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ORIGINAL PAPER

Implications of afforestation for bird communities: the importance of preceding land-use type

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Abstract Afforestation of open habitats is one of the principal land-use changes underway in Europe and elsewhere in the world at present, and it can have a considerable impact on local biodiversity. The sustainable expansion of global forest plantations requires an understanding of the factors that determine the ecological impacts of afforestation. This study set out to determine the importance of preceding land-use type in determining the outcomes of afforestation for bird communities. Paired comparisons of 5-year-old exotic conifer plantations and matching non-forested sites were studied in areas of low (peatland), intermediate (wet grassland) and high (improved grassland) management intensity. Afforestation resulted in an overall increase in total bird density in all three habitat types. The effects of forest planting on bird conservation were found to be positively related to prior management intensity at the site. The density of bird species of conservation concern increased in response to the planting of intensively managed grassland sites, but decreased in response to afforestation of peatlands and of grasslands under intermediate management intensity. This study shows that plantation forests can, in some contexts, offer opportunities for bird conservation, and the findings highlight the trade-offs that are an integral part of land-use change. Therefore, where afforestation planning includes consideration of its impact on bird communities, planting should take place predominantly on sites of low biodiversity value, such as agriculturally improved

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grasslands. Furthermore, the preservation of sites of high conservation value within areas of afforestation would confer advantages on bird communities.

Keywords Biodiversity · Forest management · Grassland · Land-use change · Peatland · Plantation forest · Sustainable forest management

Introduction

Afforestation (the conversion of open habitat to forested area) is one of the most common land-use changes currently on-going in Europe and throughout much of the world (Lambin and Geist 2008; Hansen et al. 2013). Land-use change is an important driver of global biodiversity change and research over the last two decades has identified deleterious impacts of land-use change on biodiversity and ecosystem resilience in many parts of the world (Sala et al. 2000; de Baan et al. 2013; Newbold et al. 2015). Deforestation has resulted in the net global removal of as much as 12 million hectares of forest annually since 2000 and is associated with biodiversity decline (FAO 2010; Hansen et al. 2013). However, in many parts of the world, and particularly in developed countries, land-use change also includes the establishment of forests in formerly non-forested areas. This may occur through the planting of trees on land that was not previously forested, the planting of trees on land where historically there was forest or through natural forest expansion on abandoned agricultural or industrial land (Pawson et al. 2008; Quine and Humphrey 2010; Pellissier et al. 2012), and may have positive impacts on landscape restoration and landscape scale forest biodiversity. Plantation forests now make up an estimated 264 million hectares (7 %) of global forest area and are forecast to further increase to approximately 345 million hectares by 2030 (Carle and Holmgren 2008). There is, therefore, a pressing need for research to ensure that this expansion is carried out sustainably, with minimal negative impacts on biodiversity, and to provide evidence for forest benefits in the context of ecosystem services rather than purely economic benefits (Quine et al. 2013; Thomas et al. 2015).

The effect of plantation forests on biodiversity has been the focus of considerable debate (Brockerhoff et al. 2008; Bremer and Farley 2010; Pawson et al. 2013). Some authors have described plantation forests as “biological deserts” (Stephens and Wagner 2007), and argued that “plantations are not forests” (Carrere and Fonseca 2004). While many researchers have recorded relatively low levels of biodiversity in plantation forests (Wallace and Good 1995; Lachance et al. 2005; Wilson et al. 2006; Sweeney et al. 2010b; Bunce et al. 2014; Bergner et al. 2015), this is typically in comparison with natural woodlands, and the dismissal of their potential to support biodiversity entirely is inappropriate (Stephens and Wagner 2007). Plantation forests can enhance landscape level biodiversity where natural forests are rare (Brockerhoff et al. 2005; Santos et al. 2006) and have been shown to provide suitable habitats for a wide range of forest species, including species of conservation concern (BOCC) (Humphrey et al. 2000; Gardner 2012; Brockerhoff et al. 2013; MacKay et al. 2014).

Taxa differ in their response to afforestation, and while species richness in forest plantations can be as high as in semi-natural woodlands, the two forest types may support different assemblages of species (Dickie et al. 2011; Irwin et al. 2014; Bergner et al. 2015). Furthermore, the impacts of afforestation on biodiversity are influenced by many factors including planted tree species, management intensity and preceding land-use type (Brockerhoff et al. 2008; Bremer and Farley 2010; Riffell et al. 2011; Pawson et al. 2013; Calladine et al. 2015). Where plantation forests replace natural or semi-natural ecosystems, negative impacts on biodiversity are typically documented (Brockerhoff et al. 2008; Bremer and Farley 2010; Pawson et al. 2013). Plantations established on former agricultural, or otherwise ecologically degraded land may, however, offer considerable opportunities for biodiversity conservation (Brockerhoff et al. 2008; Bremer and Farley 2010; Pawson et al. 2013). The current view arising from reviews and meta-analyses is that, for certain taxa, plantation forests are less biodiverse than other habitats, particularly grasslands (Brockerhoff et al. 2008; Bremer and Farley 2010). Studies of this kind, however, typically focus on natural grasslands rather than pasture, or treat all grasslands as one group, failing to account for biodiversity variation among different grassland habitats which may influence the net biodiversity change. While grasslands managed at low intensity can have high biodiversity, the same is not true of intensively managed grasslands (Weiner et al. 2011; Gonthier et al. 2014), a fact that has sometimes been overlooked. Given the expansion of plantation forests, and afforestation of open areas, the impact of these activities on biodiversity requires detailed investigation (Cousins et al. 2015).

The ecology, distribution and abundance of birds are sensitive to environmental conditions (Furness and Greenwood 1993; Kent et al. 2014) and terrestrial bird communities have been shaped by habitat modification resulting from human activities such as afforestation, deforestation and changes in management intensity of agricultural land (Fuller 2012; Scridel 2014). Due to increasing demands for food, fibre, water and energy these land use changes are likely to remain an important influence on bird populations in the future (Jetz et al. 2007; Eglington and Pearce-Higgins 2012). Afforestation typically results in the reduced prevalence of open habitat bird species, while benefitting forest birds (Allan et al. 1997; Dias et al. 2013), particularly in landscapes where natural forest cover is low or, as is the case in Ireland, has been significantly reduced as a consequence of anthropogenic activity (Sweeney et al. 2010b). Research has shown that structural heterogeneity is related to increased bird diversity (Barbaro et al. 2005; Hovick et al. 2014; Bergner et al. 2015). Therefore, forest management strategies can be used to maximise avian biodiversity, particularly where they aim to achieve increased structural complexity (Brockerhoff et al. 2008; Sweeney et al. 2010a; Jones et al. 2012; Lindenmayer et al. 2012).

Here, we investigate the extent to which the impact of afforestation on bird diversity depends on preceding land-use using a space-for-time substitution design with a paired-site approach. Space-for-time studies can be confounded by differences in site history, which may drive differences in observed community level responses. The use of a paired site design, where study sites are carefully matched in terms of site history and preceding land use and habitat prior to data collection, strengthens this approach considerably. In this study, bird diversity in paired forested and non-forested sites was compared across three types of pre-afforestation habitat: agriculturally improved grassland (high management intensity), wet grassland (intermediate management intensity) and peatland (low management intensity). We tested the hypothesis that the effects of afforestation on bird communities are dependent not just on the gross differences between forested and unforested sites, but also on the differences in bird communities of these habitats before afforestation takes place. We also tested the hypothesis that these effects are mediated by the impact of tree planting on habitat vegetation structure.

Methods

Study sites

Study sites were located in Ireland where afforestation is one of the fastest on-going land-use changes in Europe (Wilson et al. 2012). Europe is the only region in the world where a net increase in forest area was reported between 1990 and 2000 (FAO 2007), but our study area is representative of many areas around the world where the conversion of agricultural land to forest is a major consideration for biodiversity conservation. Forty eight study sites were selected in pairs, each comprising a matching non-forested site and a 5-year-old Sitka spruce (*Picea sitchensis*) plantation. Study sites ranged in size between 6Ha and 20Ha with forested sites having canopy heights of between 1.3 and 3.8 m. The 24 site pairs were selected in three habitat types: eight pairs in each of improved grassland, wet grassland and peatland habitat. Sites in each pair were closely matched in terms of environmental conditions such as slope, altitude, drainage, soil type, and proximity of other habitat types. Sites in each pair were within five km of each other. Potential study sites were selected from national forest databases, and archived aerial photographs were used to confirm pre-planting habitat, and to locate non-forest sites that matched the habitat of afforestation sites at the time of planting. Before final selection of study sites, ground-truthing was undertaken to confirm that all site pairs were well matched in terms of soil type, pre-afforestation vegetation type and drainage.

Improved grassland study sites were intensively managed or highly modified agricultural grasslands that had been reseeded and/or regularly fertilised. These sites were species poor, dominated by perennial rye grasses (*Lolium* spp.) and were typically located on well drained mineral soil (Fossitt 2000). Wet grassland study sites were less intensively managed than improved grassland sites, and production was typically lower. These sites were typically located on poorly drained, wet or water-logged mineral soil. Species composition varied considerably and they were not dominated by commercial grasses and had a greater presence of moisture-tolerant graminoids, particularly sedges (*Carex* spp.) and rushes (*Juncus* spp.) (Fossitt 2000). Peatland study sites were bogs or heaths comprising marginally productive grazing land on peat soil (Fossitt 2000). Vegetation composition at these sites was variable, but one or more of the following groups was always dominant: dwarf shrubs, including heather (*Calluna vulgaris* and *Erica* spp.), bilberry (*Vaccinium myrtillus*) and bog myrtle (*Myrica gale*); acidophilic graminoids, especially *Mollinia caerulea*, cotton grass (*Eriophorum* spp.) and deer grass (*Trichophorum* spp.); and mosses, particularly *Sphagnum* spp.

Bird and vegetation surveys

Birds were surveyed at non-forested and forested (5 years after afforestation) sites during the summers of 2002 and 2004 using point counts (Bibby et al. 2000). Data were collected at each site over two visits, one in May/early June and the second visit in June/early July, between the hours of 0700 and 1800. Each site was surveyed during the morning and the afternoon, with between five and nine point counts surveyed at each site, depending on site size. Points were positioned at a minimum distance of 100 m from one another and, in plantations, so that they covered a representative range of edge and interior habitat and features such as forest roads and field boundaries, where these were present. At control sites, points were situated to cover a representative range of distances from field boundaries. Point counts lasted 5 min, during which the species and position of all birds detected within 50 m of the observer were recorded. Bird surveys were not conducted in heavy or persistent rain, or in winds greater than Beaufort scale four. Clusters of birds of the same species were recorded as having a maximum of two individuals to reduce the influence of fledged families on density estimates (Bibby et al. 2000). Over-flying birds were not recorded as their presence could not be assumed to indicate an association with the site.

The data collected during point counts were used to derive estimates of the following bird community metrics: (1) total bird density, (2) total bird species richness, (3) density of bird species of conservation concern (red and amber-listed species according to Lynas et al. (2007), hereafter referred to as BOCC) density, and (4) BOCC species richness. Distance software was used to derive species densities from field observations (Buckland et al. 2001), by adjusting the numbers of birds detected during surveys according to detection functions, which estimate how detection efficiency varies with distance from the observer. Each species was assigned to one of five detection groups, which were based on aspects of the ecology and behaviour likely to influence species' detectability and on the distances at which observations in each species-habitat combination were recorded. Separate detection functions were developed for birds recorded in young plantation forest, non-forested open habitat and for those bird detected within 15 m of a hedge in non-forested sites, as the distances at which birds were detected varied between these three situations. Species richness was calculated as the cumulative number of species recorded over both visits at each site.

Structural vegetation metrics were recorded at each point count location, including percentage cover of: conifer trees, deciduous trees, shrub (woody vegetation 0.5–2.0 m in height) and ground vegetation ($\leq$0.5 m in height) as well as the height of conifer and deciduous trees. The position, canopy width and height of all hedge and non-hedge shrub and tree cover in each site were entered, together with bird survey data, onto digitised maps using ArcGIS 10 (ESRI 2010). These were used to calculate the length, area and percentage cover of habitat features in the study sites.

Data analysis

Generalised linear mixed models (GLMMs) were used to investigate whether there was an effect of afforestation on bird communities, and whether this effect varied according to preceding (pre-afforestation) habitat type. GLMMs were conducted using the 'lmer' function in the R library lme4 (Bates et al. 2005), including pair as a random effect, and treatment (forested/non-forested) as a fixed effect. Bonferroni post hoc tests from separate one-way ANOVAs to test for differences in the bird metrics between habitat type in both forested and non-forested sites, were used to confirm the statistical significance between habitat differences of the bird metrics indicated by the GLMMs.

Analysis of the responses of bird density and species richness to afforestation was undertaken to test the hypothesis that the impact of afforestation on bird community metrics was dependent not only on the gross difference between forested and non-forested sites, but also on the bird diversity supported by the pre-afforestation habitats. To this end, the net differences between bird metrics of paired non-forested and forested sites (forested site value minus non-forested sites value; hereafter referred to as the "response") were calculated for each paired site in each of the three habitat types. Differences in the response of the bird community metrics between the three habitat types were assessed using one-way ANOVAs with Bonferroni post hoc tests.

In order to investigate whether the impacts of afforestation on bird community metrics are dependent on the pre-existing vegetation structure, we modelled the relationships between the responses of community metrics together with the responses of structural vegetation metrics, using an information theoretic model averaging framework based on Akaike's Information Criterion corrected for small sample sizes (AICc). Gaussian generalised linear models (GLMs) were used to identify those structural vegetation metrics whose responses were related to the responses of the four bird community metrics. Variables included in each of these GLMs were the responses of: height and cover of both conifer and deciduous trees, shrub and moss-herb cover, as well as preceding land-use type and all first level interactions of these structural vegetation metrics responses with preceding land-use type. To determine the most important explanatory variables in the GLMs, we applied model averaging using the "dredge" function in the R library MuMIn (Bartoń 2009). Normality and homogeneity of variance were tested using Kolmogorov–Smirnov and Levene's test, respectively. ANOVAs and paired t-tests were conducted using PASW Statistic 17.

The impact of afforestation on vegetation structure in each of the three habitat types was investigated using paired *t* tests to compare non-forested and forested sites in terms of deciduous tree height and cover, ground and shrub cover.

A *t* test was also used to investigate whether afforestation resulted in a loss of beta diversity of birds (assemblage diversity between sites, Whittaker 1972). This test used the "betadisper" function on the beta diversity of the forested and non-forested sites, calculated according to principal components by the "betadiver" function, in the Vegan R library (Oksanen et al. 2010). Non-metric multi-dimensional scaling (NMDS) analysis was used to examine the variation in the bird community assemblages between forested and non-forested sites in the three habitat types. NMDS analysis was conducted using PC-ORD (version 6; MjM Software, Gleneden Beach, Oregon, USA) using Sørensen distance measures.

To examine whether the response of the bird community assemblages to afforestation in the three pre-afforestation habitats was mediated through the response to vegetation structure, we conducted redundancy analyses (RDA) using the R package Vegan (Oksanen et al. 2010). The relative importance of each of the vegetation response variables, and habitat type in structuring the response of the bird communities to afforestation were assessed using this statistical approach. In order to examine whether bird community structure was confounded by geographic location, a variable matrix of two-dimensional coordinates x and y was completed by adding all terms of the cubic regression: $(x + y) \times (x + y) \times (x + y)$ to the analyses following Legendre (1990). Collinearity was assessed by computing the variance inflation factor of the variables, and collinear variables with a variable inflation factor greater than 20 were excluded. We report the variation explained by each variable in the RDA model as the adjusted R^2 (R^2adj), which prevents the inflation of R^2 values by taking into account the number of predictor variables and sample size (Peres-Neto et al. 2006). Only significant variables identified by a forward selection procedure using the results of a Monte Carlo permutation test of 4999 random permutations with the R package packfor (Dray et al. 2007) were included in the variance partitioning analysis. Prior to forward selection, we performed a global test including all variables to ensure that the explanatory variables had an effect on the response variables. RDAs were tested for significance using an ANOVA based permutation procedure.

Results

Bird density and species richness in non-forested and forested sites

Thirty nine bird species were recorded during this study, including 6 BOCC, with 30 of these species detected in both non-forested and forested study sites (Table 1). One of these BOCC species (House sparrow) was found exclusively in non-forested improved grassland sites, while a further two (Grasshopper warbler and Kestrel) were found exclusively in forested sites).

Similar patterns of bird density and species richness were observed among habitat types at forested and non-forested sites in this study. At non-forested sites both the total bird density and species richness were highest in wet grassland sites and lowest in peatland sites ($F_{2,21} = 15.7$, $P < 0.001$ and $F_{2,21} = 32.1$, $P < 0.001$ respectively, Fig. 1). At forested study sites the total bird density was similar where the preceding habitat had either been improved or wet grassland but was significantly lower at forested sites where the preceding habitat had been peatland ($F_{2,21} = 13.3$, $P < 0.001$, Fig. 1), despite the observed increases in density following planting within peatland sites. In these sites bird species richness was also significantly lower in sites that were previously peatland than where the preceding habitat had been improved or wet grassland ($F_{2,21} = 23.1$, $P < 0.001$).

The observed patterns of BOCC density and species richness differed from patterns observed when all bird species were considered. At forested study sites BOCC density was significantly higher in sites where the preceding habitat had been improved grassland than at the other two site types ($F_{2,21} = 9.7$, $P = 0.001$, Fig. 1). At these sites, BOCC species richness was also significantly higher where the preceding habitat had been improved grassland than where it had been peatland ($F_{2,21} = 4.9$, $P = 0.018$, Fig. 1). At non-forested sites BOCC density was higher in peatlands than in wet grasslands, but not significantly different between either of these habitats and improved grassland ($F_{2,21} = 4.2$, $P = 0.03$, Fig. 1). BOCC species richness did not differ among the non-forested habitat types ($F_{2,21} = 1.1$, $P = 0.35$, Fig. 1).

Afforestation influenced all four bird community metrics under investigation in this study (total bird density and species richness, and BOCC density and species richness). The impact of afforestation was dependant on the pre-afforestation habitat type at each site, as indicated by a significant interaction between treatment and habitat type for all metrics except total bird species richness (Table 2).

Response of bird density and species richness to afforestation

The response of bird communities to afforestation was measured as the net difference between bird community metrics at the non-forested and forested study site pairs. Both the density and the species richness of total bird species increased in response to afforestation in all habitat types. The response of bird total density to afforestation varied significantly according to pre-afforestation habitat type ($F_{2,21} = 5.37$, $P = 0.013$), with a larger positive response seen in improved grassland sites compared to wet grassland sites, with the increase in total bird density in peatland sites indistinguishable from either of the other habitats (Fig. 2). There was a significant positive response in total bird species richness in all habitat types, with no difference in the magnitude of this response between habitats ($F_{2,21} = 1.52$, $P = 0.24$, Fig. 2).

Table 1 Mean (±SE) density of each bird species in forested and non-forested study sites

		Improved grassland		Wet grassland		Peatland	
		Non-forested	Forested	Non-forested	Forested	Non-forested	Forested
Blackbird	*Turdus merula*	0.26 (0.06)	0.29 (0.1)	0.49 (0.11)	0.47 (0.06)	0.04 (0.04	0
Blackcap	*Sylvia atricapilla*	0	0.02 (0.02)	0.11 (0.06)	0.17 (0.04)	0	0
Blue tit	*Cyanistes caeruleus*	0.09 (0.09)	0.04 (0.04)	1.07 (0.43)	0.12 (0.06)	0	0
Bullfinch	*Pyrrhula pyrrhula*	0.03 (0.03)	0.02 (0.02)	0.03 (0.03)	0.09 (0.05)	0	0
Chaffinch	*Fringilla coelebs*	0.52 (0.22)	0.4 (0.14)	0.56 (0.2)	0.35 (0.06)	0	0.49 (0.43)
Chiffchaff	*Phylloscopus collybita*	0.03 (0.03)	0	0.03 (0.03)	0.08 (0.07)	0	0
Coal tit	*Periparus ater*	0.36 (0.18)	0.3 (0.1)	0.66 (0.22)	0.25 (0.08)	0	0.08 (0.08)
Dunnock	*Prunella modularis*	0.19 (0.09)	0.34 (0.11)	0.16 (0.09)	0.48 (0.12)	0	0.06 (0.05)
Goldcrest	*Regulus regulus*	0.14 (0.12)	0.45 (0.18)	0.65 (0.34)	0.43 (0.18)	0.06 (0.06)	0
Grasshopper warbler[a]	*Locustella naevia*	0	0.11 (0.05)	0	0.03 (0.02)	0	0.01 (0.01)
Great tit	*Parus major*	0.16 (0.11)	0.07 (0.04)	0.04 (0.04)	0.02 (0.02)	0	0
Greenfinch	*Carduelis chloris*	0.05 (0.05)	0.05 (0.03)	0	0	0	0
Grey wagtail	*Motacilla cinerea*	0	0	0	0	0.28 (0.28)	0
Hooded crow	*Corvus cornix*	0	0.02 (0.02)	0	0	0	0.02 (0.02)
House sparrow[a]	*Passer domesticus*	0.03 (0.03)	0	0	0	0	0
Jackdaw	*Corvus monedula*	0	0	0.02 (0.02)	0	0.01 (0.01)	0
Kestrel[a]	*Falco tinnunculus*	0	0.04 (0.04)	0	0.01 (0.01)	0	0
Lesser redpoll	*Acanthis cabaret*	0.04 (0.04)	0.34 (0.2)	0.04 (0.04)	0.09 (0.03)	0.04 (0.04)	0.23 (0.07)
Linnet[a]	*Carduelis cannabina*	0.08 (0.06)	0.21 (0.09)	0	0.03 (0.03)	0	0
Long-tailed tit	*Aegithalos caudatus*	0	0	0.06 (0.06)	0.09 (0.06)	0	0
Magpie	*Pica pica*	0	0	0.03 (0.03)	0.01 (0.01)	0	0
Meadow pipit	*Anthus pratensis*	0.12 (0.09)	1.33 (0.45)	0.84 (0.2)	0.47 (0.22)	1.08 (0.3)	1.57 (0.24)
Mistle thrush	*Turdus viscivorus*	0.04 (0.04)	0.03 (0.02)	0	0	0	0
Pheasant	*Phasianus colchicus*	0.03 (0.03)	0.03 (0.02)	0.07 (0.06)	0	0	0

Table 1 continued

		Improved grassland		Wet grassland		Peatland	
		Non-forested	Forested	Non-forested	Forested	Non-forested	Forested
Pied wagtail	*Motacilla alba*	0.18 (0.12)	0	0	0	0	0
Reed bunting	*Emberiza schoeniclus*	0	0.31 (0.12)	0.28 (0.10)	0.43 (0.17)	0.03 (0.03)	0.13 (0.06)
Robin	*Erithacus rubecula*	0.67 (0.18)	0.4 (0.12)	1.21 (0.17)	1.02 (0.27)	0	0.03 (0.02)
Rook	*Corvus frugilegus*	0.07 (0.05)	0.02 (0.02)	0.03 (0.03)	0	0	0
Sedge warbler	*Acrocephalus schoenobaenus*	0.09 (0.09)	0.26 (0.14)	0	0.24 (0.1)	0.04 (0.04)	0.09 (0.05)
Siskin	*Carduelis spinus*	0	0.02 (0.02)	0	0.04 (0.04)	0	0.02 (0.02)
Skylark[a]	*Alauda arvensis*	0.16 (0.07)	0.09 (0.05)	0.08 (0.04)	0	0.4 (0.13)	0.01 (0.01)
Song thrush	*Turdus philomelos*	0.04 (0.02)	0.32 (0.13)	0.11 (0.05)	0.27 (0.12)	0	0.01 (0.01)
Stonechat	*Saxicola torquata*	0	0.08 (0.07)	0.06 (0.06)	0.07 (0.05)	0.04 (0.03)	0.24 (0.13)
Swallow[a]	*Hirundo rustica*	0.07 (0.07)	0.05 (0.04)	0.02 (0.02)	0.04 (0.03)	0	0.03 (0.02)
Whinchat	*Saxicola rubetra*	0	0	0	0.03 (0.03)	0	0.04 (0.03)
Whitethroat	*Sylvia communis*	0	0.24 (0.11)	0.06 (0.05)	0.31 (0.1)	0	0.12 (0.07)
Willow warbler	*Phylloscopus trochilus*	0.07 (0.03)	1.17 (0.3)	0.67 (0.13)	1.46 (0.22)	0	0.26 (0.07)
Woodpigeon	*Columba palumbus*	0.01 (0.01)	0.02 (0.02)	0.12 (0.1)	0.07 (0.05)	0	0
Wren	*Troglodytes troglodytes*	0.33 (0.09)	1.33 (0.48)	0.57 (0.1)	1.41 (0.17)	0.04 (0.04)	0.41 (0.11)

[a] Bird species of Conservation Concern (BOCC)

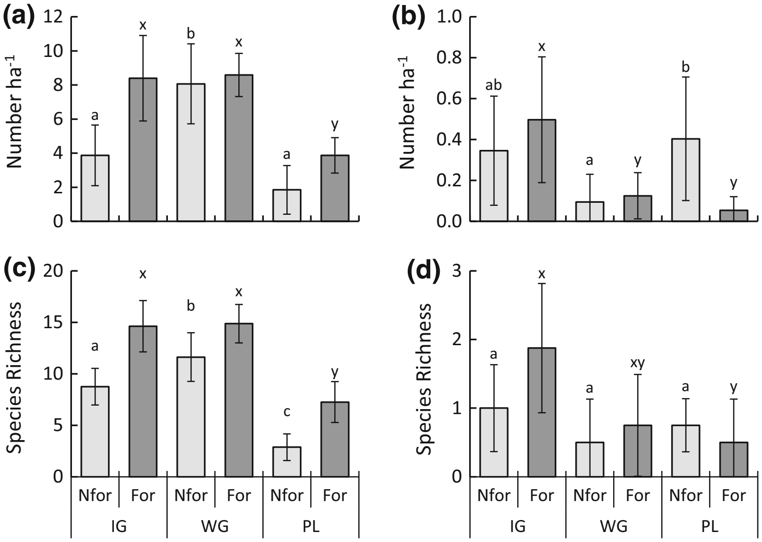

Fig. 1 **a** Total bird density, **b** BOCC density, **c** total species richness and **d** BOCC species richness, in forested (*dark bars*) and non-forested (*pale bars*) sites within different habitat types (*IG* improved grassland; *WG* wet grassland; *PL* peatland). All values are means ± 95 % confidence intervals. *Lowercase letters* (*a*, *b*, *c* for non-forested sites and x, y, z for forested sites) refer to homogenous subsets. All values are means ± 95 % confidence intervals

When we looked at BOCC species, a positive response of both density and species richness to afforestation was seen in both improved and wet grasslands, while a negative response of both density and species richness was seen in peatlands. The response of BOCC density to afforestation differed among habitats ($H_2 = 7.39$, $P = 0.025$) with no significant response observed in either improved or wet grasslands but a significant negative response observed in peatlands (Fig. 2). A similar pattern was seen in BOCC species richness, although there was no significant difference in the observed response between habitat types ($F_{2,21} = 3.36$, $P = 0.054$).

When the responses of bird communities to afforestation were modelled, preceding land-use was included in all of the top models of total bird density response, and was assigned the highest relative importance value by model averaging of all explanatory variables (Table 3). Deciduous tree height was also assigned a relatively high importance, but the importance values of other vegetation variables were relatively low (Table 3). Preceding land-use explained relatively little of the variation in the effect of afforestation on total bird species richness, with the height of deciduous trees, ground cover and conifer cover all being assigned higher importance values. No explanatory variable was included in all of the averaged models of density or species richness of BOCC, but vegetation cover contributed considerably to modelled variation in these bird metric response variables (Table 3). Conifer cover was assigned the highest relative importance for models of BOCC density, followed by shrub cover and preceding land-use type. The most important variable in determining BOCC species richness was shrub cover, closely followed by preceding land-use type and conifer cover. The interaction between shrub cover and preceding land-use type was also of relatively high importance, with shrub cover having a positive impact

Table 2 GLMMs showing the influence of afforestation, preceding land-use type and their interaction on the four bird community metrics

Explanatory variable	Total bird density		Total species richness		BOCC density		BOCC species richness	
	Estimate (±SE)	*P*	Estimate (±SE)	*P*	Estimate (±SE)	*P*	Estimate (±SE)	*P*
Intercept[a]	3.87 (0.76)	<0.0001	8.75 (0.85)	<0.0001	0.35 (0.09)	0.0006	1.00 (0.29)	0.0012
Preceding land-use—WG	4.19 (1.07)	0.0003	2.88 (1.20)	0.021	−0.25 (0.13)	0.064	−0.50 (0.41)	0.23
Preceding land-use—PL	−1.80 (1.07)	0.10	−5.88 (1.20)	<0.0001	0.06 (0.13)	0.66	−0.25 (0.41)	0.54
Afforestation	4.52 (0.88)	<0.0001	5.88 (1.07)	<0.0001	0.15 (0.12)	0.21	0.88 (0.31)	0.007
Afforestation WG	−4.00 (1.25)	0.003	−2.63 (1.51)	0.09	−0.12 (0.17)	0.48	−0.63 (0.44)	0.16
Afforestation PL	−2.73 (1.25)	0.03	−1.50 (1.51)	0.33	−0.50 (0.17)	0.005	−1.13 (0.44)	0.013

[a] Improved grassland was the reference category

IG improved Grassland; *WG* wet Grassland; *PL* Peatland

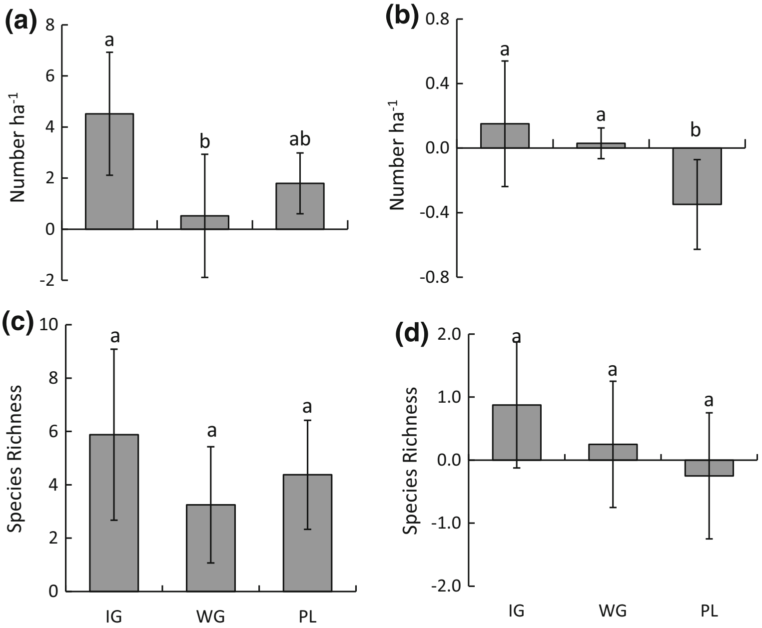

Fig. 2 The responses of **a** total bird density, **b** BOCC density, **c** total species richness and **d** BOCC species richness in paired sites (forested minus non-forested) in each of the three preceding land-use types (*IG* improved grassland; *WG* wet grassland; *PL* peatland). *Lowercase letters* refer to homogenous subsets indicated by Bonferroni post hoc tests. Where 95 % confidence intervals do not intersect the x-axis indicates a significant difference between paired sites within each habitat type. All values are means ± 95 % confidence intervals

in improved grassland, little impact in wet grassland and a negative impact in peatland on the response of BOCC species richness (Table 3).

Vegetation structure in non-forested and forested sites

The level of shrub cover was higher in forested than in non-forested sites in both improved grasslands ($t = -2.6$, df $= 7$, $P = 0.035$) and peatlands ($t = -2.6$, df $= 7$, $P = 0.035$), however, there was no significant difference between forested and non-forested sites in wet grasslands (Table 2). Ground vegetation cover was higher in forested sites than in non-forested sites in peatlands ($t = -3.6$, df $= 7$, $P = 0.009$) and improved grasslands ($z = 2.1$, $P = 0.036$). Compared to non-forested sites, deciduous tree height was greater in forested than in non-forested peatlands ($t = -3.7$, df $= 7$, $P = 0.008$), but lower in forested than non-forested sites in improved grassland and wet grassland ($t = 2.7$, df $= 7$, $P = 0.031$ and $t = 2.5$, df $= 7$, $P = 0.043$, respectively, Table 4).

Bird community structure in non-forested and forested sites

Overall, the bird communities of non-forested sites were more variable than those of forested sites, as indicated by the larger ordination space occupied by non-forested sites in the NMDS ordination (Fig. 3). This was particularly the case for improved grassland and

Table 3 Explanatory variable parameter estimates, standard errors (SE) and significance values (*P*) of each of the top models, and the relative variable importance (RVI) from the model averaging, demonstrating the responses to afforestation in improved grassland (IG) reference category), wet grassland (WG) and peatland (PL) habitat types of total bird density and species richness, BOCC density and BOCC species richness

Explanatory variable	Total Bird density			Total species richness			BOCC density			BOCC species richness		
	Estimate (± SE)	*P*	RVI	Estimate (± SE)	*P*	RVI	Estimate (± SE)	*P*	RVI	Estimate (SE)	*P*	RVI
Intercept	5.6 (1.06)	<0.0001	–	8.18 (1.02)	<0.0001	–	-0.66 (0.14)	<0.0001	–	-0.64 (0.45)	0.17	–
Preceding land-use - WG*	−4.27 (1.09)	0.01	1	−2.88 (1.1)	0.02	0.4	–	–	0.46	0.24 (0.4)	0.55	0.84
Preceding land-use—PL	−5.25 (1.37)	0.059	1	3.97 (1.46)	0.01	0.4	–	–	0.46	0.35 (0.49)	0.48	0.84
Conifer cover	–	–	0.05	–	–	0.62	0.03 (0.01)	0.0006	0.88	0.04 (0.02)	0.025	0.76
Conifer height	–	–	0.06	–	–	0.07	–	–	0.07	–	–	0.11
Deciduous cover	-0.26 (0.21)	0.047	0.31	-0.32 (0.13)	0.019	0.38	–	–	0.20	–	–	–
Deciduous height	1.26 (0.45)	0.01	0.68	1.98 (0.46)	0.0003	1	−0.08 (0.04)	0.07	0.37	–	–	–
Shrub cover	0.16 (0.08)	0.06	0.31	–	–	0.1	0.03 (0.01)	0.016	0.82	0.13 (0.13)	0.003	0.89
Shrub × WG	–	–	–	–	–	–	–	–	–	−0.13 (0.07)	0.09	0.73
Shrub × PL	–	–	–	–	–	–	–	–	–	−0.19 (0.06)	0.003	0.73
Ground Cover	–	–	0.18	−0.15 (0.06)	0.016	0.66	–	–	0.18	–	–	0.11
Ground × WG	–	–	0.15	–	–	0.05	–	–	0.12	–	–	0.11
Ground × PL	–	–	0.15	–	–	0.05	–	–	0.12	–	–	0.11

*Improved grassland was the reference category

Table 4 Cover (%) and height (m) (mean ± SE) of vegetation variables recorded at non-forested and forested Improved Grassland, Wet Grassland and Peatland sites

Parameter	Improved grassland		Wet grassland		Peatland	
	Non-forested (n = 8)	Forested (n = 8)	Non-forested (n = 8)	Forested (n = 8)	Non-forested (n = 8)	Forested (n = 8)
Conifer cover (%)	2.81 (2.81)	24.10 (6.79)	0.38 (0.38)	17.30 (2.17)	0.0 (0.0)	11.60 (2.10)
Conifer height (m)	0.13 (0.13)	2.73 (0.46)	0.15 (0.15)	2.40 (0.24)	0.0 (0.0)	1.75 (0.12)
Deciduous cover (%)	1.08 (0.39)	2.19 (0.98)	3.18 (2.10)	2.55 (1.19)	0.07 (0.05)	1.32 (0.41)
Deciduous height (m)	3.18 (0.44)	1.85 (0.52)	3.90 (0.40)	2.78 (0.57)	0.06 (0.04)	0.70 (0.18)
Shrub cover (%)	1.15 (0.59)	6.61 (2.81)	2.79 (1.10)	5.59 (1.75)	3.86 (1.55)	9.85 (2.32)
Ground cover (%)	97.6 (0.83)	93.00 (2.34)	94.7 (2.18)	94.8 (0.99)	89.8 (4.20)	94.40 (1.45)

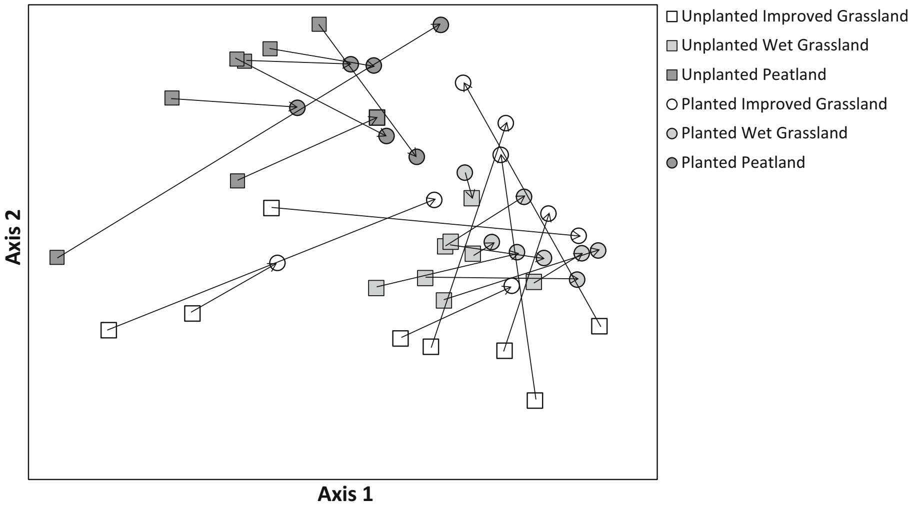

Fig. 3 NMDS ordination plot of bird densities. *Arrows* connect paired sites. Final stress from two-dimensional solution = 16.8, final instability = 0.00049. Axes 1 and 2 explain 22 and 48 % of the variation, respectively

peatland sites, with non-forested wet grassland sites occupying similar ordination space as afforested wet grassland sites. There was a significant reduction in the beta diversity of afforested sites compared to non-forested sites ($F_{1,46} = 9.2$, $P = 0.004$), with the average distance of non-forested sites from the median centre point of overall community variation being substantially higher in non-forested (0.45) than forested (0.32) sites.

When the responses of bird assemblages to afforestation were modelled, and vegetation response included in this analysis, forward selection procedures identified preceding land-use ($R^2adj = 0.073$; $P < 0.001$), shrub cover ($R^2adj = 0.039$; $P = 0.011$), and deciduous tree height ($R^2adj = 0.032$; $P = 0.012$), but not geographical location, as being significantly related to intra-pair site responses in bird community structure. These three variables accounted for 14.4 % of the observed variation in the response of bird community structure to afforestation.

Discussion

Broadly speaking, afforestation had a positive effect on bird diversity when improved grassland sites (intensively managed) were planted, relatively little impact where wet grassland sites (intermediate management intensity) were planted and a negative impact where peatland sites (low management intensity) were planted. In all three habitat types, there was an increase in total bird density and diversity following afforestation. Similarly previous studies have demonstrated little impact of pine afforestation on open farmland bird species (Sánchez-Oliver et al. 2014). However, a more appropriate assessment of the effects of this land-use change on bird conservation can be derived from comparisons of the impacts on species of conservation concern (Cousins et al. 2015). In this study, both the density and the species richness of bird species of conservation concern (BOCC) increased following afforestation of improved grassland sites, while their density decreased following afforestation of peatland sites. Although several reviews and meta-analyses have suggested that the impacts of land-use change on biodiversity may depend on the preceding land-use (Brockerhoff et al. 2008; Bremer and Farley 2010; Felton et al. 2010), this is the first study to directly address this issue using a paired and replicated study design.

The findings of this study support the view that plantation forests can, in some contexts, offer opportunities for bird diversity conservation (Humphrey et al. 2000; Brockerhoff et al. 2005, 2008; Lindenmayer et al. 2008; Quine and Humphrey 2010) particularly when they replace habitats with low bird diversity (Brockerhoff et al. 2008). This is particularly important in landscapes where natural forest cover is low, either naturally or as a consequence of deforestation, and plantation forest cover is increasing. The intensive management of improved grassland sites results in little or no complex vegetation structure other than hedgerows (Wilson et al. 2012). The development of shrub cover at these sites by the release from grazing pressure following afforestation, along with the cover provided by the young conifer trees themselves, boosts structural complexity, which increases the suitability of these sites for a wide range of species (Sweeney et al. 2010b; Wilson et al. 2010). In this way young plantation forests have the potential to enhance bird diversity in intensively managed agricultural landscapes.

By contrast, non-forested peatland sites tend to have low bird diversity, but many of thes birds present are BOCC species (Lynas et al. 2007; Grant and Pearce-Higgins 2012). Although just one species of BOCC, skylark (*Alauda arvensis*), was actually recorded in non-forested peatland sites, BOCC species are typically rare. A number of BOCC species were recorded in this study, though their numbers were too low for inclusion in statistical analysis. These were curlew (*Numenius arquata*), which is near-threatened globally and red-listed in moorland and upland farmland habitats, and red-listed in Ireland and Britain, wheatear (*Oenanthe oenanthe*) an amber-listed moorland species, and woodcock (*Scolopax rusticola*) a red-listed forest species. BOCC species in peatland habitat not recorded during this study included merlin (*Falco columbarius*), hen harrier (*Circus cyaneus*) and short-eared owl (*Asio flammeus*), which are amber-listed, golden plover (*Pluvialis apricaria*), dunlin (*Calidris alpine*) and red grouse (*Lagopus lagopus scoticus*) which are red-listed. BOCC species in wet grassland habitat not recorded in this study included lapwing and redshank both of which are red-listed. The negative impact of afforestation recorded in this study, may be somewhat underestimated as a result of rare species (such as Merlin and Golden Plover) being entirely absent from our dataset. So, although afforestation can make peatlands more attractive to many bird species, through increased structural complexity, this may come at the expense of rarer, habitat specialist species of high conservation value. In the UK (Wallace and Good 1995), mainland Europe (Andrés and Ojeda 2002) and North America (Lachance et al. 2005), afforestation of peatlands and other open habitats managed at low intensity is reported to diminish biodiversity at local and regional scales.

The relatively small impact of afforestation on bird diversity in wet grassland sites was likely due to the low intensity of management of the preceding land-use which means that these sites support structurally complex hedgerows and shrub-rich areas (Wilson et al. 2012). These residual habitats can have a disproportionate influence on the bird assemblages of farmland-dominated landscapes, relative to the area that they occupy (Berg 2002). The replacement of wet grasslands with young conifer plantations consequently had a relatively small effect on the habitat available for birds. Therefore, the observed impact of afforestation on bird diversity is dependent not only on the habitat it provides but crucially, on the habitat that is being replaced.

The selection of sites for forest planting involves trade-offs between physical land characteristics, economic considerations and agricultural and environmental policies (Upton et al. 2014). In many cases economic considerations and biodiversity objectives are not well aligned, and this conflict can have consequences for afforestation practices (Thomas et al. 2015). Where private net benefits of land use change do not occur, land use change can be encouraged through the use of additional incentives to promote forest planting in areas which offer maximum gains for biodiversity. The findings of the current study clearly demonstrate that the greatest net gains in bird diversity are achieved in the most intensively managed habitats in this study, where the bird diversity of the preceding land use is lowest. In this case the selection of improved grassland for afforestation offers the greatest potential for bird diversity gains and biodiversity benefits of the new forests. Further study into the future can evaluate how these benefits evolve over time through the forest cycle as the trees mature.

A number of authors have suggested that afforestation of degraded or intensively managed habitats may offer biodiversity benefits, however, meta-analyses have shown that this does not always hold true (Brockerhoff et al. 2008; Bremer and Farley 2010; Felton et al. 2010). The former can support considerable biodiversity (Öckinger et al. 2006; Sirami et al. 2008), and would be likely to be negatively impacted by afforestation. Also, although meta-analyses are effective in assessing general trends among diverse datasets (Gurevitch and Hedges 1999), variation in methodological approaches and under-reporting of methods in the primary studies can make the results of meta-analyses somewhat difficult to interpret (Felton et al. 2010).

This study considered impacts of afforestation on bird communities 5 years after tree-planting only. However, the bird assemblages of plantation forests have been shown to typically continue to change for decades after they are planted, particularly following canopy closure (Wilson et al. 2006; Lindenmayer et al. 2008; Sweeney et al. 2010b). Young forests, such as those described in this study, provide important breeding sites for shrub dependent species, and are likely to continue to do so across subsequent forest rotations (Sweeney et al. 2010b; Wilson et al. 2010). Afforestation over large temporal and spatial scales would result in a proportion of afforested land being continually in a similar state of biodiversity value to the one described in the present study.

Due to extensive deforestation, forest cover in Ireland was below 1 % at the beginning of the twentieth century (Mitchell 2000). For this reason, and because of Ireland's geographical location at the western edge of Europe, Ireland lacks many forest specialist bird species (Fuller et al. 2007). As forest plantations mature and their canopies close, there is a decline in open and shrub habitat specialist birds (Wilson et al. 2006; Sweeney et al. 2010b). The limited number of forest specialist birds in Ireland means that the bird communities of mature plantation forests are unlikely to include BOCC. Rather, they will be dominated by a limited number of generalist species that are relatively common in other widely-available habitat types (Wilson et al. 2006; Sweeney et al. 2010b). These common, open habitat species, and those capable of inhabiting planted forests, are the bird species typically supported by plantation forests (Lindenmayer et al. 2008; Carrascal et al. 2014; Sánchez-Oliver et al. 2014). Particularly in sites that previously supported a range of open habitat specialists, this will result in a loss of alpha diversity (species diversity within afforested sites), beta diversity (variation between sites), and gamma diversity (diversity within all sites, Whittaker 1972). A study of bird diversity responses to *Pinus radiata* plantation on former agricultural pasture demonstrated that bird species associated with open and woodland habitats were disadvantaged by forest planting (Lindenmayer et al. 2008). However, in lowland landscapes dominated by intensive agriculture, plantations established in habitats such as improved grassland may have a positive effect on bird diversity even as they age, as several of the birds they support are much more abundant in forest than in intensively managed pasture farmland.

In deforested regions with more forest specialist species, there may be greater potential for afforestation to positively affect biodiversity. Many studies have highlighted the use of plantations by BOCC species (Humphrey et al. 2000; Lynas et al. 2007). However, many forest species of conservation concern have relatively specialised habitat requirements, which may or may not be met by the tree species composition and management of commercial plantations. The impact of afforestation on biodiversity is therefore dependent, at least in part, on the species pool that is available for colonisation of the newly created forest habitats. Recognition of the requirements of the potential colonists of plantations in landscapes where the level of forest cover is low, and native forest cover is rare or absent, is important in the selection of sites and plantation types when planning for afforestation. In this regard the siting of new forest plantations within a matrix that includes old woodlands may be an important consideration (Sisk et al. 1997; Brotons et al. 2003).

Conclusions

The findings of this study provide evidence for the benefits of forest planting in intensively managed agricultural habitats, and demonstrate that planted, non-native, conifer forests can, in some contexts, offer opportunities for bird conservation. The responses of biodiversity to afforestation are complex, and these findings are relevant only for bird species. They demonstrate the importance of site history on the consequences of land-use change for bird diversity, and highlights the importance of considering preceding habitat type in the selection of sites for afforestation. The impact of afforestation on bird communities in this study was largely determined by the bird diversity at the site before planting. The bird species assemblages of intensively managed habitats are more likely to be enhanced by conversion to forest than those of less intensively managed habitats. Sustainable forest management must therefore address the trade-off between the bird diversity of newly forested sites and that of the previous land-use. Hence forest management should encourage any proposed future exotic plantations to be located in areas of high management intensity such as improved agricultural land rather than in low management intensity peatlands that typically support bird communities of high conservation value. In practice the conservation of marginal farmland habitats will rely on trade-offs between forestry and agriculture and the optimisation of the spatial allocation of afforestation for economic considerations and environmental policies. This study focussed on the early impacts of afforestation and examined forests 5 years after afforestation. The consequences for bird diversity of a land-use change such as afforestation will continue to develop over time and persist through subsequent forest rotations. The findings of this study provide evidence that it is possible to increase the potential for plantation forests to protect and enhance bird communities at a landscape scale by ensuring that afforestation is planned and managed appropriately.

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