Subarctic afforestation: effects of forest plantations on ground-nesting birds in lowland Iceland

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Abstract

1. Planting forests is a commonly suggested measure to mitigate climate change. The resulting changes in habitat structure can greatly influence the diversity and abundance of pre-existing wildlife. Understanding these consequences is key for avoiding unintended impacts of afforestation on habitats and populations of conservation concern.
2. Afforestation in lowland Iceland has been gaining momentum in recent years and further increases are planned. Iceland supports internationally important breeding populations of several ground-nesting, migratory bird species that mostly breed in open habitats. If afforestation impacts the distribution and abundance of these species, the consequences may be apparent throughout their non-breeding ranges across Europe and Africa.
3. To quantify the effects of plantation forests on the abundance and distribution of ground-nesting birds (in particular waders, *Charadriiformes*), surveys were conducted on 161 transects (surrounding 118 plantations) perpendicular to forest edges throughout Iceland. The resulting variation in density with distance from plantation was used to estimate the likely changes in bird

numbers resulting from future afforestation plans, and to explore the potential effects of different planting configuration (size and number of forest patches) scenarios.

4. Of seven wader species, densities of five (golden plover (*Pluvialis apricaria*), whimbrel (*Numenius phaeopus*), oystercatcher (*Haematopus ostralegus*), dunlin (*Calidris alpina*) and black-tailed godwit (*Limosa limosa*)) in the 200 m surrounding plantations were just over half of those further away (up to 700 m). Redshank (*Tringa totanus*) **densities were lowest <150 m from the plantation edge while** snipe (*Gallinago gallinago*) densities were 50% higher close to plantations (0-50 m) than further away (51-700 m)**, and no consistent effects of plantation height, diameter, density or type were identified**. Plantations are typically small and widespread, and simulated scenarios indicated that total declines in bird abundance resulting from planting trees in one large block (1000 ha) could result in only ~11% of the declines predicted from planting multiple small blocks (1 ha) **in similar habitats**.
5. *Synthesis and application:* The severe impact that planting forests in open landscapes can have on populations of ground-nesting birds emphasises the need for strategic planning of tree-planting schemes. Given Iceland's statutory commitments to species protection and the huge contribution of Iceland to global migratory bird flyways, these are challenges that must be addressed quickly, before population-level impacts are observed across migratory ranges.

Keywords: Anthropogenic change, conservation, edge effects, forest plantations, waders

Introduction

Loss and degradation of habitats that support wildlife is one of the major drivers of global biodiversity decline (Dirzo *et al.* 2014). These changes often result from land conversion due to human activities, such as the development and expansion of housing, roads and agriculture; processes which reduce the overall amount of natural habitat and increase fragmentation of the landscape, creating smaller and more isolated habitat patches (Foley *et al.* 2005; Torres, Jaeger & Alonso 2016). During the initial stages of land conversion, habitat loss and fragmentation are often characterized by the introduction of novel structures such as roads, electric pylons, trees and wind turbines (Amar *et al.* 2011; Sutherland *et al.* 2012; Hovick *et al.* 2014; D'Amico *et al.* 2018). Structures can have direct effects **such as** increased collision risk and changes in foraging and breeding opportunities, and indirect effects **such as** changes in microclimatic conditions or altered predator-prey and host-parasite relationships on local populations, **processes which can subsequently** influence mortality, productivity and recruitment rates (Ewers & Didham 2006; Fischer & Lindenmayer 2007; Pearce-Higgins *et al.* 2009; Prugh *et al.* 2009; Hovick *et al.* 2014; Fernández-Bellon *et al.* 2018). The presence of novel structures may also affect the distribution of individuals in the surrounding landscape through changes in demographic factors **such as** altered rates of survival or recruitment, or through behavioural change **with** individuals changing their temporal and spatial activity patterns by avoiding or choosing to be close to structures) (Ditchkoff, Saalfeld & Gibson 2006; Dinkins *et al.* 2014; Jameson & Willis 2014; Wang *et al.* 2015; Łopucki, Klich & Gielarek 2017), potentially reducing local population sizes.

In recent decades, climatic amelioration at higher latitudes has facilitated rapid forestry development in areas where tree growth was previously limited by harsher environmental conditions (Halldórsson, Oddsdottir & Sigurdsson 2008). Afforestation at these latitudes can lead to loss and fragmentation of the open habitats that dominate the landscape, with potentially important impacts on pre-existing biodiversity (Brockerhoff *et al.* 2008; Halldórsson, Oddsdottir & Sigurdsson 2008). While afforestation may benefit species that use forest habitats, species that require open landscapes may decline, particularly if the landscape surrounding forests supports fewer individuals (Halldórsson, Oddsdottir & Sigurdsson 2008). Previous studies have reported lower densities of some open-nesting **(i.e. nesting in open, non-forested habitats)** bird species close to forest edges (Hancock, Grant & Wilson 2009; Stroud, Reed & Harding 2009; Wilson *et al.* 2014; Holmes, Koloski & Nol 2020). **Lower densities of open-nesting** birds could reflect demographic effects **such as** increased distances between locations needed for foraging, breeding and chick rearing increasing travel costs and associated risks; or increased predation rates because predator activity is concentrated around forests (Wilcove, McLellan & Dobson 1986; Berg, Lindberg & Källebrink 1992; Macdonald & Bolton 2008; Svobodová *et al.* 2010), or behavioural effects **such as** avoidance of areas in which visibility is impeded. Several studies have found ground-nesting waders to nest significantly further away than expected from man-made structures and trees, without clear fitness benefits (Wallander, Isaksson & Lenberg 2006; Bertholdt *et al.* 2017; Holmes, Koloski & Nol 2020).

In Iceland, which has been largely treeless for ~1000 years, afforestation could have widespread deleterious effects on the ecological communities of currently abundant open landscapes that support internationally important biodiversity. Icelandic forestry is still in its infancy and currently forests cover ~1.9% of the land area (~190,000 ha; (Eysteinsson 2017)). Downy birch (*Betula pubescens*) is the only tree species to naturally form continuous forests in Iceland (Eysteinsson 2017) and plantation forests typically contain non-native species such as sitka spruce (*Picea sitchensis*), larch (*Larix spp.*), lodgepole pine (*Pinus contorta*) and black cottonwood (*Populus trichocarpa*), along with the downy birch (Brynleifsdóttir 2018). In 2018, the Icelandic government provided additional funding to the Icelandic forest service to increase the number of trees planted, with a goal of enhancing carbon sequestration (Ministry for the Environment and Natural Resources 2018). As forestry primarily operates through government grants to **private** landowners to plant trees within their land (Halldórsson, Oddsdottir & Sigurdsson 2008), plantations typically occur as numerous small patches in otherwise open landscapes. These features make Iceland an ideal location in which to quantify the plantation effects on **densities**

of birds in the surrounding habitats, and identify afforestation strategies that might reduce these effects.

The ongoing expansion of plantation forestry in Iceland is mostly in the vegetated lowlands, which are also the most important habitats for most ground-nesting bird populations (Gunnarsson *et al.* 2006; Jóhannesdóttir *et al.* 2014; Skarphéðinsson *et al.* 2016). The most common ground-nesting species in Iceland are meadow pipit, (*Anthus pratensis)*, and several species of wader (Jóhannesdóttir *et al.* 2014). Several avian predators that commonly prey on bird nests also breed in lowland Iceland, including ravens (*Corvus corax*) (Þórisson 2013) which have begun nesting in trees in Iceland, although this is still relatively rare (K.H. Skarphéðinsson, personal communication, November 2, 2018). Iceland also has two mammalian nest predators: arctic fox (*Vulpes lagopus*) and American mink (*Neovison vison*), **which is a non-native species** (Sillero-Zubiri, Hoffmann & Macdonald 2004; Bonesi & Palazon 2007), in addition to domestic cats which are common and likely to be occasional nest predators (Bonnington, Gaston & Evans 2013). While little is currently known about how predators **in Iceland** use plantations, any perceived risks of predator presence and reduced visibility may influence **densities of** birds in the surrounding landscape (Vliet & Wassen 2008; Amar *et al.* 2011; Wilson *et al.* 2014). Here we use surveys of open-nesting birds in lowland Iceland to assess (a) whether densities are reduced in the landscape surrounding plantations; (b) whether these effects vary among plantations with differing characteristics; and (c) the potential impact of differing future afforestation plans for lowland Iceland.

Methods

Study sites

The study was conducted in south, west and north Iceland (Fig 1). Forests that were at least 30 m in diameter, surrounded by homogenous semi-natural habitat and >100 m from houses or agricultural land were selected from aerial photos and known locations. As all forests included in the study contained or were exclusively made up of non-native species, **they** are hereafter referred to as plantations. Afforestation primarily takes place within semi-natural habitats which were classified using the farmland database *Nytjaland* as: wetland, semi-wetland, rich heathland, poor heathland or grassland (Gísladóttir, Brink & Arnalds 2014) (Table S1).

Bird surveys

In total, 161 surveys of bird distribution and density were undertaken surrounding plantations between May and June 2017, spanning the majority of the nesting and chick-rearing period of ground-nesting species in Iceland (Gunnarsson *et al.* 2017; Alves *et al.* 2019). To ensure that detectability of target species was as consistent as possible counts were conducted between 8 am and 10 pm, to avoid peaks in bird activity early in the morning and reduced activity levels in the evening (Davíðsdóttir 2010), in wind speeds < 7 m/s and avoiding periods of heavy rainfall (Hoodless, Inglis & Baines 2006). To avoid systematic bias arising from possible "push effects" of corralling birds in front of the surveyor, surveys were conducted along transects that started either at the edge of the plantation with the observer moving away (79 transects), or started away from the plantation with the observer walking towards it (82 transects). Each transect was surveyed once but, when **sufficiently large blocks of homogenous habitat were available on both sides of a plantation** (43 out of 118 plantations), two **separate** transects in opposite directions were conducted from the same plantation, each on different sides of the plantation. Transects were conducted within a single habitat type, and transect length ranged between 300 and 700 m (mean length = 581 ± 133 SD) depending on the homogeneity of the landscape **and the presence of obstructions such as lakes or rivers**, resulting in a total distance covered of 93 km. All transects were preceded by a 5-minute period in which the observer stood still to allow birds to settle, after which the transect was walked at a steady pace without stopping. All birds seen or heard within a 100 m range on either side of the transect were recorded **when first seen**, **and** their distance from the plantation **documented**. **If there was any doubt that this was the first time the bird was seen, the individual was not documented for a more conservative estimate. Subsequently, t**ransects were divided into 50 m **distance intervals** (1 ha in area) **from the forest edge**, and the number of birds recorded within each interval was calculated (Fig S1).

Plantation characteristics

For each plantation, a suite of characteristics was recorded (Table 1). As plantation **diameter** and area were strongly correlated (Pearson's r = 0.84, n = 76, p <0.001), only **diameter** was included in subsequent models (Table 1). Coniferous, broad-leaved and mixed plantations were comparable in **diameter**, height and density (Table S2) and sampling of all plantation characteristics occurred throughout the survey period and at various times during the day (Fig S2, S3).

Effects of plantation configuration on bird density

To explore the magnitude of effect of different future plantation configurations on waders in the Icelandic lowlands, segmented linear regression was used to identify the distance from the plantation edge at which the most extreme change in bird densities occurs. This 'breaking point' distance was then used to define an 'affected area' within which densities differed from the remaining 'unaffected area'. The mean densities in affected and unaffected areas were used to estimate the overall changes in abundance of these species resulting from scenarios of planting 1000 ha as one large up to 1000 small (1 ha) plantations. We calculated total bird change by combining the change in bird numbers in the forested area (assuming complete loss for open-nesting species (Halldórsson, Oddsdottir & Sigurdsson 2008)) and the affected area (altered density; Fig S5), as;

Equation 1:

Change in number of birds = No of patches (Change in numbers in forest area + Change in numbers in affected area)*

$$\Delta N = P^* (\Delta D_T + \Delta D_A)$$

$$\Delta N = P^* (T^*(D_T - D_U) + A^*(D_A - D_U))$$

where N = number of birds, P = number of plantation patches, T = plantation area, A = affected area, D_T = average bird density in plantation area **(assumed to be 0 for open-nesting species)**, D_A = average bird density in affected area, D_U = average bird density in unaffected area. All plantation patches were assumed to be circular (giving the most conservative estimate of affected surrounding area) and have an individual affected area with no overlap between patches. Confidence intervals for the change in numbers of birds were then calculated by bootstrapping the observed variation in bird density per area and repeating the equation 1000 times. **To assess how much of the Icelandic lowlands is currently within the affected area of forest plantations, the distance from plantation forests to 100,000 randomly located points was calculated using a GIS layer from the Icelandic forest service (Icelandic Forest Service 2021).**

Statistical analyses

In order to assess the change in density of birds with distance to plantation, we constructed a generalized linear mixed effect model (GLMM) with a Poisson distribution and a log-link function, with bird density as the response variable, accounting for zero inflation by using the R package glmmADMB (Fournier *et al.* 2012). A priori models were initially constructed to assess the effect of direction of transects (direction, interval and their interaction as explanatory variables) with transect **identity** nested in plantation identity included as a random factor to account for non-independence of intervals within the same transect and surrounding the same plantations. When direction showed a significant effect it was retained in subsequent models, in which the effects of interval, distance from plantation, habitat and plantation characteristics were explored for each individual species (Fig S4, Table 1). For plantation type, broadleaved, **which most closely resembles the native birch forest,** was used as the reference, and 2-5 m category as the reference height and grassland as reference habitat **which** were the most numerous categories (Table S6). Starting with a full model, sequential deletion of non-significant predictors (plantation factors and habitat removed in an order of increasing significance as determined by a priori test) (Table S5) was used to find minimum models by removing a single factor at a time, and comparing the resulting model to the previous more complex model with a chi-square test (backward stepwise regression). If removal of a given predictor resulted in a significant change in the model, it was retained in subsequent models (Harrison *et al.* 2018). In addition to backward stepwise regression, sequential adding of factors to the null model (forward stepwise regression), and subsequent comparison of the AIC values was performed to verify the model selection. All statistical analyses were undertaken in RStudio 1.0.153 (RStudio Team 2016; R Core Team 2017) with R packages "segmented" used to estimate break points in density changes over distance intervals (Muggeo 2008).

Results

Relationships between distance to plantation and bird density

On the 161 transects conducted across lowland Iceland, 3713 individual birds of 30 species were recorded (Table S4). The nine most common species (excluding gulls which do not breed in the focal habitats) used in subsequent analyses were seven waders; oystercatcher, golden plover, dunlin, common snipe (hereafter snipe), whimbrel, black-tailed godwit (hereafter godwit), redshank; and two passerines: meadow pipit and redwing (*Turdus iliacus*). These species comprised 88% of all birds recorded. Of the seven waders, snipe was the only one found in significantly higher numbers closer to plantations (Table 2, Fig 2). Snipe density declined by approximately 50% between the first (0-50 m) and second (50-100 m) distance intervals, suggesting a highly localised effect of plantations. Densities of golden plover, whimbrel, oystercatcher, dunlin and godwit all increased significantly with increasing distance from all plantations (Table 2, Fig 2). Dunlin and oystercatcher showed the largest effect (~15% increase per 50 m), followed by whimbrel (~12%), godwit (~7%) and golden plover (~4%) (Table 2, Fig 2). **Although redshank did not show a linear relationship with distance from plantation edges, redshank densities were lowest close to the plantation edge (<150 m), showing an approximately twofold increase in subsequent intervals (>150 m) (Table S3, Fig 2).** For the two passerines, redwing density decreased by ~12% per 50 m increment, and meadow pipit showed no change in density with distance from plantations (Table 2, Fig 2).

Effects of plantation characteristics on bird density

Golden plover, whimbrel and snipe were found in lower densities in the area surrounding the tallest plantations (over 10 m) compared to the 2-5 m tall plantations (Table 2). Density of redwings increased with increasing plantation **diameter** and thereby size and dunlins were found in higher densities surrounding broadleaved plantations than mixed and coniferous (Table 2). Plantation density had no significant effect on the density of any of the species, or on the relationship between bird density and distance from plantation.

Effects of plantation configuration on bird density

The effect of plantation configuration on bird densities was quantified for six wader species, **five which increased linearly with distance from plantations** (oystercatcher, golden plover, dunlin, whimbrel and godwit) **along with redshank, which does not nest in forested areas in Iceland** (Halldórsson, Oddsdottir & Sigurdsson 2008) and **was found in the lowest density within 150 m from the forest edge (Table S3, Fig 3A),** and separately for snipe and redwing which are known to nest within forests and were found in higher densities close to the plantation edges (Fig 3B). No estimates were created for meadow pipit, as their densities inside plantations are unknown. The breaking point was estimated to be in interval 5 (200-250 m from the forest edge), and the affected area for the open-nesting waders defined as the first 4 intervals (0-200 m) from the plantation edge. The mean density of the six species within each distance band within that area was, A1 (0-50 m): 17 birds/km^2; A2 (51-100 m): 29 birds/km^2; A3 (101-150 m): 30 birds/km^2; A4 (151-200 m): 51 birds/km^2 compared to 67 birds/km^2 in the remaining area (201-700 m). Consequently, **the** densities in the affected and unaffected areas were applied to equation 1 to estimate the change in bird numbers of these six open-nesting species resulting from different future plantation scenarios in vegetated open habitats in lowland Iceland (Fig S5):

Change in number of birds =

= No of patches* (Plantation area *(Density in plantation area – Density in unaffected area) + Affected area*(Density in affected area – Density in unaffected area))

*= No of patches * (Forest area (km^2) * (-67 birds/km^2) + Affected area A1 (km^2) *(- 50 birds/km^2)) + Affected area A2 (km^2) *(- 38 birds/km^2)) + Affected area A3 (km^2) *(- 37 birds/km^2)) + Affected area A4 (km^2) *(- 16 birds/km^2))*

Using this equation, we can estimate likely changes in abundance resulting from planting 1000 ha of plantation in different planting scenarios. Planting **1000 ha** of forest in one large patch instead of 50 smaller patches (4 ha each) would approximately halve the resulting decline in abundance (Fig 4). This effect increases even further as the patches become smaller, such that planting one 1000 ha forest patch would result in only a fraction (~11%) of the decline in overall abundance compared to planting 1000 small (1 ha) patches. **The analysis of the random points revealed that 6.3% of the Icelandic lowlands (<300 m a.s.l.) is currently within the affected area (<200 m) from forest plantations.**

For the combined density of redwing and snipe, the breaking point was estimated to be in interval 2 (51-100 m) away from the forest edge. The mean density of these species was 114 birds/km^2 in the first interval (0-50 m) compared to 55 birds/km^2 in subsequent intervals (51-700 m), suggesting a twofold increase in snipe and redwing numbers immediately adjacent to plantations, in addition to any breeding of individuals within those plantations.

Discussion

Planting new forests may provide potential benefits in terms of carbon sequestration, habitat for forest-dwelling species and physical protection **of human settlements and infrastructure** from adverse weather conditions. However, afforestation in open landscapes can have considerable impacts on the biodiversity those landscapes support. Iceland is considered one of the most important areas for breeding waders in Europe (Thorup 2004), and holds large proportions of the global nesting populations of golden plover (52%), whimbrel (40%), redshank (19%), dunlin (16%) and black-tailed godwit (10%) (Gunnarsson *et al.* 2006). The effects of rapid and widespread afforestation in Iceland are already becoming apparent, with five of the seven wader species in our study occurring in the lowest densities close to plantations, and areas surrounding plantations (up to 200 m) supporting around half the number of birds that occur in the same habitats further away from the plantations. There are currently hundreds of plantations throughout lowland Iceland, many of which (including the 118 used in this study) are located within semi-natural habitats. For the 76 study plantations for which recent area estimates area could be accurately measured (from aerial photographs within ±1 year of survey year) total plantation area is ~2,800 ha and the total amount of semi-natural habitat in the surrounding 200 m of **them** is ~3,600 ha. Using the equations reported here (Fig 4), we estimate that these 76 plantations could potentially have resulted in losses of ~3000 breeding waders, and thus the total losses resulting from all current plantations are likely to already be in the tens of thousands. While the abundance of waders in **forested** areas prior to the presence of plantations is unknown, previous studies in Iceland have shown much higher densities of waders (~123-276 birds/km^2, depending on the habitat type; (Jóhannesdóttir *et al.* 2014)) than we have in the unaffected area around plantations (63-187 birds/km^2). Thus, **the** estimated losses **are likely to** be conservative and the low overall densities in areas with plantations suggests that these are real losses rather than local redistributions away from plantations. While larger-scale redistributions cannot be ruled out, these migratory species are typically highly faithful to breeding sites (Newton 2010), likely because of the importance of re-locating mates (Gunnarsson *et al.* 2004) and the benefits of local site-knowledge for nesting safely and raising chicks. **Even if redistribution did occur, the surrounding habitats might eventually become saturated, and productivity and/or survival could be reduced through impacts on availability of key resources.** This underlines the urgent importance of strategic planning when it comes to afforestation (planting fewer, larger forests), along with protection of areas of great importance. Should future planting continue in the current format of many small plantations, the consequences will be far more severe than planting the same area in a smaller number of large blocks.

The changes in density of waders in open habitats surrounding forest plantations in Iceland was species-specific. The **six** species which were found in lower densities closer to plantations included species that typically nest in open landscapes such as heathland or grassland and with nests that are generally not well-concealed (oystercatcher, whimbrel and golden plover), and species that require tall vegetation in which to conceal their nests (godwit, **redshank and dunlin**) (Gunnarsson *et al.* 2006; Laidlaw *et al.* 2020), suggesting that effects of plantations will be apparent across all of lowland Iceland's semi-natural habitats. Species such as snipe **(ground-nesting; (Laidlaw *et al.* 2020))** and redwing **(tree- and ground-nesting; (Meilvang, Moksnes & Røskaft 1997))** that can nest within plantations may well increase as a result of afforestation, but estimating the magnitude of these potential increases would require data on densities within plantations which are not currently available. However, snipe was found in lower densities surrounding taller (>10 m) plantation, possibly because they only utilize plantations in the transitions stage where trees are sparse, rather than advanced forests with thick tree growth.

Effects of plantation characteristics on bird density

Two wader species (golden plover and whimbrel) were found in significantly lower densities in areas surrounding the tallest plantations (>10 m high) compared to the reference group (2-5 m high). Taller trees may provide avian predators with more or better perches (Andersson, Wallander & Isaksson 2009), and visibility (e.g. of approaching predators) is likely to be reduced in areas surrounding taller forests. Forest height can also be an indicator of forest age, which could impact bird density in the surrounding habitat, as any reduction in productivity, recruitment and survival will take some time to manifest, particularly for long-lived species with high breeding site fidelity, such as waders (Halldórsson, Oddsdottir & Sigurdsson 2008; Méndez *et al.* 2018). The number of predators using forests may also be greater in older, more established forests, and thus actual or perceived predation risks for breeding birds in the surrounding habitat may be greater (Hancock, Klein & Cowie 2020). However, it should be noted that the majority of the plantations in this study are relatively young compared to other countries, with the Icelandic Forest Service being officially founded in 1930 and forestry only gaining momentum in recent decades (Eysteinsson 2018).

Plantation density and **diameter** had no additional effect on the species that were in lower densities closer to the plantations, suggesting that the mere presence of plantations induces the observed changes in abundance, and that these effects will not increase in magnitude around larger plantations. In this study, plantations all had a minimum edge length of 30 m (i.e. 900 m^2 in area, assuming a square shape), but it is possible that this effect may operate at even smaller scales. For example, some studies have shown the presence of single trees to have an effect on breeding densities of waders in the surrounding areas (Berg, Lindberg & Källebrink 1992; Żmihorski *et al.* 2018).

Reduced densities of open-nesting species in areas surrounding trees and forests have been recorded elsewhere, with effects ranging from 50 up to 700 m in studies from the UK and the Netherlands (Stroud, Reed & Harding 2009; Vliet, Dijk & Wassen 2010; Wilson *et al.* 2014). Our results suggest that reduced densities of ground-nesting waders surrounding plantations in Iceland typically reach approximately 200 m from the edge. The extent of **the** effect could be influenced by composition of the predator community and the associated predation risks. No mammalian predators were seen during the course of this study but ravens were seen on numerous occasions, and a third (13 out of 35) of raven sightings were within 50 m of the forest edge (areas within 50 m totalled 9% of the total surveyed area), indicating that ravens may be more abundant close to forests in lowland Iceland. **C**hanges in the distribution and number of predators can be an important consequence of introducing plantations into open habitats (Hancock, Klein & Cowie 2020), and should be considered when planning future forest expansion.

Effects of plantation configuration on bird density

Estimates of the consequences of differing future planting scenarios highlight the strong potential for designing forest configurations that reduce the impact on biodiversity in the surrounding landscapes. As plantations in Iceland often appear as small patches of trees in otherwise open landscapes, rather than large forests, the total amount of affected area is considerably higher than it needs to be. The magnitude of the reduction in bird abundance close to forests is such that planting trees in few large blocks rather than many small ones could reduce total declines in abundance by more than 90%. **Therefore, when initiating new forests, concentrating on areas with the potential for large plantations, many of which still exist, would have a much lower impact than planting on smaller**

private lands (Ministry of Finance and Economic Affairs 2022). Plantation size is not the only parameter that could be considered; shape can also make a difference. Wilcove, McLellan and Dobson (1986) suggested that, in an effort to reduce the proportion of forest edge to forest interior, making forest plantations circular should be encouraged, and the same applies to reducing the proportion of the forest edge to the surrounding habitat. Future forestry planning should also consider the natural habitat on which planting takes place, given the large variation in bird density between habitats (Jóhannesdóttir *et al.* 2014). Ideally, plantations should be located where bird numbers are naturally low, such as in sparsely or non-vegetated areas, at higher altitudes and on slopes (Whittingham, Percival & Brown 2002; Skarphéðinsson *et al.* 2016), and surveys of breeding birds prior to planting would also help to identify areas of high breeding densities which should be avoided. **Although heathland habitats supported the lowest overall densities of birds in this study, densities of some open-nesting species are high in these habitats, making them of high conservation value (Katrínardóttir 2012; Jóhannesdóttir *et al.* 2014). Currently, the majority of plantation forests in Iceland have been placed in previously vegetated lowlands (dry habitats, such as heathlands and grasslands, drained wetlands and wetlands (75%)), and less in un-vegetated areas (19%) and natural forests (6%) (Traustason 2021).**

One of the assumptions **underlying** our calculations of density is that all birds within transects were detected. This is rather unlikely as **the detectability of** birds may **vary with stage of breeding or behaviour (e.g. incubating individuals hiding on the nest).** However, such detectability issues would only be a concern here if they varied with distance from plantations. Individuals very close to plantations could potentially move into the plantations and be under-recorded, but this is unlikely as none of the species for which densities increased with distance from plantation are known to occur in wooded areas, and the reduced densities were apparent over hundreds of metres from plantation edges (Fig 2). Meadow pipit, redwing and snipe were found in higher numbers close to the forest edge when walking away from, rather than towards, the plantation, suggesting that these three species could move into plantations in response to an approaching observer, but none showed reduced densities closer to plantations (Fig S4).

Forestry in Iceland is an ongoing project, and planting is expected to increase even further on an annual basis, with a goal of countering human-induced climate change. However, planting forests in open landscapes can have severe impacts on biodiversity, particularly on populations of ground-nesting birds. This serves as an example of a trade-off between two major challenges facing humanity, with contributions towards solving one, climate change (via carbon sequestration), impacting the other, biodiversity loss (Veríssimo *et al.* 2014; United Nations 2015; Sikora 2021). **Although plantations may support breeding** snipe and redwing, these species have larger global populations and ranges **(and are thus less vulnerable) than the wader species that breed only in open habitats only in Iceland,** some of which are also declining globally (International Wader Study Group 2003; Stroud *et al.* 2006; IUCN 2022), **and are therefore of high conservation value.** Waders are highly site-faithful and long-lived (Méndez *et al.* 2018) and displacement by forestry is likely to have significant fitness and population consequences. **To identify the underlying drivers behind an altered bird abundance surrounding plantation forests, and better predict future impacts, before-after-control-studies of marked individuals in areas where forests are planted, where their behaviour and demography could be tracked would be ideal**. **However, long-term tracking of displaced individuals and any subsequent changes to their fitness is very challenging, particularly in systems in which breeding success is often highly stochastic** (Laidlaw *et al.* 2020). Iceland holds large proportions of the global populations of several bird species, and four of the wader species found in lower densities close to plantation edges (godwit, whimbrel, dunlin and oystercatcher) are decreasing worldwide according to the IUCN red list (IUCN 2022). Iceland is a signatory to numerous international agreements **such as** AEWA (Agreement on the Conservation of African-Eurasian Migratory Waterbirds) and the Bern Convention on the Conservation of European Wildlife and Natural Habitats, committing it to protecting birds as well as their habitats, especially wetlands (Einarsson *et al.* 2002; Schmalensee *et al.* 2013). It is therefore imperative that strategic planning of tree-planting schemes in Iceland is developed and implemented, in order to reduce the effect on ground-nesting birds, by avoiding areas with high bird abundance and optimizing the size and shape of future forest plots.

Author contributions

TGG, JAA, JAG and AEP conceived the ideas and designed methodology; AEP and HE collected the data; AEP, JAA, JAG, TGG, SP and VM analysed the data; AEP, TGG, JAG, JAA and SP led the writing of the manuscript. All authors contributed critically to manuscript development and gave final approval for publication.

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Data accessibility statement

The data that support the findings of this study are available from Dryad digital repository.

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Figures and tables

Table 1: Variables and model structure used to quantify the effect of forests on the density of breeding birds recorded on transects through the surrounding landscape in lowland Iceland.

Variable	**Unit**	**Definition**
Bird density	Birds ha^{-1}	Number of birds recorded in each 1 ha interval of each transect
Interval	1-14	50 m distance bands from closest (1) to furthest (14) from the plantation edge
Transect	Transect number	Individual transect (one or two per plantation)
Direction	To/from	Transects were walked towards or from the plantation edge
Plantation diameter	m	Distance between two outermost trees on plantation edges, recorded from aerial photos (Icelandic Forest Service 2014) or in the field with a rangefinder
Plantation area	m^2	Area of Plantation, extracted from aerial photos
Plantation height	0-2 /2-5 / 5-10 /> 10 m	Tallest visible point of plantation, measured with a rangefinder
Plantation type	Mixed/conifer/broadleaf	Predominant tree type (coniferous, broadleaved or both)
Plantation density	Sparse/dense	Interior (up to 50 m) of plantation visible (sparse) or not (dense) from edge
Habitat	Poor heathland/rich heathland/grassland/ semi-wetland/wetland	Classification of transect habitat (Gísladóttir, Brink & Arnalds 2014)
Plantation	**Plantation number**	**Individual plantations (one or two transects per plantation)**

Full model	Bird density (birds/ha) ~ Interval + Height + Width + Type + Forest Density + **Habitat** + Direction (where applicable) + (1|**Plantation/**Transect)

Gísladóttir, F., Brink, S. & Arnalds, O. (2014) Nytjaland (Icelandic Farmland Database). *Agricultural University of Iceland Report,* **49**.

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Table 2: Estimates **(on log-scale)** from the minimum glmmADMB models with a Poisson distribution with asterisks representing significance (p<0.05 *; p<0.01 **; p<0.001 ***) of the influence on densities of nine species of distance from plantation edge, habitat, tree height, tree type and **diameter** of plantation. Transect nested within plantation was included as a random factor in all models. Direction of transect included when needed as by results from a priori models (Table S5). Factor were removed in order of increasing significance (density, **diameter**, height, type and habitat) as obtained by a priori models.

Full model: Bird density (birds/ha) ~ Interval + Type + Height + Width + Forest Density + Direction (where applicable) + Habitat + (1|plantation/transect)

Variable		**Redwing**	**Snipe**	**Golden plover**	**Whimbrel**	**Dunlin**	**Oystercatcher**	**Godwit**	**Redshank**	**Meadow pipit**
Interval		-0.13 (±0.02) ***	-0.06 (±0.02) ***	0.04 (±0.02) *	0.11 (±0.02) ***	0.14 (± 0.04) ***	0.14 (±0.05) **	0.06 (±0.03) *	0.02 (±0.03)	0.01 (±0.01)
Height	(Intercept)[a]	-1.13 (± 0.22)	-0.22 (±0.29)	-1.61 (±0.27)	-2.16 (±0.25)	-3.91 (±0.63)	-6.21 (±1.52)	-2.37 (±0.42)	-1.60 (±0.38)	-0.92 (±0.11)
	0-2 m		-0.25 (±0.38)	0.73 (±0.40)	-0.57 (±0.49)					
	5-10 m		-0.25 (±0.21)	-0.20 (±0.24)	0.07 (±0.25)					
	>10 m		-0.82 (0.28)**	-1.39 (±0.41) ***	-0.96 (±0.38) *					
Width	**km**	0.44 (±0.22) *								
Direction	Direction		-0.32 (±0.18)							-0.48 (±0.16) **
	Interval:direction	0.04 (±0.02)	0.05 (±0.02)*							0.05 (±0.02) **
Type	Broadleaved					0.80 (±0.38) *				
	Conifer					-0.68 (±0.56)				
Habitat	Poor heathland		-0.69 (±0.28)*			-2.41 (±1.08) *		-1.96 (±0.66) **	-1.43 (±0.51) **	
	Rich heathland		-0.25 (±0.22)			0.33 (±0.41)		-0.89 (±0.44) *	-0.36 (±0.37)	
	Semi-wetland		0.18 (±0.24)			0.90 (±0.45) *		0.95 (±0.38) *	-0.08 (0.42)	
	Wetland		0.63 (±0.32) *			0.97 (±0.57)		1.47 (±0.50) **	1.04 (±0.51) *	

[a] Reference height: 2-5 m; type: broadleaved; habitat: grassland, direction: away from

Figure 1: Location of 118 plantations around which transects were conducted in the summer of 2017 in areas below **300 m a.s.l.** (shown in grey) in Iceland.

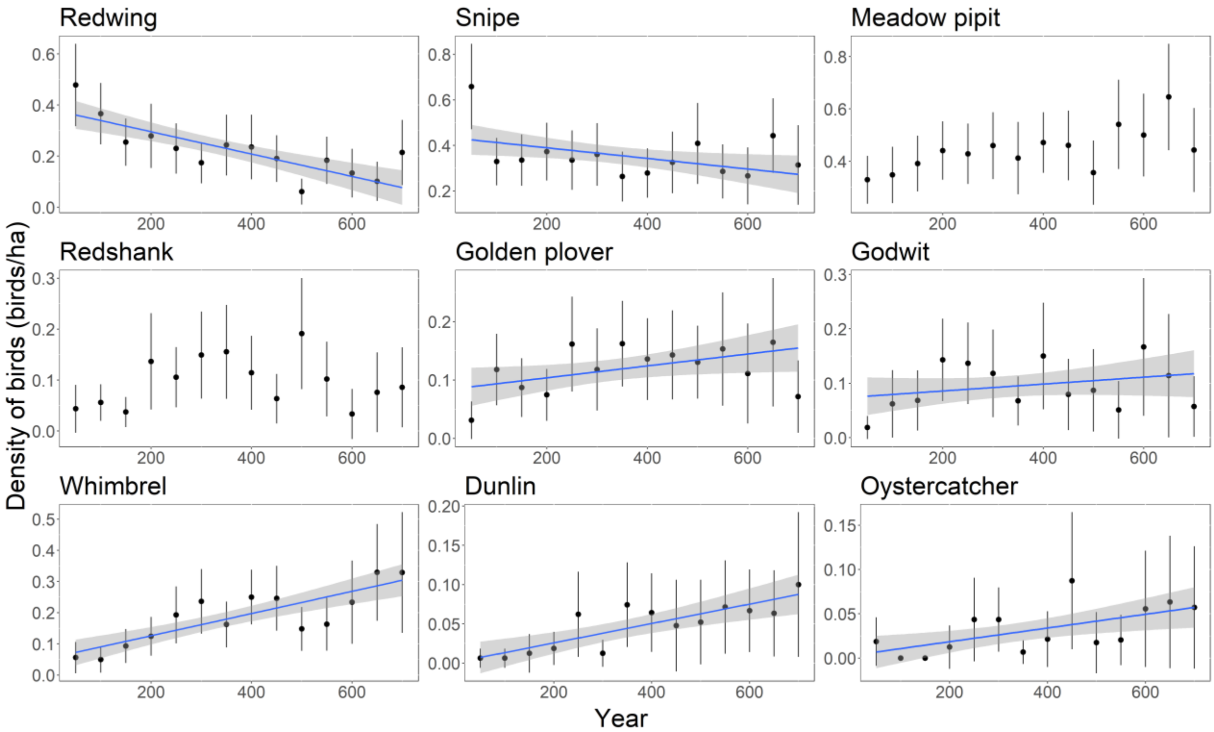

Figure 2: The mean (± SE) density of nine species with distance from plantations in 50 m intervals along transects. Regression lines **(± SE)** are shown for significant relationships.

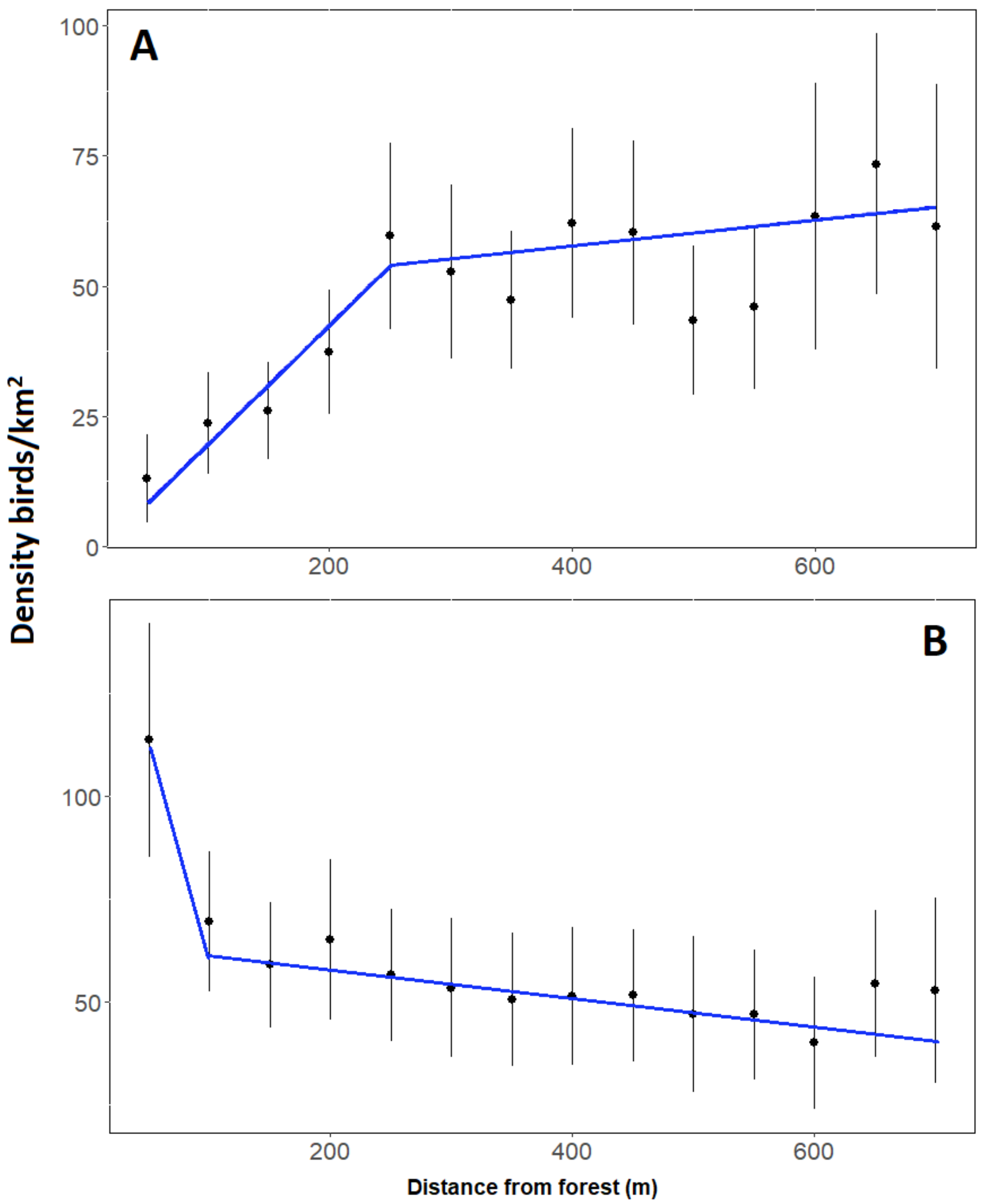

Figure 3: Combined density of A: six open-nesting wader species (oystercatcher, golden plover, dunlin, whimbrel, godwit and redshank) at different distances from plantations and B: two forest-nesting species (snipe and redwing). The regression lines are from a segmented linear regression, indicating a rapid increase in open-nesting species density until the breaking point between 200-250 m, and rapid decrease of forest-nesting species until the breaking point between 50-100 m.

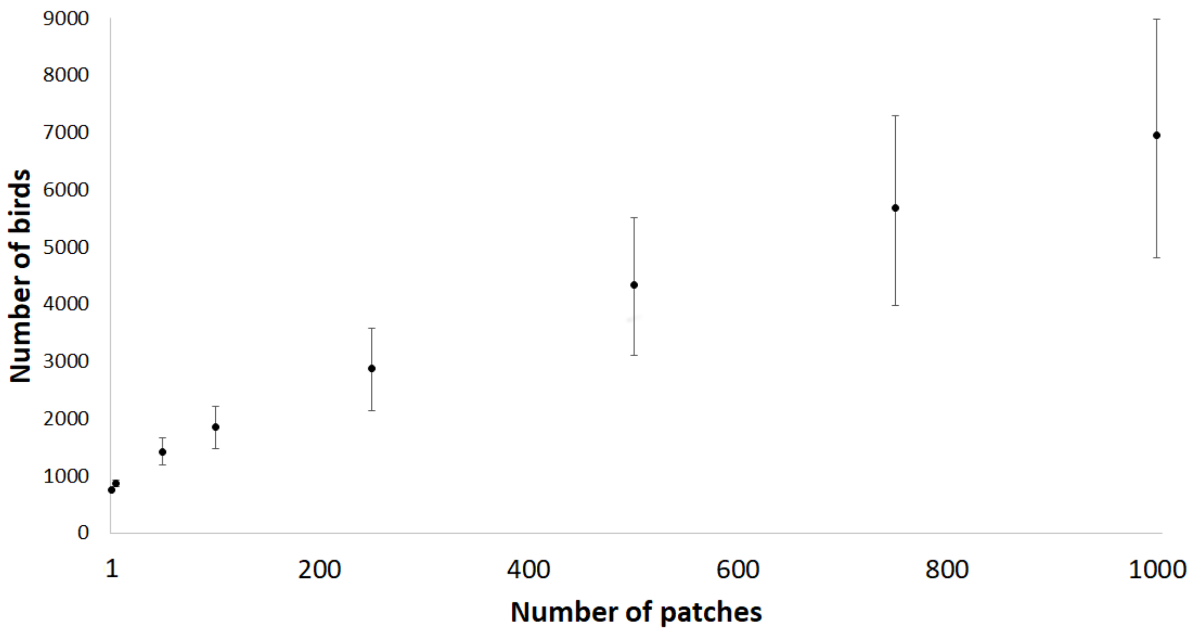

Figure 4: Estimated declines in numbers of open-nesting birds (oystercatcher, golden plover, dunlin, whimbrel, godwit and redshank) (means ± 95% Cis) in future afforestation scenarios in which 1000 ha are planted in differing numbers of equal-sized patches, as a consequence of both complete loss of birds within the plantations and reduced numbers in the affected area (within 250 m) surrounding each plantation.