er

87    et al., 2014). However, in more marginal areas for production and in less developed

88    countries, agriculture is often less intensive and widespread, and has less impact on the

89    environment and can even benefit biodiversity (Loos et al., 2014; Sutcliffe et al., 2015). In

90    Iceland, agricultural development started late and only grew beyond domestic subsistence at

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91   the beginning of the 20th Century (Júlíusson and Ísberg, 2005). Icelandic agriculture is

92   restricted by the northern location of the country, just south of the Arctic Circle, and

93   agriculture does not dominate the landscape, as only 7% of the area below 200 m a.s.l. (the

94   area which is suitable for agriculture) is currently used for cultivation (National Land Survey

95   of Iceland, 2013; Snorrason et al., 2015). However, it has been estimated that up to 63% of

96   this land could be used for cultivation (FAI, 2010). Icelandic lowlands currently comprise a

97   fine-scale mosaic of open semi-natural habitats and cultivated fields (primarily for silage

98   production), making the landscape highly heterogeneous (Jóhannesdóttir et al., 2017a). For

99   example, Iceland has over one million wetland patches smaller than one hectare, which

100  together comprise 30% of the 9000 km$^2$ of inland wetlands (50% are >5 ha), and inland

101  wetlands cover about 20% of all vegetated surfaces of Iceland (Arnalds et al., 2016). These

102  wetlands are of high value for biodiversity and they support several internationally

103  important breeding bird populations (Einarsson et al., 2002; Gunnarsson et al., 2006;

104  Jóhannesdóttir et al., 2014). Icelandic landscapes are particularly important for several

105  wader species, such as Snipe (*Gallinago gallinago*), Black-tailed Godwit (*Limosa limosa*),

106  Dunlin (*Calidris alpina*), Redshank (*Tringa totanus*), Whimbrel (*Numenius phaeopus*) and

107  Golden Plover (*Pluvialis apricaria*), for which global populations are generally declining

108  (International Wader Study  Group, 2003; Piersma et al., 2016; Pearce-Higgins et al., 2017),

109  and for which Iceland supports an estimated 3 - 34% (3, 7, 10, 12, 27 and 34%, respectively)

110  of global populations (Delany and Scott, 2004; Thorup, 2004).

111  However, wetlands in Iceland have undergone extensive drainage in recent decades, and an

112  estimated 47% of inland wetlands have now been affected by drainage (Arnalds et al., 2016).

113  This drainage was primarily undertaken to create potentially suitable agriculture land, both

114  for cultivation and grazing, and many drainage ditches are currently not associated with

115    cultivated land. Today approximately half the cultivated land in Iceland is on drained

116    wetland soils (Snorrason et al., 2015). Furthermore, a recent study showed 63% of farmers

117    intend to increase their area of cultivated land in the coming years in Iceland (Jóhannesdóttir

118    et al., 2017b). This expansion is likely to increase drainage of wetlands, with potentially

119    serious impacts on the breeding bird populations as a consequence of the resulting habitat

120    loss and reductions in landscape heterogeneity.

121    Frequent volcanic events and aeolian redistribution of dust from desert surfaces in Iceland

122    result in intense deposition of basaltic volcanic materials. The amount is geographically

123    variable depending on distance from the Mid-Atlantic ridge (where most volcanic activity

124    and main dust release areas occur), which runs from south-west to north-east Iceland

125    (Arnalds, 2015). This deposition strongly influences soil fertility (due to the resulting higher

126    pH and favourable nutrient availability). This gradient of aeolian deposition has been shown

127    to influence the distribution of breeding birds, with densities in wetland areas, in particular,

128    being greater in areas of higher aeolian deposition (Gunnarsson et al., 2015). This gradient

129    and the abundant remaining semi-natural land and high densities of breeding waders

130    (Jóhannesdóttir et al., 2014) offer a rare opportunity to quantify the influence of cultivated

131    land on bird distribution and abundance in semi-natural habitats, and how these vary in

132    areas of differing underlying productivity. Expansion of agriculture inevitably means loss of

133    other habitats and, in Iceland, wetlands have historically been the most common habitat

134    converted for production. In this study, we make use of existing variation in extent of

135    agriculture in lowland Iceland, and of the underlying productivity gradient, to examine how

136    densities of internationally important breeding wader populations on semi-natural habitats

137    vary in relation to the amount of agriculture and wetland in the surrounding landscape, and

138    how this varies across an altitudinal gradient that reflects variation in underlying productivity

139    as a consequence of historical aeolian dust deposition.

## 2. Methods

141    This study was undertaken in South-Iceland, an island in the North-Atlantic Ocean located

142    between 63° and 66° North on the mid Atlantic ridge. Agriculture in Iceland, which is mostly

143    based on livestock rearing and fodder production for their winter food (silage), is still of

144    relatively low intensity and large patches of semi-natural habitats (e.g. wetlands, bogs,

145    heathland and river-plains) are present in most agricultural areas (Fig. 2).

### 2.1 Survey locations and bird censuses

147    Single surveys of breeding birds were carried out at 200 transects in the lowlands of South

148    Iceland, in areas below 200 m a.s.l. (Fig. 2). The area is one of the most important

149    agricultural regions in Iceland, providing 36% of annual agricultural GDP in the year 2010

150    (FAI, 2010) and about 10% of land below 400 m a.s.l. in the area is cultivated land (Wald,

151    2012). Icelandic agriculture is almost entirely livestock-based (pastoral), and primarily

152    comprises hayfields that are used for grazing and fodder production (silage for winter feed)

153    for livestock farmed for meat and dairy production. Arable production is small-scale and

154    mostly comprises barley grown for fodder on the farm where it is grown, although most

155    grain fodder is imported (Helgadóttir et al., 2013). The concentration of cultivated land

156    around individual farms throughout lowland Iceland means that agricultural habitats are

157    very evenly spread throughout the region (Jóhannesdóttir et al., 2017a).

158    Land cover data for this study were extracted from the Icelandic Farmland Database, which

159    uses satellite images with extensive ground truth verification to classify the surface of

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160 Iceland into 12 different classes (Arnalds and Barkarson, 2003; Gísladóttir et al., 2014). The

161 classification represents variables that reflect productivity; mostly vegetation cover, soil and

162 drainage and is well suited for landscape analyses of biodiversity (Jóhannesdóttir et al.,

163 2014). Survey sites within the five most common vegetated habitats (40 each of wetland

164 (saturated), semi-wetland (damp), grassland, rich heathland, poor heathland, Fig. 2) were

165 selected by a stratified random method, employing ArcGis 10.1 GIS software. The selected

166 sites had to cover at least 20 ha of a single habitat type and to be at least 0.5 km apart, and

167 the altitudinal variation within transects was very small (< 20 m, Fig. S1). In addition, for

168 practical reasons of access, survey sites were selected so that they were not more than 2 km

169 from roads and tracks (Jóhannesdóttir et al., 2014). Previous studies have shown that the

170 distribution of habitat types in lowland Iceland varies little with respect to distance from

171 roads and tracks (Gunnarsson et al., 2006).

172 Breeding bird surveys were conducted in 2011 and 2012, from the middle of May until the

173 end of June, a period which encompasses incubation and early parts of chick rearing for the

174 species involved. The date on which each site was visited was random to avoid any

175 systematic bias in the counts (e.g. adults being more obvious when chicks have hatched).

176 Only adult birds were counted. Counts were performed during periods of greatest bird

177 activity, in the morning from 06:00 to 13:00 and in the afternoon from 17:00 to 22:00

178 (Davíðsdóttir, 2010). Surveys were only conducted during suitable weather conditions (wind

179 speed lower than 6 m/s and in dry weather) to avoid conditions of low bird detectability

180 (Bibby et al., 2000). At each survey site, birds were counted along a line transect, and every

181 bird within 100 m on each side of the observer was recorded (Bibby et al., 2000). The

182 placement and direction of transect line was designed to minimise any influence of adjacent

183 habitats, i.e. in the middle of the habitat patch and in the direction that had the widest

184    habitat coverage. The length of transects was often restricted by the habitat patch size.

185    Average length of the transects was 511 m (sd = 69.4 m, range 216-685 m), and their total

186    length was 101 km (Jóhannesdóttir et al., 2014).

187    The amount of agriculture and wetland habitat in the landscape surrounding each survey

188    transect was calculated for four different sized buffers (500, 1000, 1500 and 2500 m radius –

189    buffer sizes were selected arbitrarily as the size of area used by the species has not been

190    clearly identified) centred on each transect, and habitat data were extracted from the

191    Icelandic Farmland database.

192    **2.2 Data analysis**

193    Models were constructed at two levels: first, a multispecies model was used to explore

194    landscape drivers of the overall abundance of all wader species combined; second, individual

195    models were used to explore species-specific responses to landscape variables. For the

196    multispecies model we used a generalized linear mixed model (GLMM) with a Poisson error

197    distribution and a log-link function to analyse the variation in the total number of waders on

198    each transect, with transect area (natural log-scale) as an offset. Separate models were run

199    for each buffer, with the amount of cultivated land and wetland within the buffer, altitude of

200    transect and interactions between altitude and area of cultivated land, and altitude and

201    wetland area as fixed factors, including species as a random factor to control for differences

202    in community composition at each site. All waders which commonly occurred both at higher

203    and lower elevations were included in the analysis. The least common species included was

204    Redshank which occurred 112 times. For the single-species models, which were constructed

205    for the six most common wader species (Golden Plover, Dunlin, Snipe, Whimbrel, Black-

206    tailed Godwit and Redshank), generalized linear models (GLMs) with a Poisson error

207 distribution and log-link function were constructed with the same fixed effects and with

208 transect area (natural log-scale) as an offset, but with no random effects. Altitude was

209 included in the models as a surrogate of landscape composition which is related to fertility

210 and changes gradually from the coast to inland. Areas closer to the coast are flatter, have

211 more grassland, cultivated land and semi-wetlands (which tend to be drained wetlands)

212 whereas inland areas have more heathland and less vegetated land (Fig. S2; Jóhannesdóttir

213 et al., 2014; Gunnarsson et al., 2015; Arnalds et al., 2016). For data presentation, altitude

214 was split into above and below 50 m a.s.l. (Fig. 2) as there is a compositional change in the

215 landscape at approximately that altitude where it changes from flat coastal plains to higher

216 altitude inlands. Density predictions are only presented for species which showed significant

217 relationships, and density is predicted across the range of altitudes (25, 50 and 100 m). For

218 simplicity models are only presented for the 1000 m buffer, as models from different buffer

219 sizes all showed similar patterns (see Table S1 for results for all buffers). We tested for

220 spatial autocorrelation in the model residuals using Moran's I correlograms. Transects lying

221 within a lag distance were defined as neighbours using a binary weighing matrix for each

222 distance class using the ncf package (Bjornstad, 2016). Significant Moran's I ($p<0.05$) at

223 shorter pair-wise distance intervals up to 160 Distance units was taken as an indication of

224 important spatial autocorrelation in nearby transects and as an indication of violating the

225 independence of data points in our GLM models. All statistical analyses were performed in R

226 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

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275    found breeding in wetter habitats (Jóhannesdóttir et al., 2014). Expansion of agriculture into

276    areas of semi-natural habitat is ongoing in Iceland (Jóhannesdóttir et al., 2017b) and, at

277    higher altitudes, such increases may provide areas of relatively high productivity (as a result

278    of fertiliser applications and nutrient release by wetland drainage) and may increase

279    foraging opportunities for adults feeding off territory (as a result of ploughing and associated

280    increases in availability of soil invertebrates), which may allow greater breeding densities of

281    Golden Plover, Dunlin and Whimbrel to be supported. Such use of cultivated fields as

282    foraging habitats by breeding waders in upland landscapes has been reported elsewhere

283    (Pearce-Higgins and Yalden, 2003).

284    While cultivated habitats at higher altitudes may provide additional resources for the

285    breeding waders in these areas, such relationships are likely to have tipping points (e.g.

286    Fig.1). If, as intended by farmers (Jóhannesdóttir et al., 2017b), agricultural expansion

287    continues at the expense of natural wetlands, then these internationally important breeding

288    populations will likely decline, in both coastal and upland areas.

289    **4.2 Differences in underlying productivity and habitat composition**

290    The altitudinal variation in the influence of amount of cultivated land on breeding wader

291    densities is likely to reflect altitudinal variation in the underlying productivity of the land. We

292    have previously shown (Jóhannesdóttir et al., 2017a) that the relative importance of

293    cultivated land for breeding waders in lowland Iceland varies regionally, with larger numbers

294    of waders using cultivated land in the West than in the North and the South of the country.

295    This difference was linked to an underlying gradient of soil fertility which varies across

296    Iceland, due to volcanic activity being mostly restricted to the divergent tectonic plate

297    boundary that crosses Iceland on a SW-NE axis along the North-Atlantic ridge (Arnalds, 2015;

298 Gunnarsson et al., 2015). As a consequence, areas in the South and North receive larger

299 quantities of volcanic dust than areas in the west (Arnalds, 2015).

300 This variation in soil fertility also occurs along altitudinal gradients, and influences the type

301 and extent of semi-natural habitats. At coastal altitudes, more fertile and wetter habitats,

302 such as grasslands and wetlands, dominate the landscape (~75%) but, at higher altitudes,

303 heathland, forests and unvegetated land which are less suitable for breeding waders

304 comprise ~60% of the area within the buffers (Fig. S2). Thus the dominant habitats above 50

305 m a.s.l. are generally dryer and less fertile, which is likely to make cultivated land relatively

306 more beneficial as a wader foraging habitat than at lower altitudes, where more fertile

307 habitats are abundant (O´Connell et al., 1996).

308 **4.3 Conservation implications**

309 Changes in Icelandic landscapes are to be expected in the coming years as most farmers

310 intend to increase their area of cultivated land (Jóhannesdóttir et al., 2017b). This expansion

311 will inevitably impact the internationally important breeding wader populations of Iceland,

312 but the level of such impact will also depend on where the expansion will occur. The results

313 presented here highlight that increases in the area of cultivated land at lower altitudes is

314 more likely to negatively impact wader density than at higher altitudes in these regions, and

315 that the important next steps will be to identify the landscape structures and scales of

316 management that can continue to support high densities of breeding waders.

317 This information should be considered in land management, as it highlights that the

318 implications of land use changes for biodiversity can be highly context-dependent. Given the

319 international importance of the breeding wader populations that occur in Iceland, there is an

320 urgent need to develop national land management policies to prevent the unintended loss

321 of these species, which landowners value and wish to preserve (Jóhannesdóttir et al.,

322 2017b). It also highlights the key importance of maintaining the complex and heterogeneous

323 landscapes of lowland Iceland, and collaboration with stakeholders will be crucial in

324 identifying management strategies that allow these landscapes and their breeding species to

325 persist. Other potential threats to Icelandic wader populations have been identified, for

326 example afforestation of lowland areas (Pritchard and Galbraith, 2016) and spread of

327 invasive species (Davíðsdóttir et al., 2016). However, more information about the nature and

328 spatial extent of threats is needed before robust assumptions can be made about cumulative

329 impacts or interaction of threats. Results presented here demonstrate how waders are

330 affected by landscape and habitats on scales which are well beyond their territory and

331 emphasis the need to address conservation at different spatial scales. This applies to

332 different types of land use, but agriculture is especially important and its impact is likely to

333 be context dependant (Douglas et al., 2014; Buchanan et al., 2017; Franks et al., 2017).

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462

463 **Table 1 - Results of a generalized linear mixed model (GLMM) of the variation in the total number of individuals of the six**
464 **most common wader species (Golden Plover, Dunlin, Snipe, Whimbrel, Black-tailed Godwit and Redshank) on 200 survey**
465 **locations, in relation to amount of cultivated land and wetland (within the surrounding 1000 m), and the altitude of the**
466 **survey location. Transect area was included as an offset and species as a random effect. Significant factors are shown in**
467 **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 |

468

469 **Table 2 – Results of generalized linear models (GLMs) on the variation in numbers of the six most common wader species**
470 **in relation to amount of cultivated land and wetland (within the surrounding 1000 m) and the altitude of the survey**
471 **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** |

472

473
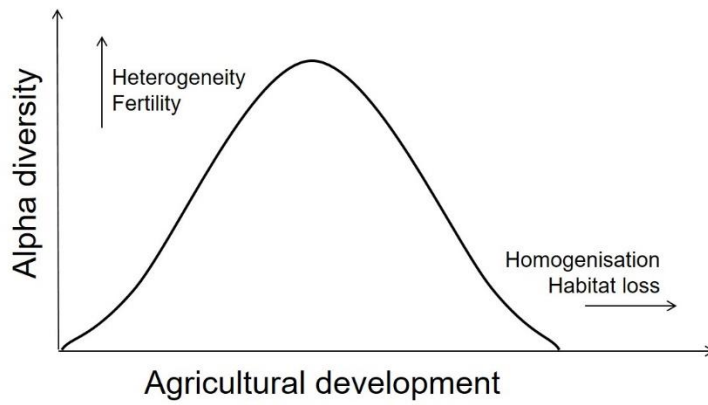
**Figure 1 –The potential relationship between agricultural development and alpha diversity. Initially, agricultural development may increase habitat and resource heterogeneity in the landscape and soil fertility may increase in some conditions, with potentially positive effects on alpha diversity. However, as agricultural intensity and extent increase, homogenisation and habitat loss can drive declines in alpha diversity.**

478
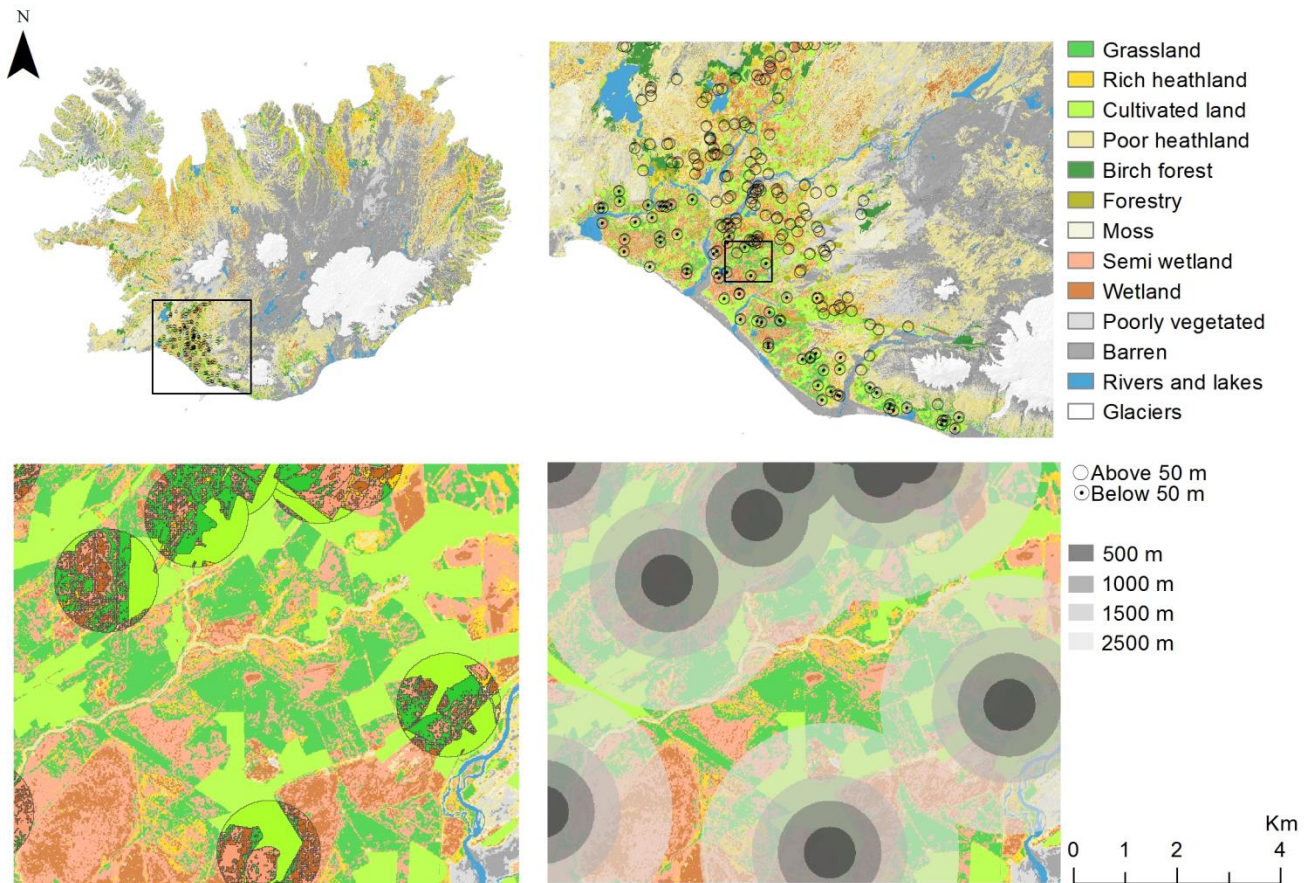
**Figure 2 - The location of the 200 bird survey transects (top left), and their distribution above and below 50 m a.s.l (top right). The two lower images display the area within the rectangle in the top right panel, and portray the fine-scale mosaic of habitats in the southern lowlands (lower left, 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).**
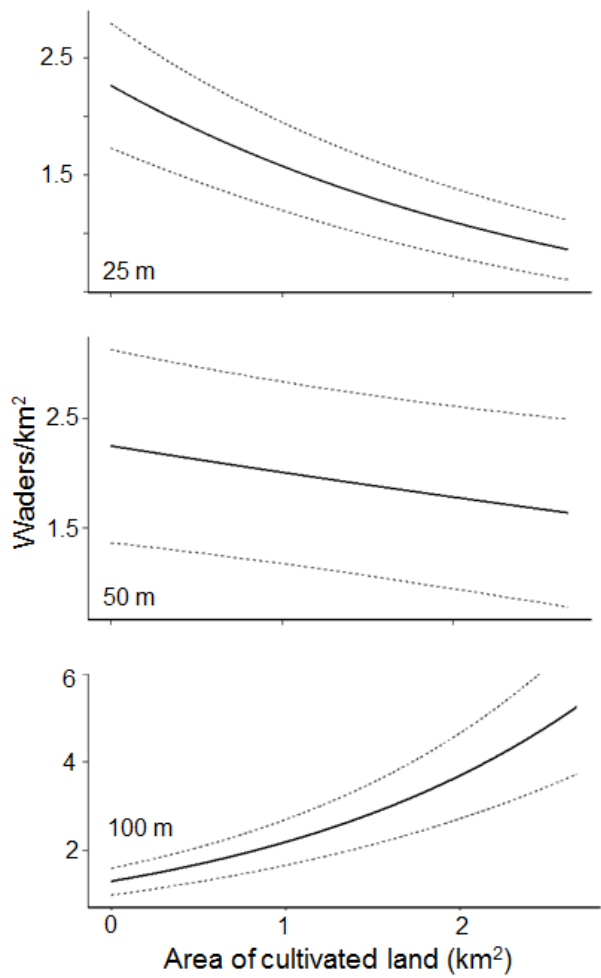
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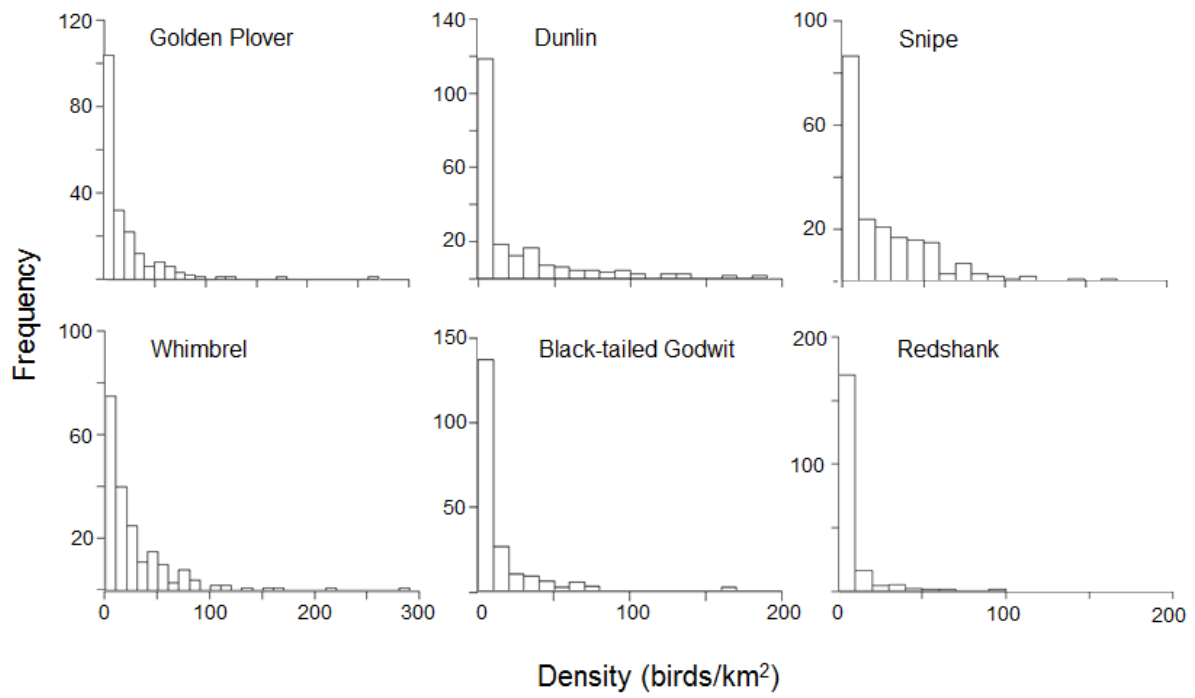
Figure 3 - Frequency distributions of the density of the six most common wader species in the lowlands of South-Iceland on the 200 transects (note variable y axis).
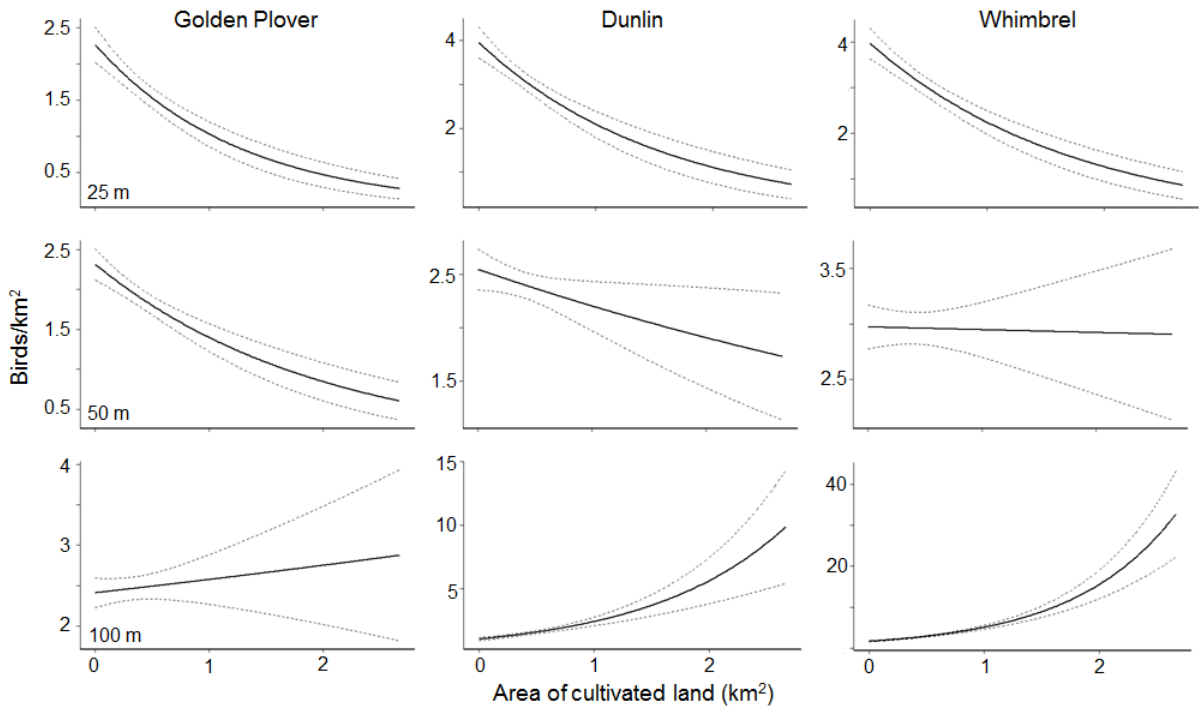
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**Figure 4 - Predicted wader densities (from the GLMM in Table 1) in relation to the area of cultivated land within the surrounding 1000 m radius buffer (size 3.13 km²) at three different altitudes (dotted lines = SE).**
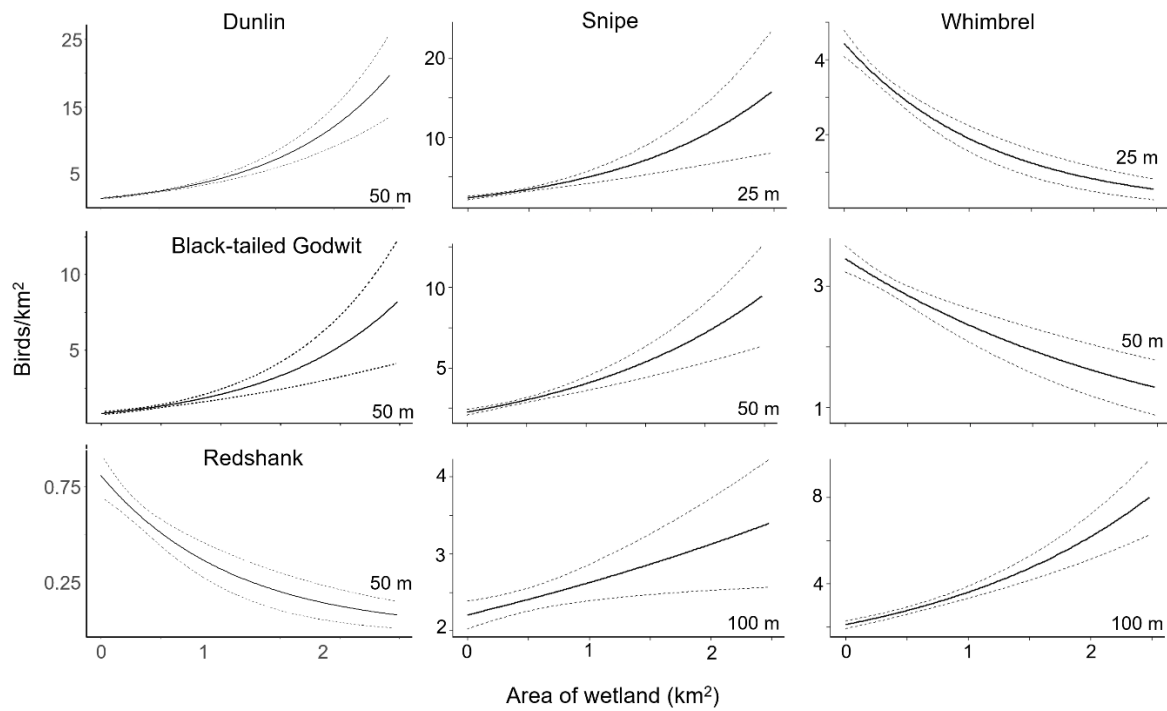
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497 **Figure 5 – Predicted wader densities (from the GLMs in Table 2) for three species with significant effects of the**
498 **interaction cultivated land area and altitude within the surrounding 1000 m at three different altitudes (dotted lines =**
499 **SE).**

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502

**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).**