Bird Study (2010) **57,** 483–494

The influence of a native tree species mix component on bird communities in non-native coniferous plantations in Ireland

OISÍN F. MCD. SWEENEY[1], MARK W. WILSON[1], SANDRA IRWIN[1], THOMAS C. KELLY[1] and JOHN O'HALLORAN[1,2]*

[1]*PLANFORBIO Programme, Department of Zoology, Ecology and Plant Science, University College Cork, Distillery Fields, North Mall, Cork, Ireland and* [2]*Environmental Research Institute, University College Cork, Cork, Ireland*

Capsule Norway Spruce plantations with Scots Pine as a secondary tree species had higher bird densities than pure Norway Spruce. Shrub cover was the most important structural variable, influencing bird density, species richness and Simpson's diversity.

Aims To investigate whether incorporating a native tree component into non-native coniferous plantations had any effect on bird communities or vegetation structure.

Methods Birds were surveyed in plantations of Norway Spruce mixed with Oak and Scots Pine, each paired with a plantation of pure Norway Spruce. DISTANCE was used to generate bird densities. Bird density, species richness and Simpson's diversity were compared between each mix type and pure Norway Spruce. GLMs were used to investigate relationships between structural components of plantations and bird data.

Results Bird communities of mixed plantations differed only slightly in their composition from pure Norway Spruce. Bird density was significantly higher in Scots Pine mixes than in Oak mixes or pure Norway Spruce. Neither species richness nor Simpson's diversity differed significantly between the plantation types. Some vegetation components differed between the plantations and shrub cover was positively associated with bird density, species richness and Simpson's diversity. The presence of rides also increased bird density.

Conclusions There is a positive effect on bird communities of including a native tree species in non-native coniferous plantations, but the magnitude of the effect is small. The influence of shrub cover on birds suggests that forest management may play an important role in determining the utility of plantations for birds. We recommend the establishment of mixed tree species plantations where possible, although, in the case of Oak mixes, the Norway Spruce appeared to suppress growth of the Oak and thus may be restricting its effect on birds. Changes in management, such as planting Oaks in clumps or heavier thinning of the coniferous component, could address this problem.

INTRODUCTION

Plantation forests are increasing in Europe (Food and Agriculture Organization 2007), while populations of woodland birds are declining across the continent (Fuller *et al*. 2005, Gregory *et al*. 2007), although trends vary between regions (Pan-European Common Bird Monitoring Scheme 2009). This situation demands that the contribution of plantations to bird conservation be maximised. In Ireland, plantation forests account for approximately 10% of total land cover and over 90% of total forest cover, which is the highest proportion of forest cover in any EU nation except Malta (Ministerial Conference on the Protection of Forests in Europe 2007). Almost 75% of these plantations comprise non-native conifers, of which Sitka Spruce *Picea sitchensis* is the most commonly planted species. In contrast, native forests account for only about 1% of total land cover (Forest

*Correspondence author. Email: j.ohalloran@ucc.ie

Service 2007). Plantation forests are therefore an extensive potential bird habitat, and their value for bird conservation requires investigation in this context.

Bird communities change throughout the plantation forest cycle and by the time commercial maturity (about 50 years) is reached the bird community in Irish plantations is dominated by a small number of species (Wilson *et al.* 2006). This suggests that plantations could be improved to benefit a wider range of bird species. Introducing native tree species as a minority component of a non-native coniferous plantation is one silvicultural technique by which plantations may potentially be improved for the benefit of biodiversity (Kerr 1999). However, there is relatively little published research addressing biodiversity in mixed species forestry. Mixed species silviculture is often practiced to maximise crop production through, for example, complementary resource use (Hartley 2002, Kelty 2006) and not through consideration of biodiversity requirements.

Using a native tree species as a secondary mix species in a non-native coniferous plantation may mimic a more natural system (Ratcliffe & Peterken 1995) and permit bird species that prefer both the primary and secondary plantation tree species to utilise the plantation (Gjerde & Saetersdal 1997, Diaz 2006). Food availability for birds may increase with the addition of a native tree species (Hartley 2002), as the number of invertebrate species that a tree hosts may be related to the length of time the tree has been present in a region (Birks 1980, Kennedy & Southwood 1984). Also, bird communities are influenced by vegetation structure (Fuller *et al.* 2007, Nikolov 2009) and structural components of a forest such as shrubs and graminoids are associated with canopy openness (Smith *et al.* 2008). Native tree species that allow more light penetration may, therefore, increase understory vegetation cover, which may in turn provide more nest-sites and food sources for birds (Quine *et al.* 2007). The additional tree species itself and the secondary effect that the mix of tree species has on forest understorey vegetation structure may therefore both influence bird communities.

The presence of non-crop broadleaf trees in a coniferous plantation has been shown to increase bird diversity and species richness, and to be utilised by the less common species in plantations (Bibby *et al.* 1989, O'Halloran *et al.* 1998, Wilson *et al.* 2010). Mixed plantations of broadleaves and conifers possess bird communities intermediate between those of pure broadleaved plantations and pure coniferous plantations (Donald *et al.* 1998). Species richness does not differ systematically between mixed plantations and pure plantations of either broadleaved or coniferous trees (Bibby *et al.* 1989, Donald *et al.* 1998, Archaux & Bakkaus 2007), but in managed boreal forests, bird species richness is positively associated with the presence of mixed stands (Jansson & Andren 2003). Similarly, in naturally occurring Mediterranean forests, mixed stands of Oak and Pine have higher bird species richness than pure Pine stands, owing to the occurrence of both Oak and Pine avifauna (Diaz 2006). In Irish Yew *Taxus baccata* forests, the presence of Oak *Quercus petraea* affects the distribution of birds throughout a stand and most bird species utilise either clearings or Oak in preference to uniform areas of yew (Carruthers & Gosler 1994).

The present study aimed to test whether the bird communities of mixed plantations differed from those of monocultures by comparing two types of mixed plantation paired with structurally similar monocultures in close geographical proximity. The study investigated the importance of structural features of plantations, as well as tree species composition, to birds. The results of this study will help inform forest management in the future. In particular, a number of questions were asked:

1. Are there differences between the bird communities of pure and mixed plantation forests?
2. Do vegetation and structural components differ between mixed and pure plantations, and what vegetation components are most important to birds in plantations?
3. Do the two native secondary mix tree species investigated have appreciably different influences on bird communities?
4. Which bird species, if any, show the greatest differences in population density between pure and mixed stands?

METHODS

Site selection

After initial exploration of a forest database to determine what types of mixed plantations existed in the landscape, Norway Spruce *Picea abies* was chosen as the primary plantation tree. Sitka Spruce would have been preferable because of its importance in the plantation forest estate in Ireland, but suitable mixed plantations were not available. Oak *Quercus* spp. and Scots Pine *Pinus sylvestris* were chosen as the secondary mix species. Plantations containing both Norway Spruce and either Oak or Scots Pine are referred to as 'mixes'. Five Oak mixes and five Scots Pine mixes were identified, each with a matching stand of pure Norway Spruce, resulting in 20 forests in total to be studied. In all study sites, the secondary mix species accounted for between 20 and 40% of the crop trees and was intimately mixed with the primary tree species (i.e. not clumped, but distributed more or less evenly throughout the stand). All forests were mature plantations of a similar age.

ARCGIS version 9.2 and a forestry database were used to select both pure and mixed plantation forests. To minimize site effects, mixed and pure paired forests were located as close to each other as possible. Most paired forests were within 5−10 km of each other, but in one instance this was not possible owing to a lack of suitable plantations, and the mix and pure forests were located approximately 50 km apart (Fig. 1). Following the selection procedure, forests were ground-truthed to check that stem density was similar between the mixed and pure plantations so that any differences detected between members of a pair could be primarily attributed to the mix component, rather than to differences in thinning intensity.

Bird surveys

Point counts (Bibby *et al.* 2000) were used to survey bird communities in all forests during the 2008 breeding season, and the same observer conducted all counts. Points had a radius of 50 m and were randomly placed on both the edge and interior of each forest, a minimum of 100 m apart. Where possible, six point counts were placed in each forest to ensure reliable density estimates and to standardise survey effort. However, two forests were too small to contain six points, so one received four and the other five. Species accumulation curves were constructed for each forest type in ESTIMATE S (Colwell 2006) and used to ensure that the lower survey effort in these two forests did not bias species richness estimation. Because some points were located close to the forest edge, and because some sites contained fewer points, the total area surveyed in the different forest types was not identical. However, the proportional difference was only 5% in terms of area sampled per site type and is, therefore, unlikely to have biased results.

Counts lasted for ten minutes, during which time all the birds seen and heard within 50 m of the observer were recorded. Distances were measured with a rangefinder where possible. Each site was visited twice, the first early in the breeding season (April–May) and the second later (May–July), an approach that is superior to a single count when censusing birds (Drapeau *et al.* 1999). Because this study was part of a larger project, there were a large number of forests to be surveyed and it was necessary to survey in both the morning and afternoon. Therefore, either the early or late visit was conducted in the morning and the other in the afternoon (i.e. each forest received both a morning and afternoon count). This approach has been used successfully to compare bird communities of different forest types (Wilson *et al.* 2006). Densities of all species were calculated for the early and late counts and the maximum of these two values was used as the density of a species.

Bird communities

Species and individuals detected in flight, and individuals of the Hirundinidae, Motacilliadae or Corvidae (with the exception of Jay *Garrulus glandarius*) were not used in the analyses as their presence in a forest could not be assumed to be evidence of breeding.

Bird communities were analysed in respect of population density, species richness and mean inverse Simpson's diversity (Simpson's diversity). ESTIMATE S (Colwell 2006) was used to resample the data randomly 500 times to generate a mean Simpson's diversity for every site to ensure that there was no effect of sample order on the index. Species richness was calculated as the cumulative number of species recorded over two visits. DISTANCE (Thomas *et al.* 2006) was used to convert field observations to bird densities. Because differences in detectability between species can bias density estimations if not accounted for (Alldredge *et al.* 2007), each species was allocated to one of four species detection groups (Table 1) that contained species which could be modelled using a single detection function. Species were allocated to groups depending on their method of detection, the distribution of detections in five distance bands (0–10 m; 11–20 m; 21–30 m; 31–40 m; and 41–50 m) and knowledge of the species' ecology. Species in these groups were then analysed together, and their detectability assumed to be similar. Because habitat may also affect the detectability of birds (Schieck 1997), cluster analysis was carried out in PC-ORD (McCune & Mefford 2006) using the vegetation data collected in each forest, and each study site was allocated to one of three habitat groups for

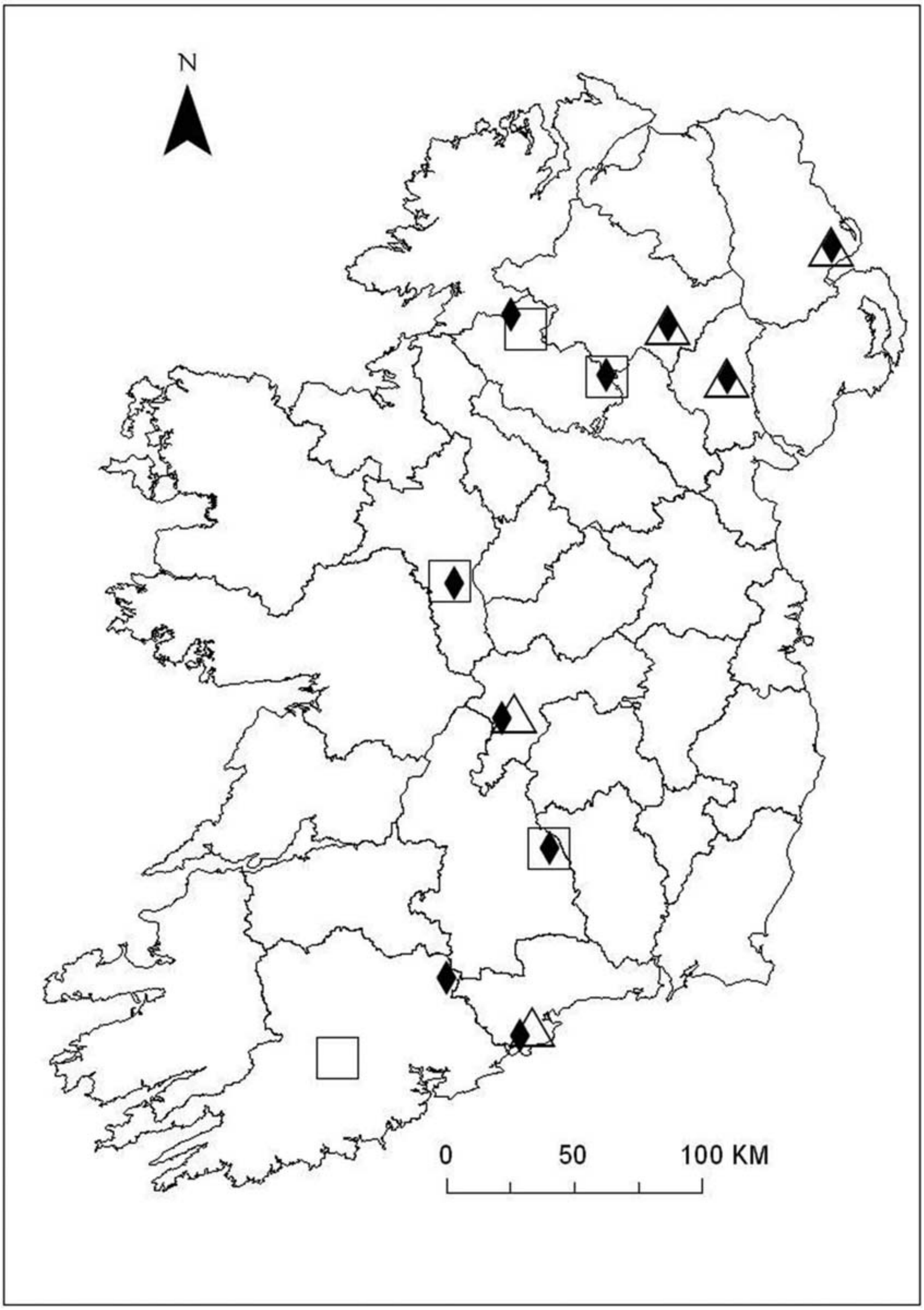

Figure 1. Map of Ireland showing study sites. ♦, pure Norway Spruce plantation; △, Norway Spruce and Oak mixed plantation; □, Norway Spruce and Scots Pine mixed plantation.

Table 1. Species detected in pure Norway Spruce (Pure NS); Norway Spruce and Oak mixed plantations (NS:O); and Norway Spruce and Scots Pine mixed plantations (NS:SP), the detection group to which each was assigned and their mean population density (No. ha^{-1} ± se). Also shown is the mean bird density for each forest type.

Species	Detection group	Scientific name	Pure NS	NS:O	NS:SP
Blackbird	1	*Turdus merula*	1.39 ± 0.34	1.14 ± 0.39	2.85 ± 0.99
Blackcap	1	*Sylvia atricapilla*	0.52 ± 0.15	0.49 ± 0.23	1.6 ± 0.62
Blue Tit	4	*Cyanistes caeruleus*	1.23 ± 0.44	4.96 ± 1.61	3.46 ± 1.82
Bullfinch	2	*Pyrrhula pyrrhula*	0.27 ± 0.18	0.28 ± 0.28	0.54 ± 0.35
Chaffinch	3	*Fringilla coelebs*	3.78 ± 0.33	4.06 ± 0.93	4.46 ± 0.60
Chiffchaff	1	*Phylloscopus collybita*	0.23 ± 0.11	0.32 ± 0.14	0.97 ± 0.56
Coal Tit	4	*Periparus ater*	19.19 ± 2.05	14.93 ± 2.58	22.82 ± 3.89
Crossbill	3	*Loxia curvirostra*	0.06 ± 0.06	0	0
Dunnock	2	*Prunella modularis*	1.05 ± 0.50	1.40 ± 0.59	2.14 ± 0.98
Garden Warbler	1	*Sylvia borin*	0.03 ± 0.03	0	0
Goldcrest	4	*Regulus regulus*	19.53 ± 1.56	16.93 ± 3.46	19.51 ± 1.84
Great Tit	3	*Parus major*	0.43 ± 0.31	0.58 ± 0.27	0.45 ± 0.26
Jay	2	*Garrulus glandarius*	1.00 ± 0.52	1.31 ± 0.77	0.74 ± 0.54
Long-tailed Tit	4	*Aegithalos caudatus*	1.27 ± 0.42	1.33 ± 0.06	1.39 ± 0.85
Mistle Thrush	1	*Turdus viscivorus*	0.44 ± 0.17	0.40 ± 0.19	0.67 ± 0.26
Pheasant	1	*Phasianus colchicus*	0	0	0.19 ± 0.12
Robin	2	*Erithacus rubecula*	4.94 ± 0.76	8.14 ± 1.91	8.53 ± 1.19
Siskin	3	*Carduelis spinus*	0.03 ± 0.03	0.06 ± 0.06	0.09 ± 0.09
Song Thrush	1	*Turdus philomelos*	0.36 ± 0.13	0.46 ± 0.33	1.68 ± 0.42
Spotted Flycatcher	2	*Muscicapa striata*	0	0	0.34 ± 0.34
Treecreeper	2	*Certhia familaris*	0.96 ± 0.27	2.51 ± 0.45	1.76 ± 0.69
Willow Warbler	1	*Phylloscopus trochilus*	0.23 ± 0.20	0.06 ± 0.06	0.21 ± 0.15
Woodcock	2	*Scolopax rusticola*	0.25 ± 0.25	0	0
Woodpigeon	1	*Columba palumbus*	1.29 ± 0.21	1.08 ± 0.42	2.92 ± 0.97
Wren	1	*Troglodytes troglodytes*	2.79 ± 0.62	3.15 ± 0.58	4.91 ± 1.16
Mean bird density			61.26 ± 2.79	63.58 ± 5.82	82.22 ± 5.88

subsequent analysis in DISTANCE. Four models were used for fitting of the detection function and AIC was used to select the best model for fitting of the detection function. These were: Uniform + Cosine; Uniform + Polynomial; Half normal + Hermite; and Hazard-rate + Cosine (Buckland *et al.* 2001).

Vegetation and structure

Percentage cover of vegetation in a 30-m radius from each bird survey point was estimated for several structural variables. These included: canopy cover; understorey cover (woody vegetation >2 m tall, but lower than the tree canopy); shrub cover (woody vegetation <2 m tall); field cover (non-woody vegetation) and ground cover (mosses and liverworts). The mean of these variables across all bird survey points was taken as the site mean.

Three 10 × 10-m vegetation plots, independent of the bird survey points, were also placed in each forest. We included three measured variables from these vegetation plots in our analysis that could potentially influence bird communities: mean dbh of all crop trees; tree basal area (m^2 per 10 × 10 plot) and the number of stems in the plot (including non-crop trees >2 m tall and >5 cm dbh).

As well as these vegetation variables, a measure of canopy openness derived from fish-eye lens photographs (expressed as a percentage) was included in the models to account for potential variation in canopy cover owing to management. A factor stating whether the forest was a mixed or pure plantation was also included in the models to investigate whether differences were due to site type *per se*. The proportion of a stand that was composed of open spaces was included, as was a factor indicating the presence or absence of rides. Rides and open space were identified using aerial photographs. We used a factor for rides because the coarse scale of the photographs made accurate measurement of ride length unreliable. Models were run with Scots Pine mixes as the baseline, so significant relationships between the response variables and the site type factors indicate differences between Scots Pine mixes and the other forest types. The mean values and ranges of all vegetation and structural variables in each forest type are shown in Table 2.

Table 2. Range and mean ± se of vegetation and structural variables in pure Norway Spruce (pure NS); Norway Spruce and Oak mixed plantations (NS:O) and Norway Spruce and Scots Pine mixed plantations (NS:SP).

	Canopy cover (%)	Understorey cover (%)	Shrub cover (%)	Field cover (%)	Ground cover (%)	dbh (cm)	Basal area (m^2)	No. stems	Proportion open space	Canopy openness (%)
Range pure NS	47.33–81.25	2.42–11.25	1.83–67.87	6.25–39.00	14.75–53.75	22.00–39.74	0.42–0.68	5.33–19.67	0.02–0.21	3.28–12.82
Mean pure NS	65.67 ± 10.81	5.95 ± 0.92	29.59 ± 7.81	18.47 ± 3.96	35.16 ± 4.60	28.60 ± 1.93	0.58 ± 0.04	9.80 ± 1.46	0.07 ± 0.02	6.22 ± 1.14
Range NS:O	55.42–66.67	5.83–22.33	12.42–61.47	2.42–30.08	20.00–55.00	22.96–33.58	0.35–0.64	6.00–11.33	0.01–0.13	2.44–5.44
Mean NS:O	59.75 ± 1.93	14.53 ± 2.78	36.55 ± 8.88	15.22 ± 4.82	34.07 ± 7.29	28.23 ± 2.14	0.53 ± 0.05	7.53 ± 0.97	0.05 ± 0.02	4.36 ± 0.67
Range NS:SP	51.25–74.50	1.67–20.08	3.50–91.83	3.08–37.20	15.92–77.50	17.30–32.66	0.44–0.66	6.00–17.00	0–0.03	5.08–11.81
Mean NS:SP	59.57 ± 9.01	10.64 ± 3.64	47.88 ± 17.87	15.49 ± 5.82	48.60 ± 10.28	25.76 ± 2.75	0.51 ± 0.05	11.07 ± 2.10	0.01 ± 0.01	7.96 ± 1.17
Significant differences	None	NS:SP & NS:O > Pure NS	NS:SP > NS:O; NS:O > Pure NS	None	NS:SP > NS:O & Pure NS	None	None	None	None	NS:SP > NS:O

Significant differences between the forests are noted, test statistics and *P*-values are given in the text.

Data analysis

Non-metric multidimensional scaling (NMS) was used to categorise the bird communities of the different forest types. This was performed in PC-ORD (McCune & Mefford 2006) using random starting coordinates and a Sørenson distance measure and by carrying out 250 runs with real data and 250 with randomised data. The step length was 0.2. All vegetation and bird data were checked for normality, homogeneity and outliers using BRODGAR (Highland Statistics Ltd, Aberdeenshire, UK), and transformations were applied where necessary.

GLM assuming Poisson distributions, were used to investigate relationships between bird metrics and vegetation. Forwards and backwards selection was used to select a model start point using minimum AIC. Models were then re-run dropping the least significant explanatory variable until all remaining variables were significant. Poisson GLM was also used to investigate whether vegetation and structural variables differed between the forest types. In this instance, forest type was the single explanatory variable and each structural variable in turn the response variable. Analyses were carried out using BRODGAR (Highland Statistics Ltd, Aberdeenshire, UK).

RESULTS

Density, species richness and Simpson's diversity

A total of 25 bird species were used in the analysis. Of these, 23 were detected in pure Norway Spruce, 20 in Oak mixes and 22 in Scots Pine mixes. Of the 25 species, 16 attained their highest population densities in the Scots Pine mixes, 4 in the Oak mixes and 5 in pure Norway Spruce (Table 1). Ordination revealed no clear differences between the bird communities of mixed and pure plantations. To visualise more clearly any differences between the bird communities of the different forest types, we graphically represented the proportion of the total bird density contributed by each species. Although the community structure was roughly similar between the forest types, the two most common species, Coal Tit *Periparus ater* and Goldcrest *Regulus regulus*, accounted for a slightly smaller proportion of the total bird density in both types of mixed plantations than in pure Norway Spruce (Fig. 2).

The models revealed no significant differences in either species richness or Simpson's diversity between the mixed plantations and pure Norway spruce. Total bird density was significantly higher in the Scots Pine mixes than in Oak mixes ($z = -2.33$, $P = 0.02$) or pure Norway spruce ($z = -3.16$, $P < 0.01$) (Table 3, Fig. 3).

Vegetation and birds

There was no significant difference between canopy cover, field cover, tree basal area, mean dbh, number of stems or the proportion of open space between the different forest types. Both Oak mixes ($z = 5.008$, $P < 0.01$) and Scots Pine mixes ($z = 3.019$, $P < 0.01$) had significantly higher understorey vegetation cover than pure Norway Spruce, but there was no significant difference in understorey cover between Oak mixes and Scots Pine mixes. Scots Pine mixes had significantly higher shrub cover than both Oak mixes ($z = 2.814$, $P < 0.01$) and pure Norway Spruce ($z = 5.531$, $P < 0.01$), and Oak mixes had significantly higher shrub cover than pure Norway Spruce ($z = 2.161$, $P = 0.03$). Scots Pine mixes had significantly higher ground cover than both Oak mixes ($z = 3.617$, $P < 0.01$) and pure Norway Spruce ($z = 3.954$, $P < 0.01$), but there was no significant difference between Oak mixes and pure Norway Spruce. The canopy of Scots Pine mixes had a significantly higher degree of openness than Oak mixes ($z = 2.531$, $P < 0.01$). However, there was no difference in canopy openness between Scots Pine mixes and pure Norway Spruce or between Oak mixes and pure Norway Spruce (Table 2).

The results of all models investigating the relationships between bird metrics and vegetation are summarized in Table 3. The only explanatory variable related to Simpson's diversity was shrub cover, which had a positive influence ($P = 0.019$). The explained deviance of the model was 56%. Shrub cover was also positively related to species richness ($P = 0.032$), with 57% of deviance explained. Total bird density was positively related to shrub cover ($P < 0.01$) and the presence of rides in forest stands ($P < 0.01$), and negatively related to field cover ($P < 0.01$); 87% of the variation was explained by the model in this instance.

DISCUSSION

We found no consistent differences in bird communities between mixed and pure plantations, although the trend was for both Scots Pine and Oak mixes to have higher species richness, Simpson's diversity and total bird density than pure Norway Spruce plantations. Finding mixed plantations proved to be very difficult, and the power of the study to detect differences between the sites types was restricted by the heterogeneity within site

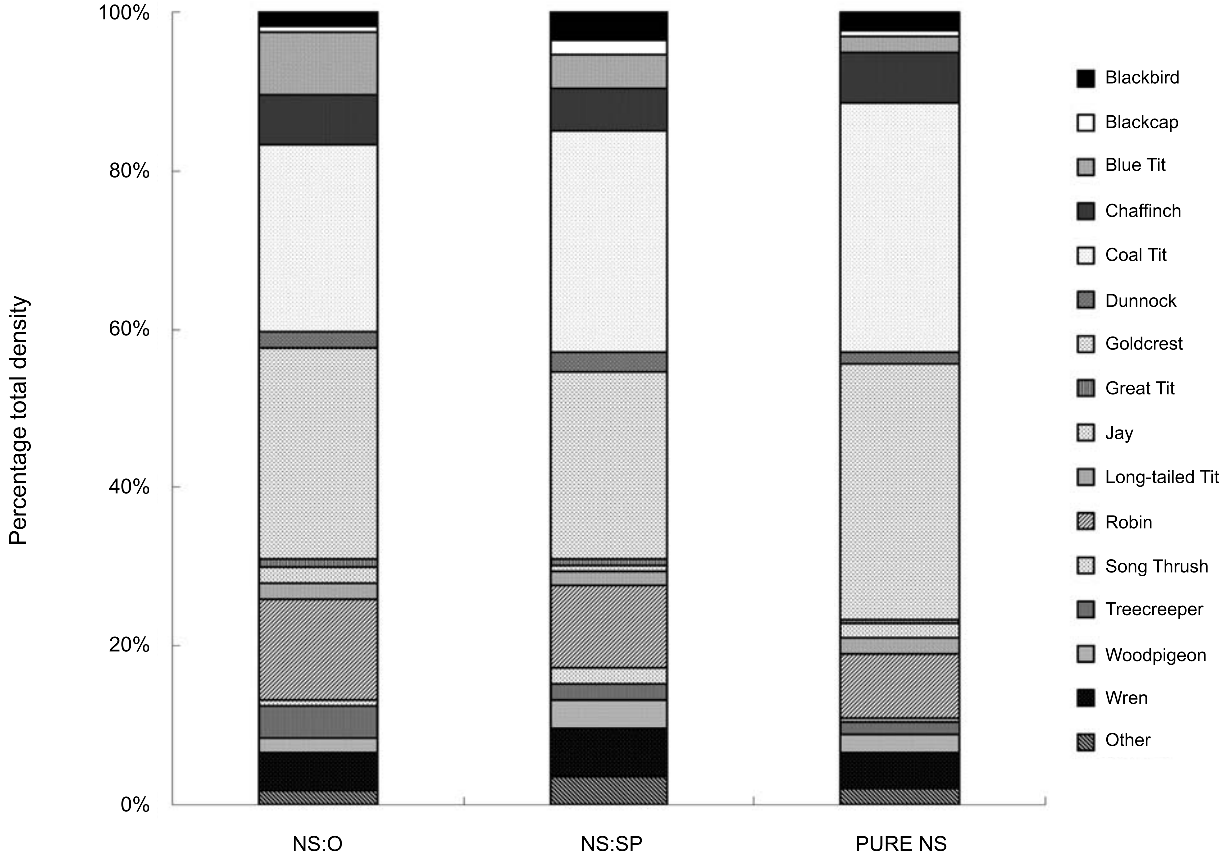

Figure 2. Stacked bar chart, using species densities, illustrating the bird communities in Norway Spruce and Oak mixed plantations (NS:O); Norway Spruce and Scots Pine mixed plantations (NS:SP) and pure Norway Spruce (PURE NS) plantation forests.

Table 3. Results of GLMs investigating relationships between Simpson's diversity, bird species richness and bird density with vegetation and structural variables in three plantation forest types.

Response variable	Null deviance	Residual deviance	Intercept	Significant explanatory variable	Estimate	*z*	*P*
Simpson's diversity	9.863	4.374	1.960	Shrub cover	0.006	2.355	0.019
Species richness	8.023	3.442	2.490	Shrub cover	0.005	2.150	0.032
Bird density	51.869	6.681	4.029	Shrub cover	0.004	3.477	<0.01
				Ride presence	0.175	2.703	<0.01
				Oak mix	−0.180	−2.328	0.020
				Pure Norway spruce	−0.213	−3.159	<0.01
				Field cover	−0.007	−2.778	<0.01

types and by the small sample size. It should also be noted that the ability to translate these findings into recommendations for future plantation forest management depends on the observed patterns in Norway Spruce being a good model for Sitka Spruce, as the latter is by some distance the most abundant plantation forest tree species in Ireland. Sitka Spruce accounts for over 50% of all plantation trees, compared with just 4% for Norway Spruce (Forest Service 2007). The composition of the bird communities of Norway and Sitka Spruce has been shown to be broadly similar (O'Halloran *et al.* 1998), and Norway Spruce may even support more bird species than Sitka Spruce, which allows less light penetration (Batten 1976). The higher species diversity in

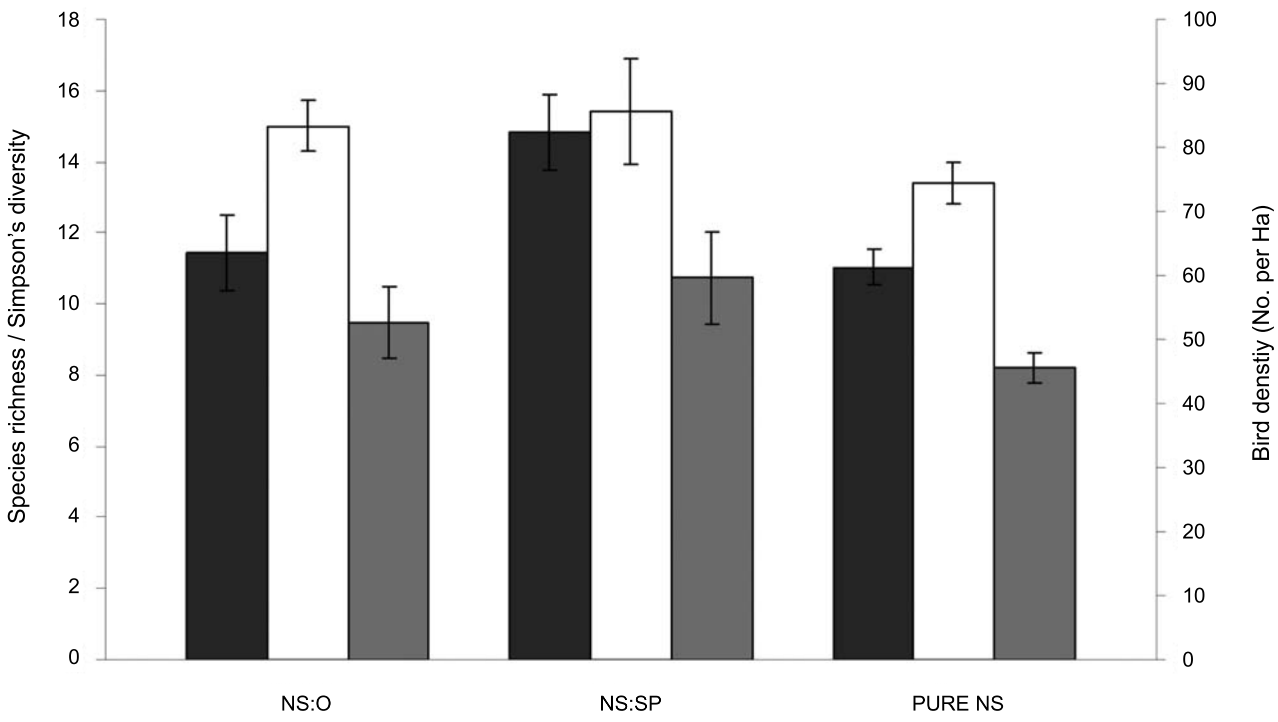

Figure 3. Total bird density (black bars), species richness (open bars) and Simpson's diversity (grey bars) (± se) in Norway Spruce and Oak mixed plantations (NS:O); Norway Spruce and Scots Pine mixed plantations (NS:SP) and pure Norway Spruce (PURE NS) plantation forests.

Norway Spruce could be a result of its status as a native species over much of Europe, where many of the bird species considered in this study are also commonly found. Sitka Spruce, in contrast, is a native of North America. The impact of a native tree mix component on bird communities may, therefore, be even more pronounced in Sitka Spruce plantations than in those composed of Norway Spruce.

The relationship between shrub cover and bird density, species richness and Simpson's diversity suggests that the ecological state of the forest, rather than the tree species *per se*, probably exerts the greatest influence on the bird communities of plantations. It is well documented that structural attributes affect populations of various bird species in forests (Quine *et al.* 2007). Shrubs provide both nesting and foraging sites for many forest breeding birds, in both native and plantation forests (Fuller 1995), and a covering of shrubs under the canopy therefore increases the carrying capacity of a stand for a wider range of birds, increasing density, species richness and diversity. The population densities of species that are highly arboreal, such as Coal Tit and Goldcrest, varied less between the forest types because shrubby vegetation is not as important to their life-histories. The presence of rides in a stand was also significantly associated with bird density. Rides act as elongated clearings in forests and, like roads and glades, allow increased light penetration and enhance non-crop plant diversity (Smith *et al.* 2007), which may in turn result in higher numbers of birds using such areas for foraging. We did not find a significant influence of the area of open space on birds, but this may be because of the fact that most forests possessed very little open space, with only a small number of stands having a large amount of open space owing to the presence of areas of windthrow or parking bays. Although it is recommended to leave some open space for biodiversity considerations (Forest Service 2000), plantations are managed primarily for timber production and therefore open space is probably minimised. It is not immediately obvious why field cover should negatively influence bird density, and this result may be because of the relationship between shrub and field cover: in forests where shrub cover was high, field cover tended to be low and *vice versa*.

Understorey vegetation, including shrub cover, is affected by light intensity, which is in turn influenced by canopy openness (Smith *et al.* 2008). Although we found no current difference in canopy openness between Scots Pine mixes and pure Norway Spruce, the greater amounts of shrub and understorey vegetation in the mixed plantations suggest that historical differences in growth rates of the crop trees may have previously allowed greater light penetration. Initially, the fact that pure Norway Spruce canopies were slightly more open than those in Oak mixes appears difficult to explain. However, this can probably be explained by sampling technique: the camera was mounted on a tripod, which was situated approximately 1 m above the ground. Therefore, understorey vegetation, which was significantly higher in Oak mixes than in pure Norway Spruce, also influenced the measure of openness.

That openness may affect non-crop vegetation, which in turn influences bird communities (Wilson *et al.* 2010), suggests that forest management has an important role to play in maximising the utility of plantations for birds, as thinning increases light transmittance through a coniferous canopy (Hale 2003). However, this runs contrary to the findings of a study in Scotland, where management in the form of thinning had little effect on breeding bird communities (Calladine *et al.* 2009). It may be that variation in thinning intensity between treatments in this study was too low to exert a strong influence on light penetration and thus understorey vegetation; a result of forest managers wishing to maximise crop tree growth for pulp production and minimise growth of competitive non-crop understorey species (J. Calladine, pers. comm.).

We controlled for the influence of management where possible by selecting forests that were structurally similar, thus indicating a similar management history. Some structural variation did exist between the paired sites, as illustrated by the ranges and mean values in Table 2 but, as neither stem density, dbh nor basal area differed significantly between the forest types, observed differences are unlikely to be driven by differences in thinning regimes.

A study of British forests has shown that mixed plantations possess bird communities intermediate between those of pure coniferous and pure broadleaved stands (Donald *et al.* 1998). This pattern was not evident in this study, where differences between the pure Norway Spruce and the mixed plantations were small. This could be partially because of the paucity of specialist woodland bird species in Ireland, which results in much of the breeding bird fauna utilising a variety of habitats, including coniferous plantations. In contrast, several woodland species that are not part of the Irish breeding bird fauna, such as Pied Flycatcher *Ficedula hypoleuca*, Nuthatch *Sitta europaea* and Great and Lesser Spotted Woodpeckers *Dendrocopos major* and *D. minor*, exhibited close associations with broadleaved stands in Britain (Donald *et al.* 1998).

Several species have been identified that occur in Irish coniferous plantations but that are more closely associated with broadleaf vegetation: Blackcap *Sylvia atricapilla*, Blue Tit *Cyanistes caeruleus*, Common Bullfinch *Pyrrhula pyrrhula*, Common Chiffchaff *Phylloscopus collybita*, Great Tit *Parus Major*, Long-tailed Tit *Aegithalos caudatus*, Eurasian Treecreeper *Certhia familiaris* and Willow Warbler *Phylloscopus trochilus* (Wilson *et al.* 2010). To this list Garden Warbler *Sylvia borin* and Spotted Flycatcher *Muscicapa striata* may be added (Fuller 1995). We found that all of these species, except Willow Warbler and Garden Warbler, achieved their highest population densities in mixed plantations, with some (e.g. Blackcap, Blue Tit and Treecreeper) two to three times as abundant in mixed plantations as they were in pure Norway Spruce. Garden Warbler was only recorded once in dense shrubs in an area of windthrow at the edge of a pure Norway Spruce plantation that was situated close to Lough Erne, the Irish breeding stronghold of the species (Herbert 1991). Bibby *et al.* (1989) suggest that one method of judging the success of conifer plantation management could be the presence of birds associated with broadleaves in such plantations. In this regard, Oak and Scots Pine mixes were superior to pure Norway Spruce. In the case of the Oak mixes the obvious explanation for the higher population densities of broadleaf associated species is the presence of broadleaf trees. However, Scots Pine is a conifer and, therefore, another mechanism is likely to explain the increase in these species in the Scots Pine mixes. Enhanced growth of non-crop vegetation owing to increased light penetration associated with a more open canopy may have resulted in the higher understorey and shrub cover that was recorded. The habitat provided by such non-crop vegetation is probably responsible for the increase in population density of broadleaf associated birds in Scots Pine mixes (Bibby *et al.* 1989; Wilson *et al.* 2010). This explanation is supported by the fact that the highest population densities of most recorded species (16 of the 25 species analysed), not just those that prefer broadleaf trees, were found in the Scots Pine mixes. Grazing also affects bird communities through altering vegetation structure (Donald *et al.* 1998; Fuller *et al.* 2007), but as no grazing animals were observed in any of the study sites, this is unlikely to have been a contributing factor to the observed differences between the forest types.

Some of the differences between the Oak and Scots Pine mixes may be because of the different growth rates of the secondary tree species. In the Scots Pine mixes the Scots Pine was a component of the canopy, while frequently in the Oak mixes the Oak acted as an understorey. It is not recommended to grow Oak and Norway Spruce in the same plantation because of the possibility of suppressing the Oak component (Joyce 2002), and this has occurred in all of our study sites. Management to encourage more vigorous growth of the Oak component, either by thinning the coniferous component or by planting Oak in clumps where individual trees are not in direct competition with the primary plantation species, may increase the utility of Oak mixes to birds. Another possible solution, which may be preferable from a commercial point of view, is to mix conifers and broadleaves at a larger scale by planting pure stands adjacent to each other (Archaux & Bakkaus 2007).

Because of the longer rotation time of Oaks, the Oak component of our study sites would be left after felling the conifers, provided they escaped damage from harvesting activities. Any subsequent rotation may, therefore, contain a secondary Oak component that is much more similar in size to the surrounding conifers. Unfortunately, few, if any, such stands currently exist in the Irish landscape and testing the potential influence of such stands on birds is, therefore, not yet possible.

Conclusions and management recommendations

We found no significant difference in species richness or Simpson's diversity between the Oak and Scots Pine mixes and pure Norway Spruce. However, Scots Pine mixes supported a higher density of birds than either Oak mixes or pure plantations. The mixes and pure Norway Spruce sites differed from one another in respect of several structural variables, of which the most important was shrub cover, which had a positive influence on bird density, species richness and Simpson's diversity. This suggests plantation managers aiming to improve the quality of forest habitat for breeding birds can do so by increasing shrub cover within their forests. Because the bird communities supported by mixes are slightly more diverse than those in monocultures, we recommend the establishment of mixed plantations (with a native tree component) where possible. In the case of Oak mixes, current management regimes do not allow effective development of the Oak component. Such plantations could be improved for birds either by more intensive thinning of the conifer component, or by planting Oaks in clumps in order to reduce shading from surrounding conifers.

ACKNOWLEDGEMENTS

This project was funded by COFORD under the National Development Plan 2007–2013. Thanks to Coillte Teoranta for access to forests and for the use of their database, and to the Forest Service of Northern Ireland for access to their forests. Foresters in both Coillte and the Forest Service were very helpful in helping to determine management history. Thanks also to Dr Linda Coote and Karen Moore for the use of their vegetation data, and to two anonymous referees, who made several comments that improved the original manuscript.

REFERENCES

Alldredge, M.W., Simons, T.R. & Pollock, K.H. 2007. Factors affecting aural detections of songbirds. *Ecol. Appl.* **17:** 948–955.

Archaux, F. & Bakkaus, N. 2007. Relative impact of stand structure, tree composition and climate on mountain bird communities. *Forest Ecol. Manag.* **247:** 72–79.

Batten, L.A. 1976. Bird communities of some Killarney woodlands. *P. Roy. Irish Acad. B* **76:** 285–313.

Bibby, C.J., Aston, N. & Bellamy, P.E. 1989. Effects of broad-leaved trees on birds of upland conifer plantations in North Wales. *Biol. Conserv.* **49:** 17–29.

Bibby, C.J., Burgess, N.D. & Hill, D.A. 2000. *Bird Census Techniques*. Academic Press, London.

Birks, H.J.B. 1980. British trees and insects: a test of the time hypothesis over the last 13,000 years. *Am. Nat.* **115:** 600.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. & Thomas, L. 2001. *Introduction to Distance Sampling: Estimating Abundance of Biological Populations.* Oxford University Press, Oxford, UK.

Calladine, J., Humphreys, E.M., Strachan, F. & Jardine, D. 2009. Forestry thinning in commercial conifer plantations has little effect on bird species richness and breeding abundance. *Bird Study* **56:** 137–141.

Carruthers, T.D. & Gosler, A.G. 1994. Distribution of breeding birds in relation to habitat in the Muckross yew wood, Killarney. *Ir. Birds* **5:** 157–164.

Colwell, R.K. 2006. *EstimateS: Statistical Estimation of Species Richness and Shared Species from Samples*, Version 7.5. University of Connecticutt, Storrs, CT.

Diaz, L. 2006. Influences of forest type and forest structure on bird communities in oak and pine woodlands in Spain. *Forest Ecol. Manag.* **223:** 54–65.

Donald, P.F., Fuller, R.J., Evans, A.D. & Gough, S.J. 1998. Effects of forest management and grazing on breeding bird

communities in plantations of broadleaved and coniferous trees in western England. *Biol. Conserv.* **85:** 183–197.
Drapeau, P., Leduc, A. & McNeil, R. 1999. Refining the use of point counts at the scale of individual points in studies of bird–habitat relationships. *J. Avian Biol.* **30:** 367–382.
Food and Agriculture Organization. 2007. *State of the World's Forests 2007*. Food and Agriculture Organisation of the United Nations, Rome, Italy.
Forest Europe. 2007. *State of Europe's forests 2007*. Available at http://www.foresteurope.org/filestore/foresteurope/Publications/pdf/state_of_europes_forests_2007.pdf (accessed 4 November 2010).
Forest Service. 2000. *Code of Best Forest Practice*. Forest Service, Johnstown Castle Estate Co. Wexford, Ireland.
Forest Service. 2007. *National Forest Inventory – Republic of Ireland*. Forest Service, Johnstown Castle Estate Co. Wexford, Ireland.
Fuller, R.J. 1995. *Bird life of Woodland and Forest*. Cambridge University Press, Cambridge, UK.
Fuller, R.J., Noble, D.G., Smith, K.W. & Vanhinsbergh, D. 2005. Recent declines in populations of woodland birds in Britain: a review of possible causes. *Brit. Birds* **98:** 116–143.
Fuller, R.J., Smith, K.W., Grice, P.V., Currie, F.A. & Quine, C.P. 2007. Habitat change and woodland birds in Britain: implications for management and future research. *Ibis* **149:** 261–268.
Gjerde, I. & Saetersdal, M. 1997. Effects on avian diversity of introducing spruce *Picea* spp. plantations in the native pine *Pinus sylvestris* forests of western Norway. *Biol. Conserv.* **79:** 241–250.
Gregory, R.D., Vorisek, P., Van Strien, A., Gmelig Meyling, A.W., Jiguet, F., Fornasari, L., Reif, J., Chylarecki, P. & Burfield, I.J. 2007. Population trends of widespread woodland birds in Europe. *Ibis* **149:** 78–97.
Hale, S.E. 2003. The effect of thinning intensity on the below-canopy light environment in a Sitka Spruce plantation. *Forest Ecol. Manag.* **179:** 341–349.
Hartley, M.J. 2002. Rationale and methods for conserving biodiversity in plantation forests. *Forest Ecol. Manag.* **155:** 81–95.
Herbert, I.J. 1991. The status and habitat of the Garden Warbler at Crom estate, Co. Fermanagh, and a review of its status in Ireland. *Ir. Birds* **4:** 369–376.
Jansson, G. & Andren, H. 2003. Habitat composition and bird diversity in managed boreal forests. *Scand. J. Forest Res.* **18:** 225–236.
Joyce, P.M. 2002. *Establishing Broadleaves. COFORD Connects, Silviculture and Forest Management*, No. 5. COFORD, Dublin, Ireland.
Kelty, M.J. 2006. The role of species mixtures in plantation forestry. *Forest Ecol. Manag.* **233:** 195–204.
Kennedy, C.E.J. & Southwood, T.R.E. 1984. The number of species of insects associated with British trees: a re-analysis. *J. Appl. Eco.l* **53:** 455–478.
Kerr, G. 1999. The use of silvicultural systems to enhance the biological diversity of plantation forests in Britain. *Forestry* **72:** 191–205.
McCune, B. & Mefford, M.J. 2006. *PC-ORD. Multivariate analysis of ecological data*. MjM Software, Gleneden Beach, OR.
Nikolov, S.C. 2009. Effect of stand age on bird communities in late-successional Macedonian pine forests in Bulgaria. *Forest Ecol. Manag.* **257:** 580–587.
O'Halloran, J., Walsh, P.M., Giller, P.S., Kelly, T.C. & Duffy, B. 1998. An assessment of avian biodiversity and opportunities for enhancement in Ireland's forests: preliminary results. *Ir. Forestry* **55:** 2–14.
Pan-European Common Bird Monitoring Scheme 2009. *The State of Europe's Common Birds 2008*. PECBMS, Prague, Czech Republic.
Quine, C.P., Fuller, R.J., Smith, K.W. & Grice, P.V. 2007. Stand management: a threat or opportunity for birds in British woodland? *Ibis* **149:** 161–174.
Ratcliffe, P.R. & Peterken, G.F. 1995. The potential for biodiversity in British upland spruce forests. *Forest Ecol. Manag.* **79:** 153–160.
Schieck, J. 1997. Biased detection of bird vocalizations affects comparisons of bird abundance among forested habitats. *Condor* **99:** 179–190.
Smith, G.F., Iremonger, S., Kelly, D.L., O'Donoghue, S. & Mitchell, F.J.G. 2007. Enhancing vegetation diversity in glades, rides and roads in plantation forests. *Biol. Conserv.* **136:** 283–294.
Smith, G., Gittings, T., Wilson, M., French, L., Oxbrough, A., O'Donoghue, S., O'Halloran, J., Kelly, D., Mitchell, F., Kelly, T., Iremonger, S., McKee, A.-M. & Giller, P. 2008. Identifying practical indicators of biodiversity for stand-level management of plantation forests. *Biodivers. Conserv.* **17:** 991–1015.
Thomas, L., Laake, J.L., Strindberg, S., Marques, F.F.C., Buckland, S.T., Borchers, D.L., Anderson, D.R., Burnham, K.P., Hedley, S.L., Pollard, J.H., Bishop, J.R.B. & Marques, T.A. 2006. *Distance 5.0*, Release 2. Research Unit for Wildlife Population Assessment, University of St. Andrews, St. Andrews, UK.
Wilson, M.W., Pithon, J., Gittings, T., Kelly, T.C., Giller, P.S. & O'Halloran, J. 2006. Effects of growth stage and tree species composition on breeding bird assemblages of plantation forests. *Bird Study* **53:** 225–236.
Wilson, M.W., Gittings, T., Kelly, T.C. & O'Halloran, J. 2010. The importance of non-crop vegetation for bird diversity in Sitka Spruce plantations in Ireland. *Bird Study* **57:** 116–120.

(MS received 25 February 2010; revised MS accepted 27 April 2010)