Biodivers Conserv (2010) 19:2329–2342
DOI 10.1007/s10531-010-9844-7

ORIGINAL PAPER

Are bird density, species richness and community structure similar between native woodlands and non-native plantations in an area with a generalist bird fauna?

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Received: 12 January 2010 / Accepted: 18 March 2010 / Published online: 2 April 2010

Abstract This study compared the bird assemblages of native semi-natural woodlands and non-native Sitka spruce (*Picea sitchensis*) plantations in Ireland to identify what vegetation variables most influenced birds and to identify management targets in plantations to maximise future bird conservation. Point counts were conducted in 10 Oak (*Quercus* spp.) and 10 Ash (*Fraxinus excelsior*) native woodlands and in five Mid-rotation (20–30 years old) and five Mature (30–50 years old) Sitka spruce plantations. Ordination was used to characterise woodland types according to their constituent bird species. Total bird density (calculated using *Distance* software) and species richness were assessed for the different woodland types. Oak and Ash woodland bird assemblages were separated from Mid-rotation and Mature plantations by the ordination. There was no difference in total bird density between any of the woodland types. Oak woodlands had significantly higher species richness than either Mid-rotation or Mature Sitka spruce plantations. Ash had higher species richness than Mature Sitka spruce plantations. Understorey vegetation was negatively associated with total bird density, which also varied with survey year. Understorey vegetation was positively associated with species richness. Reasons for the relationships between vegetation and bird assemblages are discussed. Management should seek to increase shrub and understorey vegetation in the Mid-rotation phase to improve the contribution of plantations to bird conservation.

Keywords Bird communities · Exotic plantations · Forest management · Ireland · Native woodlands · Vegetation structure

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Introduction

Plantation forests provide potential habitat for birds that utilise woodland habitat, and native woodlands—those occurring naturally in a region—offer a reference point against which to compare the bird assemblages of non-native plantations. While direct comparisons between plantations and more natural woodlands are not always appropriate (Brockerhoff et al. 2008), such comparisons are useful in identifying facets of the woodlands that differ between the woodland types. Because management affects the utility of plantations to birds (Lantschner et al. 2008; Luck and Korodaj 2008; but see Calladine et al. 2009), such comparative studies may therefore provide useful information on aspects of plantations that can be improved with a view to sustainable forest management and biodiversity conservation.

Bird assemblages can differ between native woodlands and non-native plantations (Donald et al. 1998; Sax 2002) and plantations may host fewer species at lower densities than native woodlands (Marsden et al. 2001; Lindenmayer et al. 2002; Barlow et al. 2007b; Farwig et al. 2008). However, non-native plantations may also, in certain situations, possess similar bird species richness to native woodlands (Sax 2002; Magura et al. 2008). Because specialist woodland bird species are more likely to be absent from plantations than generalists (Zurita et al. 2006; Paritsis and Aizen 2008), Ireland offers an excellent opportunity to test whether patterns of bird assemblages in plantations are more similar to native woodlands in regions lacking a specialist woodland bird fauna than in regions that have a specialist woodland bird fauna.

Ireland has experienced one of the highest afforestation rates in the EU in recent times (FAO 2007). Non-native plantations cover approximately 10% of land area, of which Sitka spruce (*Picea sitchensis*) monocultures account for over 50%. Only 15% of plantations are composed of native broadleaf species, with Oak (*Quercus* spp). and Ash (*Fraxinus excelsior*) accounting for a third of this figure (Forest Service 2007). The extensive native broadleaved woodland that colonised Ireland following the end of the last ice-age (Mitchell 2006) has gradually been reduced by man to the current level of 1% of land area (Cross 1998) and non-native plantations are now therefore the most prevalent woodland habitat. Much of Ireland's native woodland cover contains either Oak or Ash as the dominant canopy tree species. In Britain, Oak supports more invertebrate species than Ash (Birks 1980; Kennedy and Southwood 1984) and, as a result, food availability for breeding birds may differ between these woodland types, which may in turn influence bird assemblages.

The increasing coverage of plantation forests in Europe (FAO 2007), coupled with a documented decline in woodland bird species throughout the continent (Fuller et al. 2005; Gregory et al. 2007; Hewson et al. 2007), means that efforts are required to evaluate the bird assemblages of plantations and, if necessary, improve their utility to a wider range of bird species. Although many of Europe's woodland specialist birds are absent from Ireland, information on how birds utilise plantations in Ireland and which species, if any, are absent from plantations is relevant on a European scale.

The study aimed to evaluate the bird assemblages of Sitka spruce plantations approaching commercial maturity by comparing them with those of native Oak and Ash woodlands, and to make research-based recommendations for future management of plantations. In particular three questions are addressed:

1. Are there differences in the bird assemblages of unmanaged Oak and Ash native woodlands?

2. What differences exist in the bird assemblages of native Oak and Ash woodlands and non-native managed plantation forests?
3. What vegetation and structural variables are most important in explaining the observed patterns in bird assemblages?

Methods

Site selection

Bird assemblages were surveyed at 30 forests throughout Ireland: 10 Sitka spruce plantations, 10 Oak dominated native woodlands (Oak) and 10 native woodlands with a high proportion of Ash in the canopy (Ash) (Fig. 1). The native woodlands correspond to the WN1 and WN2 classification of Irish woodland habitat (Fossitt 2000). ArcGIS and local maps were used to identify study sites. Ten second-rotation Sitka spruce plantations in two age classes (five in each age class) were selected: Mid-rotation (20–30 years) and commercially mature (Mature, 30–50 years). Sitka spruce was the primary crop tree in all

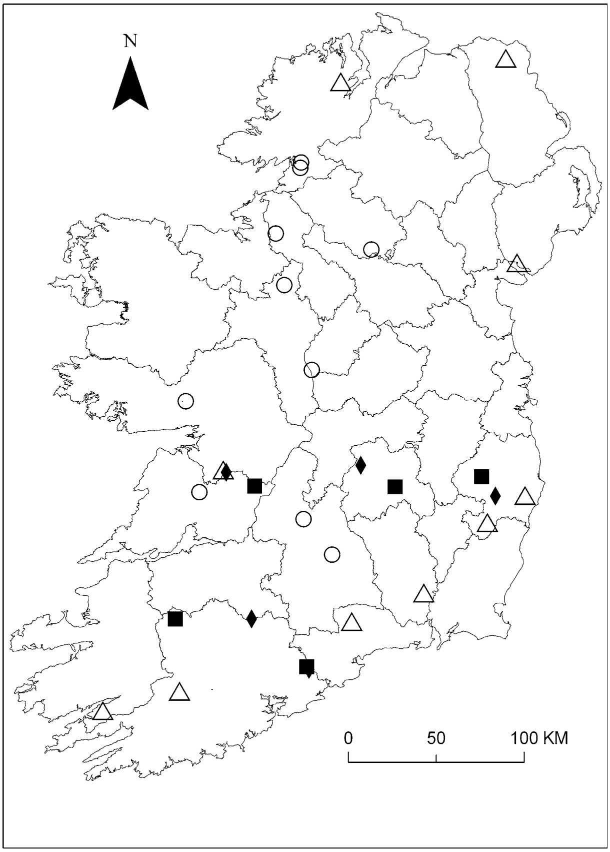

Fig. 1 Distribution of Oak (*open triangle*) and Ash (*open circle*) native woodlands and Mid-rotation (*filled square*) and Mature (*filled diamond*) Sitka spruce plantations surveyed in this study

plantations. The Oak and Ash woodlands were selected on the basis of their presence on 1840s Ordnance Survey maps, the oldest available for the Republic of Ireland, or, in the case of woodlands in Northern Ireland, on a database of ancient and long-established woodland (The Woodland Trust 2007). This was in order to minimise potential differences in bird assemblages as a result of differences in woodland age. However, due to a lack of suitable sites, we included two woodlands that were not present on the 1840s maps or the database. Following analysis we found that these woodlands did not differ significantly from the others and so results are presented for all woodlands. The native woodlands all currently receive little or no management intervention. All fieldwork was carried out during the breeding seasons of 2007 and 2008.

Point counts

Point counts (Bibby et al. 2000) were used to survey birds at all study sites. Where possible, six points were located in each site to standardise survey effort, but one Ash woodland was too small to accommodate six points and received five. Species accumulation curves were constructed for each forest type using EstimateS (Colwell 2006) and data were checked to ensure that this unequal sampling effort did not bias species richness estimation.

Points were randomly placed a minimum of 100 m apart in edge and interior habitat in each study site, and were located in the field using a Garmin GPS 76. Counts were conducted on calm days (wind speeds under Beaufort scale 4) without persistent or heavy rain. Each point was surveyed twice: early in the breeding season (April–May) and later (May–June). Because this study was part of a larger project, there were a large number of sites to be surveyed and counts therefore took place in the morning (0800–1200) and afternoon (1400–1800). Each forest received one morning and one afternoon visit. This approach has previously been successfully used to study Irish birds (Wilson et al. 2006). Counts lasted for 10 min, and all birds seen or heard within 50 m of the observer were recorded and their distances noted. Distances were typically estimated, but a range finder was used when possible.

Bird assemblages

Individuals detected in flight were excluded from analysis, as were individuals of the Corvidae (with the exception of Jay, *Garrulus glandarius*) Hirundinidae and Motacillidae as their presence at a study site could not be assumed to indicate a breeding association.

Bird assemblages were analysed in terms of community composition as determined by Non-metric Multidimensional Scaling (NMS) ordination, species richness, and total population density (number of individuals per hectare). Species richness was calculated as the cumulative number of species recorded in each site between the early and late visits.

Density estimation and data analysis

Distance (Thomas et al. 2006) was used to convert bird observations to species densities. Because detectability may differ between species (Alldredge et al. 2007) each bird species was allocated to one of four species detection groups (Table 1) and these groups analysed separately in *Distance*. Allocation depended on the method of detection, the distribution of detections in five distance bands (0–10, 11–20, 21–30, 31–40, and 41–50) and knowledge

Table 1 Species recorded in Mid-rotation and Mature Sitka spruce plantations and in Oak and Ash native woodlands, their population densities (No. ha^{-1} ± SE) and the number of forests (Forests present) in which each species was detected. The detection group (DG) to which each species was allocated is also indicated

Species	DG	Scientific name	Mid-rotation	Forests present (max = 5)	Mature	Forests present (max = 5)	Oak	Forests present (max = 10)	Ash	Forests present (max = 10)
Blackbird	1	*Turdus merula*	1.17 (0.30)	5	0.40 (0.10)	5	2.52 (0.62)	10	2.10 (0.14)	10
Blackcap	1	*Sylvia atricapilla*	0.89 (0.39)	4	0.32 (0.19)	3	0.96 (0.36)	8	1.20 (0.17)	10
Blue Tit	4	*Cyanistes caeruleus*	0.36 (0.36)	1	0.48 (0.48)	1	6.61 (1.28)	10	5.55 (1.27)	10
Bullfinch	2	*Pyrrhula pyrrhula*	0	0	0	0	0.40 (0.27)	2	0.54 (0.33)	3
Chaffinch	3	*Fringilla coelebs*	2.61 (0.67)	5	4.51 (0.92)	5	4.25 (0.60)	10	3.93 (0.75)	10
Chiffchaff	1	*Phylloscopus collybita*	0.50 (0.14)	4	0.05 (0.05)	1	0.58 (0.12)	9	0.38 (0.13)	6
Coal Tit	4	*Periparus ater*	18.64 (2.96)	5	15.44 (3.18)	5	6.56 (1.44)	10	7.00 (0.89)	10
Cuckoo	1	*Cuculus canorus*	0.12 (0.12)	1	0	0	0.06 (0.06)	1	0.03 (0.03)	1
Dunnock	2	*Prunella modularis*	0.95 (0.28)	4	0	0	0.16 (0.11)	2	0	0
Garden Warbler	1	*Sylvia borin*	0	0	0	0	0.03 (0.03)	1	0	0
Goldcrest	4	*Regulus regulus*	24.72 (3.15)	5	20.30 (3.81)	5	7.39 (0.62)	10	7.14 (0.78)	10
Great Tit	3	*Parus major*	0.05 (0.05)	1	0.33 (0.17)	3	1.06 (0.26)	9	2.18 (0.45)	10
Jay	2	*Garrulus glandarius*	0.26 (0.16)	2	0.54 (0.26)	3	0.70 (0.28)	6	0.86 (0.38)	6
Long-tailed Tit	4	*Aegithalos caudatus*	1.05 (0.68)	2	0	0	2.22 (0.89)	4	2.14 (0.74)	8
Mistle Thrush	1	*Turdus viscivorus*	0.06 (0.06)	1	0.15 (0.10)	2	0.15 (0.05)	5	0.39 (0.17)	6
Pheasant	1	*Phasianus colchicus*	0	0	0	0	0.09 (0.06)	2	0.18 (0.15)	2
Robin	2	*Erithacus rubecula*	7.26 (0.74)	5	4.64 (1.25)	5	9.38 (0.60)	10	7.74 (0.82)	10
Siskin	3	*Carduelis spinus*	0.05 (0.05)	1	0	0	0.08 (0.05)	2	0	0
Song Thrush	1	*Turdus philomelos*	0.42 (0.21)	3	0.21 (0.21)	1	0.84 (0.17)	8	0.54 (0.06)	10
Sparrowhawk	2	*Accipiter nisus*	0	0	0	0	0.25 (0.13)	3	0	0
Spotted Flycatcher	2	*Muscicapa striata*	0	0	0	0	0.24 (0.17)	2	0.26 (0.18)	2
Stock dove	1	*Columba oenas*	0	0	0	0	0.03 (0.03)	1	0	0
Treecreeper	2	*Certhia familaris*	0	0	0.35 (0.14)	3	1.66 (0.43)	9	2.10 (0.56)	9

Table 1 continued

Species	DG	Scientific name	Mid-rotation	Forests present (max = 5)	Mature	Forests present (max = 5)	Oak	Forests present (max = 10)	Ash	Forests present (max = 10)
Whitethroat	2	*Sylvia communis*	0.13 (0.13)	1	0.27 (0.27)	1	0.07 (0.07)	1	0	0
Willow Warbler	1	*Phylloscopus trochilus*	0.22 (0.22)	2	0.11 (0.07)	2	0.55 (0.32)	4	0.26 (0.08)	6
Woodpigeon	1	*Columba palumbus*	0.06 (0.06)	1	0.50 (0.21)	4	0.61 (0.11)	10	1.22 (0.20)	9
Wren	1	*Troglodytes troglodytes*	2.64 (0.91)	5	2.63 (0.79)	5	2.93 (0.48)	10	3.06 (0.35)	10
Mean density			63.23 (7.15)		51.23 (5.43)		50.36 (3.62)		48.79 (3.40)	

of a species' ecology. Therefore, species with broadly similar detectability were analysed together. To minimise the potential influence of habitat structure on the detection function, we also analysed native woodlands and plantations separately in *Distance*.

Akaike's Information Criteria (AIC) was used to select between four models for fitting of the detection function in *Distance*: Uniform + Cosine, Uniform + Polynomial, Half normal + Hermite and Hazard-rate + Cosine (Buckland et al. 2001). Population densities of all species for both the early and late counts were calculated for each site and the reported density of a species was the maximum of these two values.

Habitat variables and model building

Vegetation variables were estimated visually in a 30 m radius at each point. Variables measured were: canopy cover and height; understorey cover and height (a layer of woody vegetation below the canopy >2 m tall); shrub cover (woody vegetation <2 m tall) and field cover (herbaceous vegetation). The mean of the recorded variables from each point was used as the site score. We also included mean tree diameter at breast height (DBH), mean tree basal area and mean number of stems collected in three 10×10 metre plots in each forest. Year of survey was included in the models to test whether any significant relationships were due to inter-year differences, as were latitude and longitude to ensure that geographical differences were not driving observed patterns. The length of rides and the area of open space in the study sites were calculated from aerial photographs. In the case of rides, because the resolution was coarse and therefore length was unlikely to be calculated precisely, we added ride as a factor (present or absent in a study site) in models.

Data analysis

NMS using species' densities was carried out in PC-ORD (McCune and Mefford 2006) on the 'slow and thorough' setting, and used to investigate species composition in the different woodlands. NMS was undertaken using Sørenson distance measure and random starting coordinates with six axes. Dimensionality was reduced by one at each cycle. Initial step length towards minimum stress was 0.2. The stability criterion was 0, with 10 iterations to evaluate stability. A Monte Carlo test was carried out using 250 runs.

Indicator species analysis (Dufrene and Legendre 1997) was also carried out in PC-ORD to illustrate those species whose presence characterised each age class. Indicator values were derived from both the abundance and frequency of occurrence of a species in each woodland type to produce an indicator value. This value was tested for statistical significance using a Monte Carlo test. Only species with an indicator value of ≥20% and with $P < 0.05$ were considered.

ANOVA and Tukey HSD post hoc test were used to test for differences in bird density between the site types. Kruskal–Wallis with Dunn's post hoc test was used to test for differences in species richness between sites.

Before modelling, data were checked for normality, colinearity and outliers using Brodgar (Highland Statistics LTD 2007). Data transformations (log, cube root and fourth root) were applied where appropriate to reduce the effect of outliers and normalise the data. General Linear Modelling (GLM) assuming a Poisson distribution (or, in the event of overdispersion, a quasi-Poisson distribution) was used to used to investigate relationships between species richness and the habitat variables, and between density and the habitat variables. Backwards and forwards selection was used to select starting models which were identified using minimum Akaike's Information Criteria (AIC). The least significant explanatory variables were then dropped until all explanatory variables were significantly associated with the response variable. All analyses were carried out in Brodgar (Highland Statistics LTD 2007).

Results

Ordination and indicator species analysis

Having excluded species detected in flight and those groups that were not of interest, 27 species were included in the analysis. Twenty species were recorded in Mid-rotation and 17 in Mature Sitka spruce plantations. Twenty-one species were recorded in Ash woodlands and all 27 in Oak woodlands (Table 1).

The ordination represents a gradient from high canopy cover and simple understorey and ground vegetation structure in the Sitka spruce plantations, through to Oak and Ash woodlands which had higher shrub, field and understorey cover. Mid-rotation and Mature Sitka spruce plantations separated clearly from Oak and Ash woodlands along both Axis 1 (31% of variation) and Axis 2 (58% of variation). However, Oak and Ash woodlands did not separate from each other along either axis, nor did Mid-rotation and Mature plantations. Indicator species for Mid-rotation were Coal Tit (32%), Dunnock (68%), Goldcrest (34%) and Robin (25%). Indicators for Mature were Coal Tit (39%) and Goldcrest (42%). Indicator species were the same for Oak and Ash woodlands and included Blue Tit (Oak 51%, Ash 43%), Great Tit (Oak 26%, Ash 60%), Robin (Oak 32%, Ash 27%), Treecreeper (Oak 36%, Ash 46%) and Woodpigeon (Oak 25%, Ash 46%) (Fig. 2).

Bird density and species richness

We found no significant difference in total bird density between the woodland types ($F_{3,26} = 1.21$, $P > 0.05$). However, species richness was significantly different between woodlands ($H_c = 84.18$, D.F. = 3, $P < 0.01$), with Oak woodlands having significantly higher species richness than Mid-rotation ($Q = 2.70$, $P < 0.05$) and Mature ($Q = 3.25$, $P < 0.01$) Sitka spruce plantations and Ash woodlands having significantly higher species richness than Mature Sitka spruce plantations ($Q = 3.12$, $P < 0.05$). Species richness did not differ significantly between the other site types.

Year of study was positively related to total bird density ($t = 2.36$, $P = 0.03$) while understorey cover was negatively related to total bird density ($t = -2.53$, $P = 0.02$), although the explained deviance of the model was relatively low (24%). In contrast, understorey cover was associated with increasing species richness in a GLM with 55% of the deviance explained ($Z = 2.93$, $P < 0.01$).

Discussion

Oak and Ash woodlands

We found little difference in the bird assemblages of Oak and Ash woodlands. Both woodland types had similar indicator species, species richness and bird density. Hence the

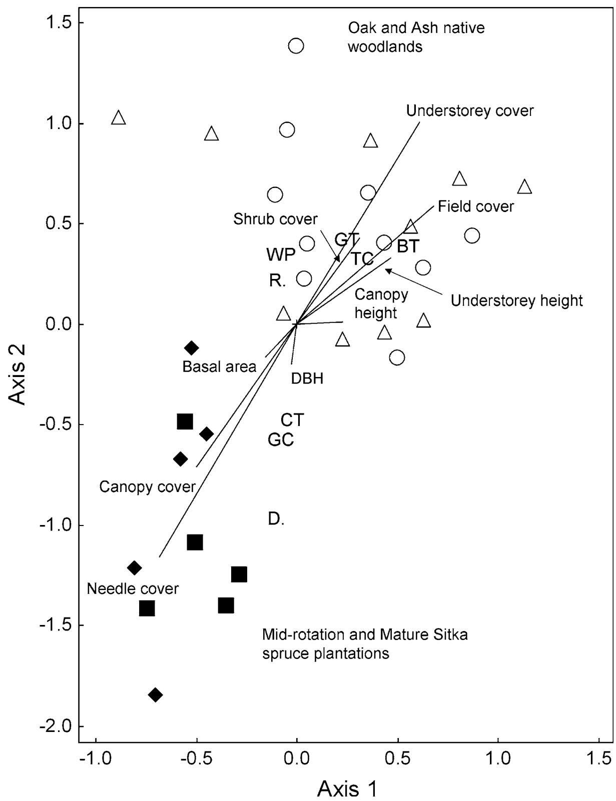

Fig. 2 NMS biplot of species densities in Mid-rotation (*filled square*) and Mature (*filled diamond*) Sitka spruce plantations, and in Oak (*open triangle*) and Ash (*open circle*) native woodlands. Main vegetation and structural gradients are shown with lines. Axis 1, $r^2 = 0.31$, Axis 2, $r^2 = 0.58$, cumulative $r^2 = 0.90$. Indicator species with an indicator value of 20% or more with $P < 0.05$ are marked on the plot. BT = Blue tit; CT = Coal tit; D. = Dunnock; GC = Goldcrest; GT = Great tit; R. = Robin; TC = Treecreeper; WP = Wood Pigeon. Rough site groups are also indicated on the plot. Final stress for the 2-dimensional solution = 13.57

two major native woodland types in Ireland provide similar habitat for birds and vegetation structure, rather than the dominant tree species, is likely the important factor driving between-site differences in species richness as suggested by the relationships between the response and explanatory variables. The fact that Oak hosts more invertebrate species than Ash (Kennedy and Southwood 1984) may be less important to breeding birds than total invertebrate biomass on the tree. Further research is required to clarify whether this is indeed the case.

Native and plantation woodlands

The clear separation of Oak and Ash native woodlands from Sitka spruce plantations via ordination illustrates distinct structuring of the bird assemblages of native and plantations woodlands. This provides support for the idea that plantations are complementary habitats (Donald et al. 1998; Barlow et al. 2007a). The difference in species richness suggests that the carrying capacity of plantations is lower than that of native woodlands for most bird species. That much of the generalist terrestrial bird fauna that characterises Ireland is present at low densities in plantations is an important finding and suggests that differences between plantations and native woodlands will be more pronounced in areas with a specialised woodland bird fauna.

A small number of species (primarily Coal Tit and Goldcrest) present at high densities dominate the bird fauna of plantations. Similar patterns of low diversity and dominance of a few species in coniferous plantations have been reported previously (Bibby et al. 1989; Fuller and Browne 2003), but not in as pronounced a way as reported in this study where Coal Tit and Goldcrest accounted for approximately 60% of the total bird density in plantations.

Other species common to plantations, such as Chaffinch and Robin, achieved similar densities in native woodlands whereas densities of Coal Tit and Goldcrest were much lower in native woodlands than in plantations. Both Coal Tit and Goldcrest are largely arboreal and small-bodied and Goldcrests feed on very small invertebrates of the orders Hemiptera and Collembola (Fuller 1995; Snow and Perrins 1998) which are abundant in Sitka spruce plantations (Straw et al. 2006). Besides also feeding on invertebrates, Coal Tits utilise spruce seeds taken from cones (Snow and Perrins 1998). Such diet preferences may render plantations more suitable for these small bodied species, rather than larger species which may not utilise the smallest prey items. This may help to explain the high population densities of Coal Tit and Goldcrest present in plantations.

Several species recorded in this study have been identified as occurring in Irish Sitka spruce plantations but being closely associated with non-crop broadleaved elements (Wilson et al. 2010). Each of these species (Blackcap, Blue Tit, Bullfinch, Chiffchaff, Great Tit, Long-tailed Tit, Treecreeper and Willow Warbler) was recorded at its highest density in either Oak or Ash woodlands, in some cases being several times as abundant as in plantations. Garden Warbler and Spotted Flycatcher can be added to this list of species that prefer broadleaved vegetation (Snow and Perrins 1998). The occurrence of broadleaf associated species may be one way in which the quality of plantations can be evaluated (Bibby et al. 1989), and by this measure plantations are currently lower quality habitat for birds than native woodlands. This offers a solid method by with which the effectiveness of future plantation management can be evaluated in terms of its success in bird conservation.

Two species of conservation concern were detected in this study, the Spotted Flycatcher and the Stock Dove. Both are on the Amber list of birds of conservation concern in Ireland and the Spotted Flycatcher is also a Species of European Concern (Lynas et al. 2007). The Spotted Flycatcher was found in both Oak and Ash woodlands but not in Sitka spruce plantations, while the Stock Dove was found in only one Oak woodland. The Spotted Flycatcher requires open areas and perches for foraging so the typically uniform nature of Sitka spruce plantation canopies may be less suitable. In the case of Stock Dove, native woodlands probably offer tree hollows for nesting (Snow and Perrins 1998).

Vegetation structure and bird assemblages

Bird species richness is associated with vegetation structure (Cherkaoui et al. 2009; Nikolov 2009), and changes in the structural diversity of woodland is one possible contributing factor to observed declines in British woodland bird populations (Fuller et al. 2007; Gill and Fuller 2007; Hopkins and Kirby 2007). Our finding, that species richness was significantly related to understorey cover, emphasises the importance of woodland vegetation structure to birds.

Canopy cover is negatively associated with understorey vegetation in plantation forests (Smith et al. 2008), which suggests that measures to reduce canopy cover and allow more light penetration could benefit bird diversity through the promotion of heterogeneous vegetation layers (Ding et al. 2008) which, in turn, provide nesting and foraging opportunities for a wide range of bird species (Quine et al. 2007). Mature coniferous plantations may have low structural diversity in the field and shrub layers (Ferris et al. 2000) and so may represent a lower quality habitat for birds than unmanaged, structurally heterogeneous native woodlands.

The negative association between understorey cover and total bird density initially appears paradoxical when viewed in light of the positive influence of understory vegetation on species richness. However, understorey vegetation tended to be sparse in Sitka spruce plantations (the maximum value was 8%) yet total bird density was slightly higher than in Oak and Ash native woodlands where understorey vegetation was abundant (maximum value 67%). The model thus negatively associated understorey vegetation with bird density.

Blue Tit, Great Tit and Treecreeper, indicator species identified for Oak and Ash woodlands, are all associated with structural aspects of woodlands. Blue Tit and Great Tit are hole nesting species (Fuller 1995) and it is likely that populations of cavity nesting species are limited in plantations as a result of short rotation times and a lack of old, cavity rich trees (Newton 1994). Treecreepers do not require holes but utilise loose bark and fissures (Fuller 1995), which are also likely to be more common on older trees. The herbivorous diet of Woodpigeons means that native woodlands, with more shrub and understorey vegetation, likely provide higher quality foraging opportunities, hence the identification of this species as an indicator of native woodlands. The occurrence of Robin as an indicator for both native woodlands and Mid-rotation plantations reflects this species' ability to utilise a wide range of habitats (Fennessy and Kelly 2006). Dunnock, common in the pre-thicket and thicket age classes (5–15 years) of plantations (Wilson et al. 2006), was also an indicator of Mid-rotation Sitka spruce plantations. This was surprising as it is a species more associated with scrub (Fuller 1995). It may be that the species manages to persist from early age classes into the Mid-rotation age class, but the oldest plantations become unsuitable, hence the species absence from the Mature stage of the plantation forest cycle.

The Oak and Ash woodlands that were used in this study are all considerably older than any of the plantations. Commercially over-mature (90–150 years) stands of conifers in Great Britain are utilised by birds that are associated with broadleaves (Bibby et al. 1989; Donald et al. 1998). Were Irish plantations allowed to mature to a similar age as native woodlands, bird assemblages of Sitka spruce plantations may eventually come to resemble those of native woodlands as structural diversity increases. Currently, some plantations are being left to mature beyond commercial felling age to provide seed for stock and for recreation purposes, and it would be interesting to survey the bird assemblages of such plantations in the future to test whether they closer resemble those of native woodlands. However, current typical forestry practice involves clearfelling and replanting, and over-mature stands are therefore only likely to occur in areas that are inaccessible or no longer economically viable to harvest.

Year of study

We found a positive association between study year and total bird density. Because this study was part of a wider project that also investigated other woodland types, it was not possible to survey all study sites during the same breeding season. Differences between years were not consistent, although the woodlands with the lowest densities tended to be those surveyed in 2007 and those with the highest in 2008. Year on year differences may be due to high structural complexity in some of the 2008 native woodlands which included some long-established woodland. The winter of 2007 was also unusually mild (Met Éireann 2010) which may have reduced over-winter bird mortality and resulted in higher bird density in 2008.

Management to benefit bird conservation

A striking feature of these results is the similarity of the bird assemblages of the Mid-rotation and Mature Sitka spruce age classes. Species richness is low in comparison to native woodlands by the time plantations are 20 years old and remains low until felling, which may be 20–30 years later. The Mid-rotation age class therefore provides a management target to increase the utility of plantations to birds.

We have demonstrated the importance of structural components of woodlands, particularly understorey cover, on bird species richness. Thus, management to promote these features and therefore increase the carrying capacity of plantations will likely increase the utility of plantations for bird conservation. Because few woodland specialist species occur in Ireland, and because many of the species in the study occurred in both native and plantation woodlands, there is potential for plantations to host a large proportion of Ireland's terrestrial bird fauna. To achieve this in the relatively short lifetime of a plantation, stands entering the Mid-rotation age class should be targeted for thinning in wide lines or patches to allow light penetration and encourage the establishment of pioneer species such as Birch (*Betula* spp.) and Bramble (*Rubus fructicosus*) and epiphytes such as Ivy (*Hedera helix*). This would mirror more closely the structure of native woodlands and provide both nesting and foraging opportunities for birds, including species of conservation concern such as the Spotted Flycatcher. Alternatively, implementation of forestry practices such as selection systems, where varying numbers of trees are removed at any one time, or the planting of polycultures, may improve structural diversity in plantations (Kerr 1999). The effectiveness of management may then be judged by the population densities of bird species associated with broadleaved vegetation.

Allowing some individual trees or stands of trees to remain and senesce following harvesting may increase nest site availability for cavity nesting species in the long term. The excavation of nest holes by the Great Spotted Woodpecker (*Dendrocopos major*) which appears to be re-colonising Ireland (Coombes 2009) may also increase cavities in such trees in the long term. In the short term, the provision of nest boxes which both Blue Tit and Great Tit are known to readily use (Fuller 1995; Mänd et al. 2009), would likely increase the utility of plantations to cavity nesting species.

Conclusions

We have demonstrated that the bird assemblages of native woodlands and those of older Sitka spruce plantations are distinct, even in a country with a highly generalised bird fauna. The differences are most likely due to differences in vegetation structure between the woodland types. However, because of the generalist bird fauna typical of Ireland, it is likely that relatively small measures (e.g. carrying out thinning in the Mid-rotation phase) could improve the utility of plantations to birds, and allow more broadleaf-associated species to achieve higher population densities.

Acknowledgements This project was funded by COFORD under the National Development Plan 2007–2013. Our thanks go to Coillte Teoranta, the Forest Service of Northern Ireland and the National Parks and Wildlife Service for allowing access to forests. Several private landowners also kindly permitted access to forests on their land. Thanks to Linda Coote and Karen Moore for access to unpublished data, and to several post-graduate students, post-docs and an anonymous reviewer whose suggestions greatly improved the manuscript.

References

Alldredge MW, Simons TR, Pollock KH (2007) Factors affecting aural detections of songbirds. Ecol Appl 17:948–955

Barlow J, Gardner TA, Araujo IS et al (2007a) Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. Proc Natl Acad Sci USA 104:18555–18560

Barlow J, Mestre LAM, Gardner TA et al (2007b) The value of primary, secondary and plantation forests for Amazonian birds. Biol Conserv 136:212–231

Bibby CJ, Aston N, Bellamy PE (1989) Effects of broadleaved trees on birds of upland conifer plantations in North Wales. Biol Conserv 49:17–29

Bibby CJ, Burgess ND, Hill DA (2000) Bird census techniques. Academic Press, London

Birks HJB (1980) British trees and insects: a test of the time hypothesis over the last 13, 000 years. Am Nat 115:600

Brockerhoff E, Jactel H, Parrotta J et al (2008) Plantation forests and biodiversity: oxymoron or opportunity? Biodivers Conserv 17:925–951

Buckland ST, Anderson DR, Burnham KP et al (2001) Introduction to Distance Sampling: estimating abundance of biological populations. Oxford University Press, Oxford

Calladine J, Humphreys EM, Strachan F et al (2009) Forestry thinning in commercial conifer plantations has little effect on bird species richness and breeding abundance. Bird Study 56:137–141

Cherkaoui I, Selmi S, Boukhriss J et al (2009) Factors affecting bird richness in a fragmented cork oak forest in Morocco. Acta Oecol 35:197–205

Colwell RK (2006) *EstimateS:* statistical estimation of species richness and shared species from samples. User's Guide and application. http://purl.oclc.org/estimates

Coombes RH (2009) Woodpeckers move in. In: Wings 55, Winter 2009

Cross JR (1998) An outline and map of the potential natural vegetation of Ireland. Appl Veg Sci 1:241–252

Ding T-S, Liao H-C, Yuan H-W (2008) Breeding bird community composition in different successional vegetation in the montane coniferous forests zone of Taiwan. Forest Ecol Manag 255:2038–2048

Donald PF, Fuller RJ, Evans AD et al (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

Dufrene M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol Monogr 67:345–366

FAO (2007). State of the World's forests 2007. Food and Agriculture Organisation of the United Nations

Farwig N, Sajita N, Böhning-Gaese K (2008) Conservation value of forest plantations for bird communities in western Kenya. Forest Ecol Manag 255:3885–3892

Fennessy GJ, Kelly TC (2006) Breeding densities of Robin *Erithacus rubecula* in different habitats: the importance of hedgerow structure. Bird Study 53:97–104

Ferris R, Peace AJ, Humphrey JW et al (2000) Relationships between vegetation, site type and stand structure in coniferous plantations in Britain. Forest Ecol Manag 136:35–51

Forest Service (2007) National Forest Inventory—Republic of Ireland, Forest Service. Johnstown Castle Estate Co, Wexford

Fossitt JA (2000) A guide to the habitats of Ireland. The Heritage Council, Kilkenny

Fuller RJ (1995) Bird life of woodland and forest. Cambridge University Press, Cambridge

Fuller RJ, Browne S (2003) Effects of plantation structure and management on birds. In: Humphrey J, Ferris R, Quine C (eds) Biodiversity in Britain's planted forests. Results from the Forestry Commission's biodiversity assessment project. Forestry Commission, Edinburgh, pp 93–99

Fuller RJ, Noble DG, Smith KW et al (2005) Recent declines in populations of woodland birds in Britain: a review of possible causes. Br Birds 98:116–143

Fuller RJ, Smith KW, Grice PV et al (2007) Habitat change and woodland birds in Britain: implications for management and future research. Ibis 149:261–268

Gill RMA, Fuller RJ (2007) The effects of deer browsing on woodland structure and songbirds in lowland Britain. Ibis 149:119–127

Gregory RD, Vorisek P, Van Strien A et al (2007) Population trends of widespread woodland birds in Europe. Ibis 149:78–97
Hewson CM, Amar A, Lindsell JA et al (2007) Recent changes in bird populations in British broadleaved woodland. Ibis 149:14–28
Highland Statistics LTD (2007). Brodgar. Software package for data exploration, univariate analysis, multivariate analysis and time series analysis.Aberdeenshire, Scotland
Hopkins JJ, Kirby KJ (2007) Ecological change in British broadleaved woodland since 1947. Ibis 149:29–40
Kennedy CEJ, Southwood TRE (1984) The number of species of insects associated with British trees: a re-analysis. J Appl Ecol 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
Lantschner M, Rusch V, Peyrou C (2008) Bird assemblages in pine plantations replacing native ecosystems in NW Patagonia. Biodivers Conserv 17:969–989
Lindenmayer DB, Cunningham RB, Donnelly CF et al (2002) Effects of forest fragmentation on bird assemblages in a novel landscape context. Ecol Monogr 72:1–18
Luck GW, Korodaj TN (2008) Stand and landscape-level factors related to bird assemblages in exotic pine plantations: implications for forest management. Forest Ecol Manag 255:2688–2697
Lynas P, Newton SF, Robinson JA (2007) The status of birds in Ireland: an analysis of conservation concern 2008–2013. Irish Birds 8:149–167
Magura T, Báldi A, Horváth R (2008) Breakdown of the species–area relationship in exotic but not in native forest patches. Acta Oecol 33:272–279
Mänd R, Leivits A, Leivits M et al (2009) Provision of nestboxes raises the breeding density of Great Tits *Parus major* equally in coniferous and deciduous woodland. Ibis 151:487–492
Marsden SJ, Whiffin M, Galetti M (2001) Bird diversity and abundance in forest fragments and *Eucalyptus* plantations around an Atlantic forest reserve, Brazil. Biodivers Conserv 10:737–751
McCune B, Mefford MJ (2006) PC-ORD. Multivariate analysis of ecological data. MjM Software Gleneden Beach, Oregon, USA
Met Éireann (2010). http://www.met.ie/climate/monthly-summary.asp
Mitchell F (2006) Where did Ireland's trees come from? Biol Environ 106:251–259
Newton I (1994) The role of nest sites in limiting the numbers of hole-nesting birds: a review. Biol Conserv 70:265–276
Nikolov SC (2009) Effect of stand age on bird communities in late-successional Macedonian pine forests in Bulgaria. Forest Ecol Manag 257:580–587
Paritsis J, Aizen MA (2008) Effects of exotic conifer plantations on the biodiversity of understory plants, epigeal beetles and birds in *Nothofagus dombeyi* forests. Forest Ecol Manag 255:1575–1583
Quine CP, Fuller RJ, Smith KW et al (2007) Stand management: a threat or opportunity for birds in British woodland? Ibis 149:161–174
Sax DF (2002) Equal diversity in disparate species assemblages: a comparison of native and exotic woodlands in California. Global Ecol Biogeogr 11:49–57
Smith G, Gittings T, Wilson M et al (2008) Identifying practical indicators of biodiversity for stand-level management of plantation forests. Biodivers Conserv 17:991–1015
Snow DW, Perrins CM (1998) The birds of the Western Palearctic: concise edition. Oxford University Press, Oxford
Straw N, Fielding N, Green G et al (2006) Seasonal changes in the distribution of green spruce aphid *Elatobium abietinum* (Walker) (Homoptera: Aphididae) in the canopy of Sitka spruce. Agric For Entomol 8:139–154
Thomas L, Laake JL, Strindberg S et al (2006) Distance 5.0. Release 2. Research unit for wildlife population assessment. University of St. Andrews, UK
The Woodland Trust (2007) Back on the map: an inventory of ancient and long-established woodland for Northern Ireland. Preliminary report. The Woodland Trust, Bangor
Wilson MW, Pithon J, Gittings T et al (2006) Effects of growth stage and tree species composition on breeding bird assemblages of plantation forests. Bird Study 53:225–236
Wilson MW, Gittings T, Kelly TC et al (2010) The importance of non-crop vegetation for bird diversity in Sitka spruce plantations in Ireland. Bird Study 57:116–120
Zurita GA, Rey N, Varela DM et al (2006) Conversion of the Atlantic Forest into native and exotic tree plantations: effects on bird communities from the local and regional perspectives. Forest Ecol Manag 235:164–173