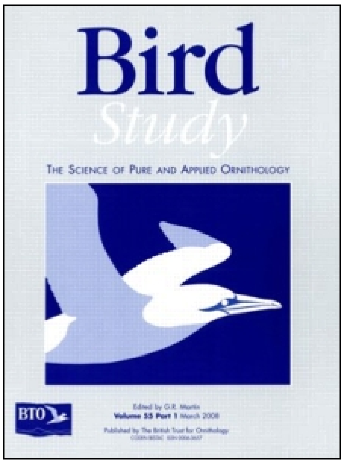
This article was downloaded by: *[University College Cork]*
On: *21 September 2010*
Access details: *Access Details: [subscription number 922096566]*
Publisher *Taylor & Francis*
Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Bird Study
Publication details, including instructions for authors and subscription information:
http://www.informaworld.com/smpp/title~content=t904369352

Breeding bird communities of second-rotation plantations at different stages of the forest cycle

Oisín F. McD. Sweeney[a]; Mark W. Wilson[a]; Sandra Irwin[a]; Thomas C. Kelly[a]; John O'Halloran[ab]
[a] PLANFORBIO Programme, Department of Zoology, Ecology and Plant Science, University College Cork, Cork, Ireland [b] Environmental Research Institute, University College Cork, Cork, Ireland

Online publication date: 30 July 2010

To cite this Article Sweeney, Oisín F. McD. , Wilson, Mark W. , Irwin, Sandra , Kelly, Thomas C. and O'Halloran, John(2010) 'Breeding bird communities of second-rotation plantations at different stages of the forest cycle', Bird Study, 57: 3, 301 — 314

To link to this Article: DOI: 10.1080/00063651003801713

URL: http://dx.doi.org/10.1080/00063651003801713

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: http://www.informaworld.com/terms-and-conditions-of-access.pdf

This article may be used for research, teaching and private study purposes. Any substantial or systematic reproduction, re-distribution, re-selling, loan or sub-licensing, systematic supply or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

Bird Study (2010) **57,** 301–314

Breeding bird communities of second-rotation plantations at different stages of the forest cycle

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 Early stages of the plantation forest cycle have distinct bird communities and bird density was significantly higher in the second rotation than in the first for a given age class.
Aims To characterize the bird communities in Irish second-rotation plantations and to compare them with those of first-rotation plantations.
Methods Point counts were used to survey 20 plantation forests in four age classes (Pre-thicket; Thicket; Mid-rotation; and Mature) in the breeding season of 2007. DISTANCE software was used to generate bird densities. Ordination, indicator species analysis, and GLM were used to analyse the bird communities.
Results Bird communities of Pre-thicket and, to a lesser extent, Thicket age classes were distinct from those of more mature forests. Bird communities of Mid-rotation and Mature age classes were indistinguishable from each other and were therefore combined into a single age class (Closed canopy). Pre-thicket held significantly lower total bird density, but significantly higher migrant bird density, than this Closed canopy age class. Bird density was significantly higher in the second rotation in all age classes except for Pre-thicket, but migrant density was significantly higher in Pre-thicket in the second rotation. There was no difference in species richness between the first and second rotation.
Conclusions Differences between rotations are probably due to changes in vegetation structure, and the increase in second-rotation forests in Ireland is likely to be a positive development for bird communities. Especially encouraging is the higher migrant bird density in second-rotation Pre-thicket, as some of these species are in decline throughout Europe. However, the largest differences in population density between rotations were exhibited by common species and such species will likely benefit most from future increases in the area of second-rotation plantation forests.

Questions remain about the contribution of plantation forests to biodiversity, particularly in second-rotation forests, which have received little attention. Bird communities are an important component of forest ecosystems (Sekercioglu 2006), influencing seed dispersal (Gómez 2003, Martinez *et al.* 2008), pollination (Cronk & Ojeda 2008, Mortensen *et al.* 2008) and exerting top-down control over insect communities (Skoczylas *et al.* 2007, Gunnarsson *et al.* 2009). Plantations in temperate regions may be as valuable a habitat for birds as agricultural land (Christian *et al.* 1998, O'Halloran *et al.* 1998) and can even compare favourably with natural forest habitats (Maicas & Fernandez Haeger 2004, Santos *et al.* 2006).

Following the end of the last ice-age, tree colonization resulted in extensive broadleaved tree cover in Ireland. This was gradually reduced, largely through the actions of humans from the Bronze Age through to the present day, to the current 1% of land area (Mitchell 1995, Cross 1998). However, Ireland has experienced some of the highest rates of commercial afforestation in Europe in recent years (Food and Agriculture Organisation of the United Nations 2007), and such forests now cover approximately 10% of the land area. The proportion of plantation forest, as compared with that of native forest, is extremely high in a European context and greater even than in

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

Britain (Forest Europe 2007). Almost 75% of plantations are composed of non-native conifers, with Sitka Spruce *Picea sitchensis*, accounting for over 50% of the forest area (Forest Service 2007). Although afforestation is ongoing (Forest Service 2007), many stands are reaching commercial maturity (approximately 35–50 years) and will soon be harvested. As there is a legal requirement in Ireland to restock felled areas (Forest Service 2000), these sites will be subsequently replanted and second-rotation forests will eventually come to characterize the forest estate. Ireland, therefore, provides an ideal opportunity to investigate the bird communities of second-rotation plantation forests.

Bird communities in first-rotation plantations change across the forest cycle. Species typical of open habitats, including many migrants, are present in young stands and are replaced by more generalist and forest-adapted species as forests mature (Humphrey *et al.* 2003, Wilson *et al.* 2006). Globally, non-native plantations can support populations of some important bird species (Brockerhoff *et al.* 2008), and this is true of Irish plantations (Wilson *et al.* 2009). Few studies have explicitly investigated bird communities in second-rotation plantations (Bibby *et al.* 1985, Patterson *et al.* 1995), and such information is important to inform management decisions as second-rotation plantations will inevitably increase world-wide, potentially influencing bird communities.

In this paper, we investigate the bird communities of second-rotation plantation forests in four different age classes in terms of species richness, total bird density and migrant bird density. This study has three key aims:

1. To characterize the bird community of four age classes in second-rotation plantation forests.
2. To explore vegetation structure as a possible explanation for any observed differences.
3. To compare the bird communities in four age classes between first- and second-rotation plantation forests.

METHODS

Study sites

ARCGIS (ESRI ArcMap V3.2 & 9.2) was used to identify second-rotation plantations of Pre-thicket (5 years), Thicket (8–15 years), Mid-rotation (20–30 years) and commercially mature, referred to hereafter as Mature (30–50 years) age classes. A forestry database was provided by Coillte Teoranta, the Irish semi-state forestry body. A total of 20 plantations were surveyed, comprising five forests from each age class. A clustered approach was used where four sites (one from each age class) were located in close proximity to minimize the potential influence of abiotic and climatic variation. It should be noted that this project is a continuation of earlier work that studied the biodiversity of first-rotation plantations (Iremonger *et al.* 2006). Therefore, second-rotation plantations were selected that resembled, as closely as possible, the previous land-use of first-rotation plantations. This was so that any differences that were observed between rotations were not confounded by large variations in site productivity. Clusters were located to ensure a representative geographical spread across the country (Fig. 1). Sitka Spruce was the primary plantation tree (>90%) in all sites. All fieldwork was undertaken during the breeding season of 2007.

Point counts

Birds were surveyed using point counts (Bibby *et al.* 2000). Six point counts were located in each forest and were randomly placed a minimum of 100 m apart in edge and interior habitat. Points were located in the field using a global positioning system (Garmin GPS76). Counts were conducted on days without strong wind (less than Beaufort scale 4) or persistent rain. Each point was surveyed twice: once early in the breeding season (April–May) and once later (May–June). This study was carried out as part of a large-scale project on the biodiversity of plantation forests and, because time was limiting, it was necessary to survey forests in both the morning and afternoon. Therefore, one of the visits was carried out between 08:00 and 11:00 hours, and the other between 14:00 and 17:00 hours. Each point received both a morning and an afternoon count. This approach has been used before and may help to reduce any diurnal bias owing to particular species being more or less active at a particular time of day (Wilson *et al.* 2006). Point counts lasted for 10 minutes, during which time all birds seen and heard within 50 m of the observer were recorded and their distances from the observer noted. Bird distances were usually estimated, but a Bushnell range finder was used where possible.

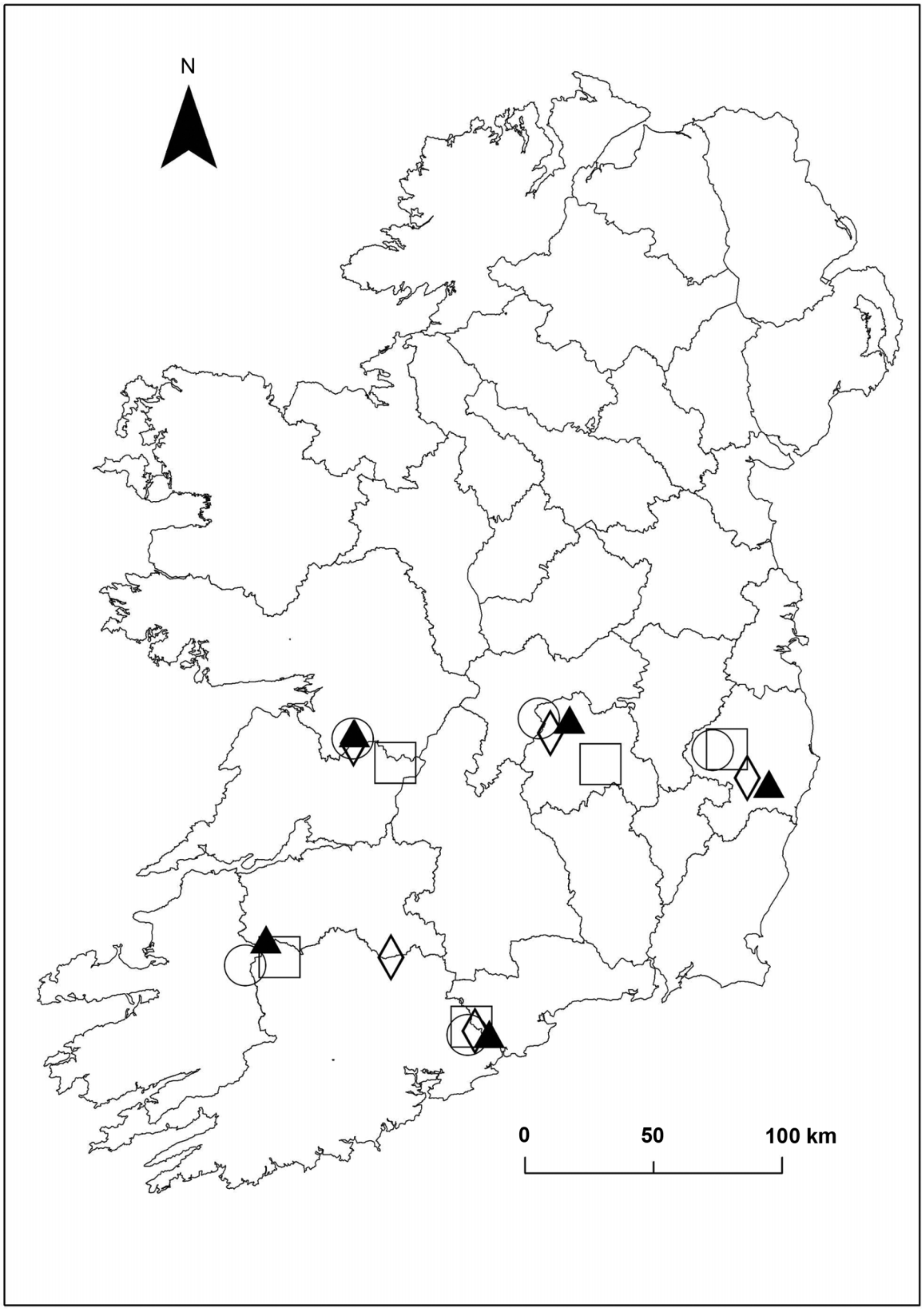


Figure 1. Distribution of study clusters throughout Ireland. ▲, Pre-thicket; ○, Thicket; □, Mid-rotation; ◇, Mature.

Bird communities

Bird communities were characterized in terms of community composition, species richness and total population density (expressed as number per hectare). Species richness was calculated as the cumulative number of species recorded at each site between the two visits. Owing to their significance from a conservation perspective, and their importance to the breeding bird fauna of temperate regions, migrant species were analysed both as a component of total bird density and separately. Six migrant species were recorded in this study: Blackcap *Sylvia atricapilla*, Common Chiffchaff *Phylloscopus collybita*, Common Cuckoo *Cuculus canorus*, Common Grasshopper Warbler *Locustella naevia*, Common Whitethroat *Sylvia communis*, and Willow Warbler *Phylloscopus trochilus*.

Individuals that were detected in flight were excluded from analysis, along with individuals of the Corvidae (with the exception of Eurasian Jay *Garrulus glandarius*), Hirundinidae and Motacillidae as their presence cannot be assumed to indicate a breeding association with forests.

Vegetation recording at the point count scale

Vegetation variables were estimated visually in a 30-m radius from each point and expressed as percentage cover. These variables included canopy cover and height, cover and height of the understorey (a vegetation layer taller than the shrub layer but beneath the canopy), shrub cover (woody vegetation under 2 m), field cover (non-woody vegetation under 2 m in height), ground cover (mosses and liverworts) and needle litter cover. For each of these variables, the mean value across both visits was calculated for each point. The value for each site was calculated as the mean percentage cover from all point counts.

Density estimation and data analysis

DISTANCE (Thomas *et al.* 2006) was used to derive species densities from field observations. Both the identity of a species (Alldredge *et al.* 2007) and the habitat in which it is observed (Schieck 1997) may affect the detectability of birds. Ideally, each species–habitat combination should therefore be analysed using a separate detection function, but we did not have enough bird observations for each species to achieve this. Each species was therefore assigned to one of four species detection groups (Table 1), which depended on the method of detection, the distribution of detections in five 10-m distance bands and knowledge of the species' ecology. Therefore, species in the same detection group were judged to have roughly similar detectability. We analysed Pre-thicket and Thicket separately as these age classes differed considerably in structure from each other and from more mature age classes, and analysed Mid-rotation and Mature together as these age classes were similar in terms of forest structure. AIC was used to select between four models for fitting of the detection function: Uniform + Cosine, Uniform + Polynomial, Half normal + Hermite and Hazard-rate + Cosine (as recommended by Buckland *et al.* [2001]). For each site, the population densities of all species for both the early and late counts were calculated, and the density of a species taken as the maximum of these two values.

A non-parametric Kruskal–Wallis with Dunn's post-hoc test was used to investigate differences in species richness, total bird density and migrant density among the different age classes as these data did not meet the assumptions of parametric statistics. Statistical analyses were carried out in BRODGAR (Highland Statistics Ltd., Newburgh, UK), SPSS V12.0.1 (SPSS Inc., Chicago, IL) or by hand.

Non-metric multidimensional scaling (NMS; see Endnote a) using species densities was used to compare the species composition between age classes as it can deal with non-normal and zero-rich data (McCune & Grace 2002). The biplot function was used to plot the vegetation data onto the ordination of species densities to visualize the environmental gradient between sites. Indicator species analysis (Dufrene & Legendre 1997) was used to determine which species characterized each age class. Indicator values were derived from the relative abundance and relative frequency of the species in each age class to produce an indicator value. This value was then tested for statistical significance using a Monte Carlo test. Only species with an indicator value of $\geq 40\%$ and with $P < 0.05$ were considered. Ordination and indicator species analyses were conducted using PC-ORD (McCune & Mefford 2006).

Rank-abundance curves were used to investigate differences in bird community structure in a particular forest age class. The slope of a rank-abundance curve is an indicator of the evenness of a community, shallower slopes indicating more even communities (Magurran 2004). The slopes of the rank abundance curves in a particular age class were compared in turn using a Kolmogorov–Smirnov two-sample test.

Table 1. Species listed alphabetically according to their common names, their population densities (birds ha^{-1} ± se) in four first-rotation (data derived from Wilson *et al.* [2006]) and second-rotation forest age classes and their rate of natural population change as identified by Coombes *et al.* (2009). The detection group (DG) to which each species was assigned is also noted.

				Pre-thicket		Thicket		Mid-rotation		Mature	
Species	Scientific name	DG	Annual population change (%)	First rotation	Second rotation	First rotation	Second rotation	First rotation	Second rotation	First rotation	Second rotation
Blackbird	*Turdus merula*	1	+0.77	0.48 ± 0.34	0.53 ± 0.18	2.45 ± 0.63	1.31 ± 0.30	1.46 ± 0.40	1.17 ± 0.30	0.49 ± 0.18	0.40 ± 0.10
Blackcap (M)	*Sylvia atricapilla*	1	+16.08*	0.04 ± 0.04	0.06 ± 0.06	0.32 ± 0.12	0.35 ± 0.28	0.46 ± 0.46	0.89 ± 0.39	0	0.32 ± 0.19
Blue Tit	*Cyanistes caeruleus*	4	+1.57*	0.08 ± 0.08	0	0.38 ± 0.38	1.14 ± 0.76	0.06 ± 0.06	0.36 ± 0.36	0	0.48 ± 0.48
Bullfinch	*Pyrrhula pyrrhula*	2	+6.66*	0.17 ± 0.17	0.11 ± 0.11	0.73 ± 0.35	0	0.08 ± 0.08	0	0.08 ± 0.08	0
Chaffinch	*Fringilla coelebs*	3	+1.04*	0.82 ± 0.48	1.69 ± 0.33	3.34 ± 0.96	8.52 ± 1.26	6.17 ± 1.80	2.61 ± 0.67	5.79 ± 0.67	4.51 ± 0.92
Chiffchaff (M)	*Phylloscopus collybita*	1	−0.77	0.17 ± 0.17	0.06 ± 0.06	0.66 ± 0.55	0.92 ± 0.38	0.26 ± 0.11	0.5 ± 0.14	0.16 ± 0.07	0.05 ± 0.05
Coal Tit	*Periparus ater*	4	+2.09*	0.26 ± 0.26	0.84 ± 0.42	1.54 ± 0.53	12.30 ± 2.78	4.93 ± 1.21	18.64 ± 2.96	4.42 ± 0.27	15.44 ± 3.18
Cuckoo (M)	*Cuculus canorus*	1	+1.78	0	0	0	0	0	0.12 ± 0.12	0	0
Dunnock	*Prunella modularis*	2	+0.34	0.46 ± 0.21	1.61 ± 0.54	1.17 ± 0.48	3.47 ± 0.91	0.13 ± 0.08	0.95 ± 0.28	0	0
Goldcrest	*Regulus regulus*	4	+2.63*	1.46 ± 0.85	0.33 ± 0.22	3.64 ± 1.05	11.33 ± 2.02	9.00 ± 0.73	24.72 ± 3.15	9.19 ± 2.04	20.30 ± 3.81
Goldfinch	*Carduelis carduelis*	3	+9.87*	0.23 ± 0.23	0.09 ± 0.09	0.10 ± 0.10	0	0	0	0	0
Grasshopper Warbler (M)	*Locustella naevia*	1	+4.12	0.03 ± 0.03	0.11 ± 0.11	0	0	0	0	0	0
Great Tit	*Parus major*	3	+2.77*	0.12 ± 0.12	0.44 ± 0.13	0.27 ± 0.27	0.36 ± 0.15	0.53 ± 0.18	0.05 ± 0.05	0.09 ± 0.09	0.33 ± 0.17
Greenfinch	*Carduelis chloris*	3	−0.7	0	0	0.53 ± 0.53	0	0	0	0	0
Jay	*Garrulus glandarius*	2	DD	0	0	0	0.23 ± 0.22	0	0.26 ± 0.16	0	0.54 ± 0.26
Lesser Redpoll	*Carduelis cabaret*	3	+12.72*	1.92 ± 0.37	0.54 ± 0.17	2.41 ± 0.84	0	0.37 ± 0.22	0	0.35 ± 0.20	0
Linnet	*Carduelis cannabina*	3	1.88	1.07 ± 0.56	0.80 ± 0.60	0	0	0	0	0	0
Long-tailed Tit	*Aegithalos caudatus*	4	1.29	0	0	0.07 ± 0.07	0.67 ± 0.67	0.15 ± 0.15	1.05 ± 0.68	0	0
Meadow Pipit	*Anthus pratensis*	2	−1.18*	2.02 ± 0.70	1.49 ± 1.23	0.16 ± 0.16	0.45 ± 0.45	0	0	0	0
Mistle Thrush	*Turdus viscivorus*	1	−3.30*	0	0.06 ± 0.06	0.33 ± 0.21	0.12 ± 0.07	0.20 ± 0.14	0.06	0.40 ± 0.33	0.15 ± 0.10
Pheasant	*Phasianus colchicus*	1	+2.86*	0	0.23 ± 0.23	0	0.07 ± 0.07	0	0	0.06 ± 0.06	0
Reed bunting	*Emberiza schoeniclus*	3	+3.04*	1.19 ± 0.91	0.17 ± 0.17	0	0	0	0	0	0
Robin	*Erithacus rubecula*	2	−1.08*	0.80 ± 0.38	5.18 ± 0.81	5.30 ± 0.85	11.31 ± 1.22	5.57 ± 1.19	7.26 ± 0.74	2.77 ± 0.97	4.64 ± 1.25
Sedge Warbler (M)	*Acrocephalus schoenobaenus*	1	+2.99*	0.11 ± 0.11	0	0	0	0	0	0	0
Siskin	*Carduelis spinus*	3	DD	0.33 ± 0.27	0	0.33 ± 0.23	0.12 ± 0.11	0.07 ± 0.07	0.05 ± 0.05	0.32 ± 0.18	0
Sky Lark	*Alauda arvensis*	1	−2.67*	0.05 ± 0.05	0	0	0	0	0	0	0
Song Thrush	*Turdus philomelos*	1	+0.55	0.11 ± 0.11	0.12 ± 0.07	1.66 ± 0.68	1.07 ± 0.43	0.50 ± 0.43	0.42 ± 0.21	0.05 ± 0.05	0.21 ± 0.21
Sparrowhawk	*Accipiter nisus*	2	DD	0	0.1 ± 0.10	0	0	0.07 ± 0.07	0	0.20 ± 0.15	0
Stonechat	*Saxicola torquata*	2	+6.32*	0.12 ± 0.12	0.43 ± 0.43	0	0	0	0	0	0
Treecreeper	*Certhia familaris*	2	−2.19	0.10 ± 0.10	0	0	0.23 ± 0.23	0.13 ± 0.07	0	0.12 ± 0.05	0.35 ± 0.14
Whitethroat (M)	*Sylvia communis*	1	+3.78	0.16 ± 0.16	3.36 ± 1.48	0	0	0	0.13 ± 0.13	0	0.27 ± 0.27
Willow Warbler (M)	*Phylloscopus trochilus*	1	+3.20*	1.00 ± 0.12	3.67 ± 0.55	1.84 ± 0.65	3.24 ± 0.58	0.15 ± 0.09	0.22 ± 0.22	0.22 ± 0.09	0.11 ± 0.07
Woodpigeon	*Columba palumbus*	1	+2.30*	0	0	0.45 ± 0.27	0.47 ± 0.18	0.17 ± 0.06	0.06 ± 0.06	0.12 ± 0.07	0.50 ± 0.21
Wren	*Troglodytes troglodytes*	1	+1.73*	1.86 ± 0.46	4.55 ± 0.37	2.45 ± 0.61	3.59 ± 0.40	2.00 ± 0.65	2.64 ± 0.91	0.58 ± 0.16	2.63 ± 0.79

*Statistically significant increase or decrease, $P < 0.01$; M, migrant species; DD, data-deficient species.

Comparisons between rotations

The findings of this study were compared with those of a recent study of first-rotation forests in Ireland (Wilson *et al.* 2006) to investigate differences in both vegetation and the bird community between rotations. Mann–Whitney *U*-tests were used to compare vegetation, while GLMs assuming a Poisson distribution were used to compare species richness, total bird density and migrant density between first- and second-rotation forests. Poisson GLM was deemed most suitable as species richness was count data, and densities were derived from count data (Zuur *et al.* 2009). To perform this test, we used a model with only one explanatory variable, rotation, and carried out a GLM for each combination of age class and response variable (species richness; total bird density; and migrant density). In each of these models, the significance of just one explanatory variable (rotation) was tested against the null model. Models were checked for over-dispersion and corrected if necessary by fitting a quasi-Poisson model. To check whether any difference between rotations was due to a natural population increase in the time period (five years) between the studies, densities were corrected using annual rates of population increase calculated by the Countryside Bird Survey (Coombes *et al.* 2009) (Table 1), and models run both with the original and corrected data.

RESULTS

Community structure in second-rotation forests

A total of 51 species was recorded in second-rotation plantation forests in this study. Of these, 31 species were used in the analysis. Of the 31 species, 24 were detected in Pre-thicket, 21 in Thicket, 20 in Mid-rotation and 17 in Mature forests (Table 1).

NMS ordination explained 96% of the variation in the species density data in second-rotation forests with Axis 1 accounting for 89% and Axis 2, 7%. The ordination identified three main groups of sites: Pre-thicket separated from the rest of the age classes along Axis 1 and showed a large amount of inter-site variation across Axis 2. Thicket separated from Pre-thicket across Axis 1 and, to a lesser extent, across Axis 2. Thicket also separated from Mid-rotation and Mature across Axis 1. However, Mid-rotation and Mature did not separate clearly from each other along either axis one or two (Fig. 2). These two age classes were therefore combined into a Closed canopy age class for further analyses. There was no significant difference between the slopes of the rank-abundance curves in any of the age classes (Kolmogorov–Smirnov: Pre-thicket versus Thicket, $z = 0.48$, $P > 0.05$; Pre-thicket versus Closed canopy, $z = 1.02$, $P > 0.05$; Thicket versus Closed canopy, $z = 0.93$, $P > 0.05$) (Fig 3).

Indicator species for Pre-thicket included Lesser Redpoll *Carduelis cabaret* (Indicator value 80%, $P < 0.01$) and Whitethroat (80%, $P < 0.01$). Indicators for Thicket were Chaffinch *Fringilla coelebs* (62%, $P < 0.01$); Coal Tit *Periparus ater* (41%, $P < 0.01$); Hedge Accentor (Dunnock) *Prunella modularis*, (63%, $P < 0.05$); Song Thrush *Turdus philomelos* (57%, $P < 0.05$); and European Robin *Erithacus rubecula* (50%, $P < 0.01$), while indicator species for the Closed canopy age class were Coal Tit *P. ater* (56%, $P < 0.01$) and Goldcrest *Regulus regulus* (66%, $P < 0.01$).

Species richness, total bird density and migrant bird density

There was no significant difference in mean species richness between Pre-thicket, Thicket or Closed canopy ($H = 1.28$, $P > 0.05$). Total bird density was significantly different between the age classes ($H = 11.17$, $P < 0.01$). Both Thicket ($Q = 2.78$, $P < 0.05$) and Closed canopy ($Q = 2.69$, $P < 0.05$) had significantly higher bird density than Pre-thicket, but there was no significant difference between Thicket and Closed canopy ($Q = 0.52$, $P > 0.05$). Migrant density also differed significantly between the age classes ($H = 12.88$, $P < 0.01$), being significantly lower in Closed canopy than in Thicket ($Q = 2.53$, $P < 0.05$) and Pre-thicket ($Q = 3.02$, $P < 0.01$). However, there was no significant difference in migrant density between Thicket and Pre-thicket ($Q = 0.86$, $P > 0.05$) (Table 2).

Comparison with first-rotation forests

Shrub cover in Pre-thicket was significantly higher in the second rotation than the first ($U = 0.0$, $P < 0.05$) while field cover was significantly higher in the first rotation than in the second ($U = 0.0$, $P < 0.05$). Canopy cover and height did not differ significantly between rotations. In Thicket, only field cover differed significantly between rotations, being higher in the first rotation than the second ($U = 0.0$, $P < 0.05$). In Closed canopy, both canopy cover ($U = 16.0$, $P < 0.05$) and field cover ($U = 10.0$, $P < 0.01$) were significantly higher in the first rotation than in the second (Table 3).

Species richness did not differ significantly between rotations in any of the three age class (Pre-thicket,

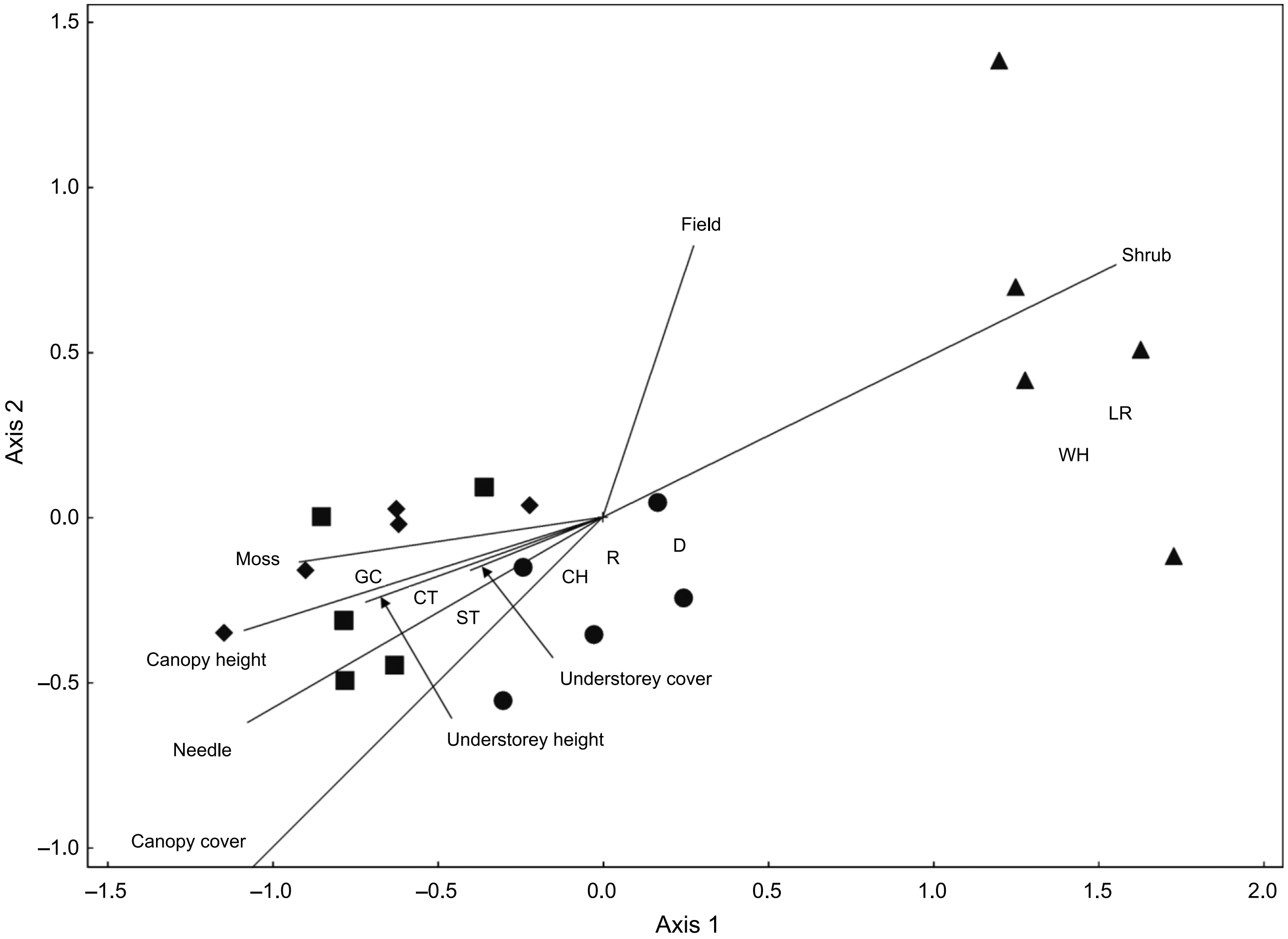


Figure 2. Non-metric multidimensional scaling biplot of site bird species densities and vegetation components in second-rotation Sitka spruce plantations. ▲, Pre-thicket; ●, Thicket; ■, Mid-rotation; ◆, Mature; Axis 1, $r^2 = 0.89$; Axis 2, $r^2 = 0.070$; final stress for 2D solution = 6.961; final instability = 0.00000; species with an indicator value of 40% or more and with a *P*-value of < 0.05 are displayed; CH, Chaffinch *Fringilla coelebs*; CT, Coal Tit *Periparus ater*; D, Hedge Accentor (Dunnock) *Prunella modularis*; GC, Goldcrest *Regulus regulus*; LR, Lesser Redpoll *Carduelis cabaret*; R, European Robin *Erithacus rubecula*; ST, Song Thrush *Turdus philomelos*; WH, Common Whitethroat *Sylvia communis*.

$z = -0.063$, $P > 0.05$; Thicket, $z = -0.522$, $P > 005$; Closed canopy $z = -0.947$, $P > 0.05$). Total bird density was significantly higher in the second-rotation in all three age classes (Pre-thicket, $t = 2.137$, $P < 0.01$; Thicket, $t = 3.860$, $P < 0.01$; Closed canopy, $t = 4.963$, $P < 0.01$), and migrant bird density was significantly higher in the second rotation in Pre-thicket ($t = 3.394$, $P < 0.01$). There was no significant difference in migrant density between rotations in the other age classes (Thicket, $z = 0.433$, $P > 0.05$; Closed canopy, $z = -0.217$, $P > 0.05$) (Table 2).

Correcting the data for natural population increase resulted in a decrease of between 5 and 10% in total bird density in each age class (Fig. 4). When re-analysed, there was no significant difference in total bird density between rotations in Pre-thicket ($t = 1.88$, $P = 0.07$), but total bird density remained significantly higher in the second rotation in both Thicket ($t = 3.637$, $P < 0.01$) and Closed canopy ($t = 4.361$, $P < 0.01$). Migrant density remained significantly higher in the second rotation in Pre-thicket ($t = 3.309$, $P < 0.01$).

The difference in density between rotations in Thicket and Closed canopy was largely driven by two abundant species: Coal Tit and Goldcrest (Table 1). Because of their numbers in the field, density estimates generated using DISTANCE are particularly susceptible to observer bias for these species. To test whether the

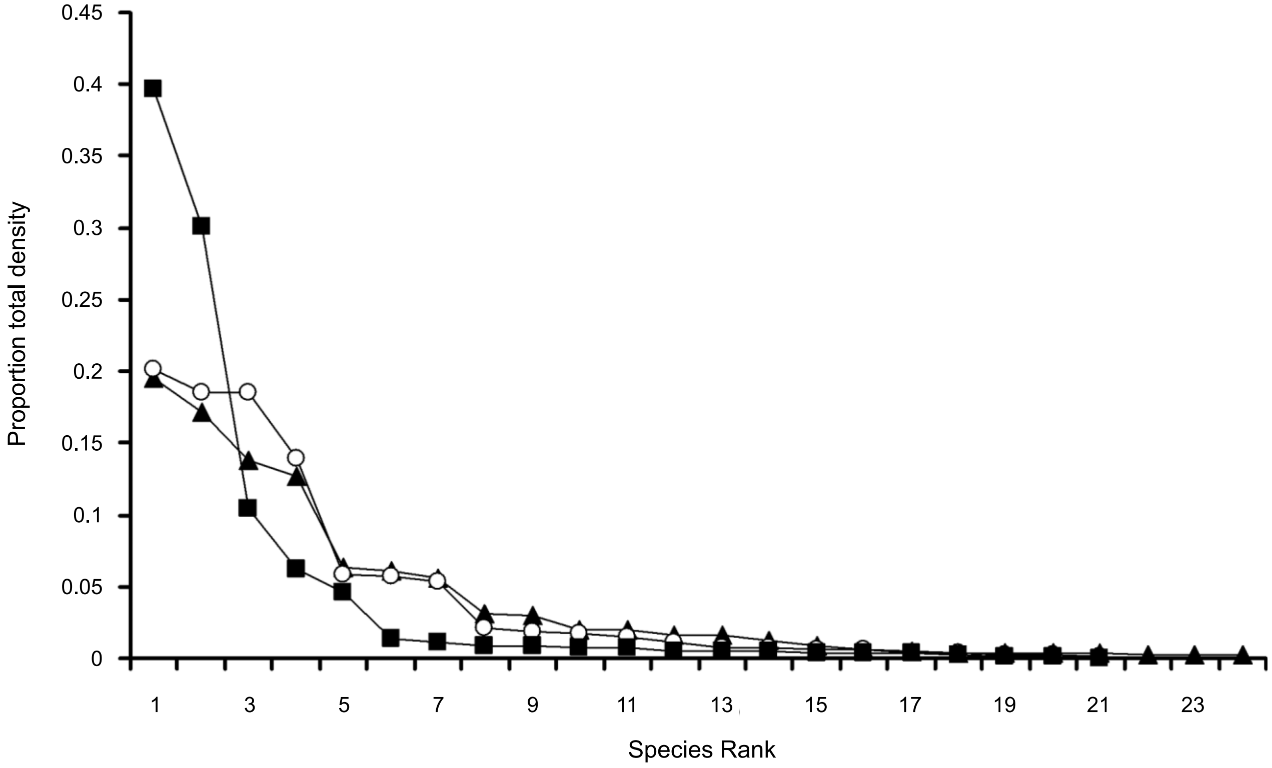


Figure 3. Rank-abundance curves of the bird populations in Pre-thicket (▲), Thicket (○) and Closed canopy (■) second-rotation Sitka Spruce plantations.

Table 2. Mean species richness, total bird density and migrant bird density (± se) in three age classes in first-rotation (data derived from Wilson *et al.* [2006]) and second-rotation forests.

	Species richness		Total bird density (birds ha^{-1})		Migrant bird density (birds ha^{-1})	
Age class	First rotation	Second rotation	First rotation	Second rotation	First rotation	Second rotation
Pre-thicket	12.75 ± 2.17	12.60 ± 1.21	15.16 ± 2.67	26.57 ± 4.98*	1.51 ± 0.14	7.26 ± 1.93*
Thicket	14.50 ± 1.32	13.20 ± 1.50	30.11 ± 4.56	61.24 ± 4.84*	2.82 ± 0.57	4.51 ± 0.67
Closed canopy	12.75 ± 1.79	11.20 ± 0.77	29.05 ± 3.79	56.73 ± 4.62*	0.43 ± 0.09	1.34 ± 0.44

Species richness was calculated as the cumulative number of species recorded at each site between the morning and afternoon visits; *statistically significant difference between rotations ($P < 0.01$).

Table 3. Canopy height and percentage cover (± se) of vegetation variables from first (from Wilson *et al.* [2006]) and second-rotation plantation forest in three age classes.

	Canopy height		Canopy cover		Shrub cover		Field cover	
Age class	First rotation	Second rotation	First rotation	Second rotation	First rotation	Second rotation	First rotation	Second rotation
Pre-thicket	2.2 ± 0.2	2.8 ± 0.3	24.7 ± 6.7	29.8 ± 3.1	11.4 ± 5.4	46.3 ± 4.2*	89.0 ± 4.9*	31.3 ± 10
Thicket	5.7 ± 0.6	5.9 ± 0.4	62.0 ± 7.0	75.3 ± 5.1	15.0 ± 6.9	12.0 ± 3.0	48.1 ± 10.0*	17.2 ± 3.4
Closed canopy	12.6 ± 0.6	13.1 ± 1.1	73.0 ± 2.9*	64.8 ± 2.4	4.2 ± 1.4	5.5 ± 1.9	37.5 ± 8.8**	11.7 ± 5.9

Age class names differ from those used in Wilson *et al.* (2006): Pre-thicket = Younger; Thicket = Intermediate; Closed canopy = Older; *Statistically significant difference between rotations ($P < 0.05$); **statistically significant difference between rotations ($P < 0.01$).

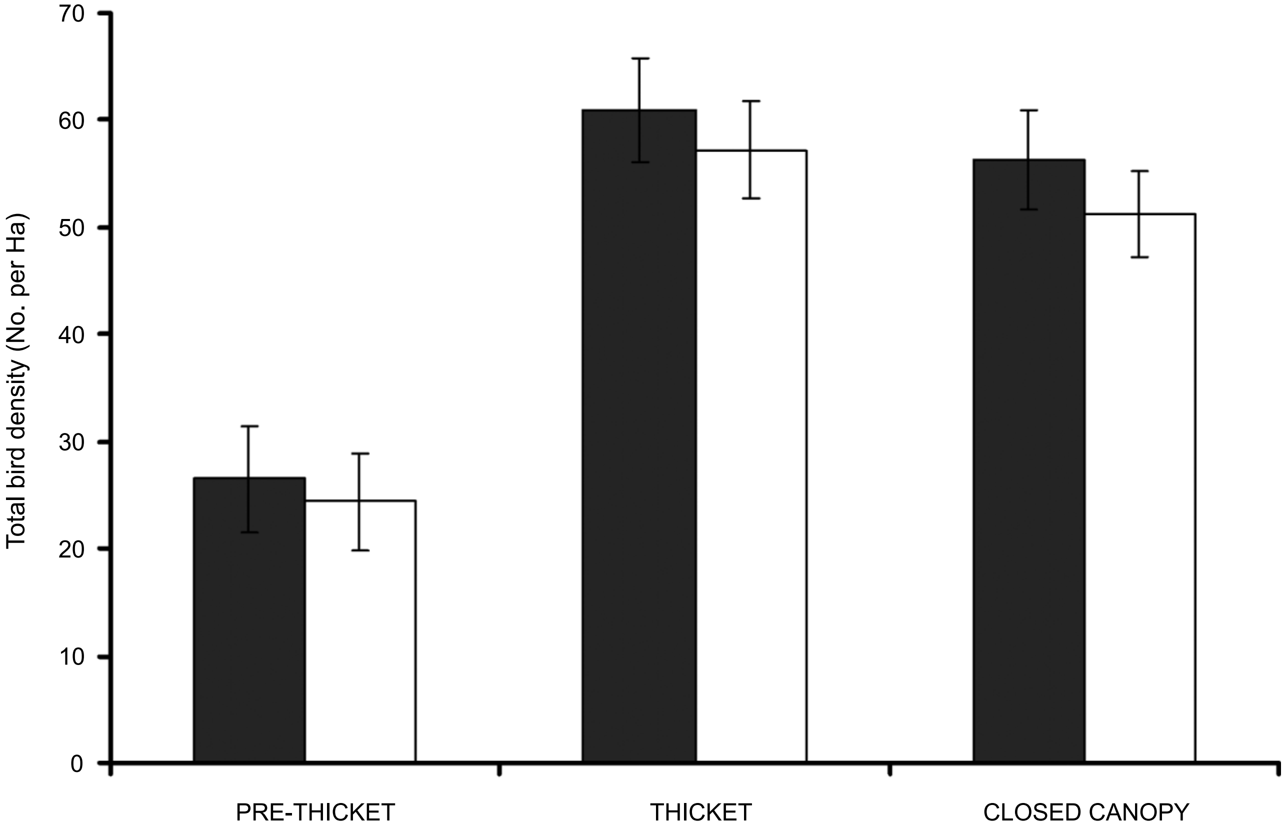


Figure 4. Total bird density (± se) before (dark bars) and after (open bars) correcting for natural population increase.

observed differences were influenced by these species, the values for these species were removed and the data, corrected for population increase, re-analysed. Total bird density was significantly higher in the second rotation in Pre-thicket and Thicket (Pre-thicket, $t = 2.183$, $P < 0.04$; Thicket, $t = 2.047$, $P = 0.05$) in the second rotation, but there was no significant difference between rotations in Closed canopy ($t = 0.363$, $P = 0.72$) (Fig. 5). Species richness and migrant density were unaffected by the removal of these species from analysis.

DISCUSSION

Bird communities in second-rotation forests

Prior to canopy closure, plantations are occupied by bird species characteristic of open habitats (Askins *et al.* 2007), which are replaced by generalist and forest adapted species as canopy closure progresses (Humphrey *et al.* 2003, Wilson *et al.* 2006). In this study, Redpoll and Whitethroat – both species that are closely associated with open habitats – were identified as indicators for Pre-thicket. Coal Tit, Chaffinch, Dunnock, Song Thrush and Robin – indicators for Thicket – are all typical of wooded habitats. Coal Tit was also an indicator for Closed canopy, and the fact that Coal Tit had a higher indicator value for this age class reflects the fact that this species, as well as Goldcrest, favours mature coniferous forests (Snow & Perrins 1998). The results of this study are therefore consistent with those of previous research that has identified changes in bird assemblages as plantations mature.

Early successional forests can be important in the conservation of open habitat specialists (Dettmers 2003, Wilson *et al.* 2006, Burton 2007). Some of the species, including some long-distance migrants, that were found predominantly in Pre-thicket in this study have undergone recent population declines elsewhere in their ranges (Hewson & Noble 2009). Our results therefore support the suggestion that young forests provide important breeding sites for open habitat birds. Common Linnet *Carduelis cannabina* and Common Grasshopper Warbler *Locustella naevia* were both found in Pre-thicket in this study and are on the Amber list

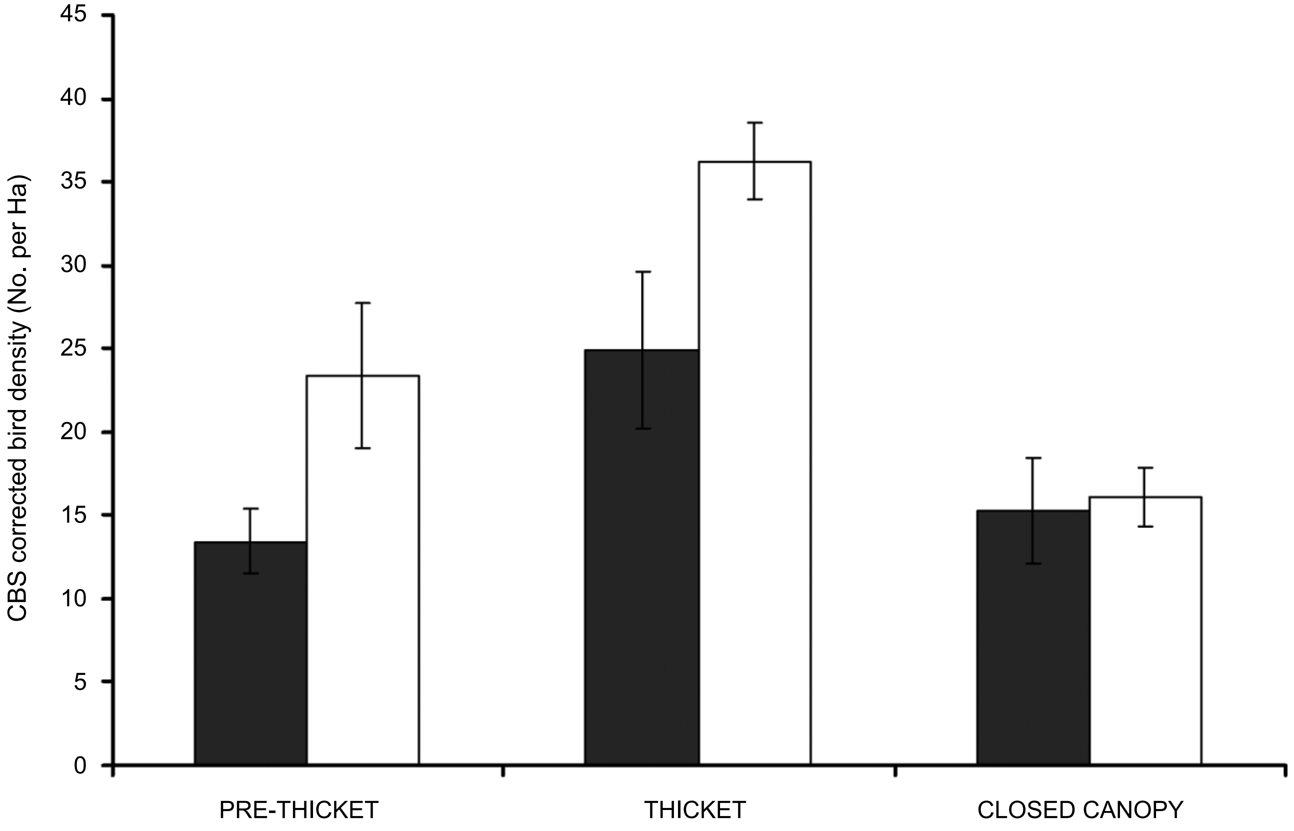


Figure 5. Total bird density (± se) corrected for natural population increase and excluding Coal Tit and Goldcrest in three age classes in first (dark bars) and second (open bars) rotation Sitka Spruce plantations.

in Ireland. Common Linnet is also a Species of European Concern (Lynas *et al.* 2007). No species of conservation concern were recorded in forests in older age classes in this study.

Thicket supported the highest bird density; similar to the findings of a previous study that used broader age classes (Patterson *et al.* 1995). This may be because of the fact that, unlike other age classes, Thicket held relatively high densities of both migrants and resident species. In contrast, migrant density was lower in Closed canopy (Table 2).

Bird species richness was similar between the different age classes despite some turnover in species as plantations matured. Twenty-four species were recorded in Pre-thicket and 21 in Closed canopy, with 13 species common to both age classes. This species turnover is illustrated by the ordination, where Pre-thicket separated clearly from the other age classes. This pattern has also been shown for plantation forests in Britain (Fuller & Browne 2003). These authors point out that the separation of Pre-thicket highlights the importance of this age class to the bird diversity of the commercial forest cycle as the bird assemblage is markedly distinct, whereas those of the other age classes more closely resemble each other.

Closed canopy tended to be occupied by a suite of generalist and forest-adapted species while Pre-thicket was occupied by less common open-habitat specialists, as well as some species found in other age classes. This overlap may be because of the lack of forest bird specialists in Ireland. Island biogeographical factors (Kelly 2008), an east-to-west decrease in bird species richness within Europe (Fuller *et al.* 2007), and historical loss of species owing to extensive deforestation (Yalden & Carthy 2004, Rackham 2006) are possible explanations for this pattern. The generalist nature of the Irish avifauna means that plantation forests support a significant proportion of the terrestrial bird fauna (O'Halloran *et al.* 1998).

Although their slopes were not significantly different, the rank-abundance curves suggest a change in community structure between Pre-thicket and Thicket and the Closed canopy age class. The steep curve in the Closed canopy age class shows that, as plantations mature, the bird community becomes dominated by a small number of common species despite the fact that species richness remains similar throughout the remainder of the forest cycle.

Migrant bird densities in Closed canopy forests were lower than in other age classes because most migrant passerines to Ireland are typical of non-forest habitats (Fuller 1995, Snow & Perrins 1998, Robinson 2005). In Great Britain, the proportion of migrants in first-rotation plantations is greatest in young and mature forests, with lower numbers present in intermediate stages (Donald *et al.* 1998). The mature forests with high migrant densities in that study were between 50 and 90 years old, whereas the maximum age of Closed canopy forests in our study was 50 years. Most commercial plantations in Ireland are felled at or before this age. However, the forest migrants such as Common Redstart *Phoenicurus phoenicurus*, Wood Warbler *Phylloscopus sibilatrix* and Pied Flycatcher *Ficedula hypoleuca*, typical of forest habitats and partially responsible for the observed increase in migrants in later growth stages in Great Britain, are all but absent from Ireland. It is not completely clear whether this pattern is because of biogeographical factors such as Ireland's distance from migration pathways, or to historical deforestation. The fact that the aforementioned migrants breed in large numbers on the western seaboard of Britain (Robinson 2005), but are almost entirely absent in eastern counties of Ireland (such as Wicklow) that possess some apparently suitable habitat, suggests that deforestation alone cannot account for their absence. The absence of these species may limit the potential for increases in migrant density in later age classes, even if Irish plantations were allowed to develop beyond commercial maturity, but this could be tested by allowing some plantations to over-mature.

Vegetation structure and differences between rotations

The ordination (Fig. 2) represents a gradient from immature, structurally diverse Pre-thicket forests characterized by high shrub cover and a low, open canopy on the right, through to commercially mature plantations characterized by high needle and moss cover and low shrub cover on the left. There is little difference in forest structure between Mid-rotation and Mature forests and hence little change in bird habitat in the last 20 years of a forest's rotation, which helps to explain the overlap in the bird communities of these age classes.

Shrubs benefit birds by increasing habitat heterogeneity (Berg 2002, Diaz 2006) and providing nest-sites and invertebrate prey (Quine *et al.* 2007). In light of this, the fact that the forests with the highest levels of shrub cover, Pre-thicket, also had the lowest total bird density in both rotations initially appears counter-intuitive. Low bird density has previously been noted in young plantations (Bibby *et al.* 1985, Donald *et al.* 1998) and may be because of the lower surface area of the crowns and trunks of small trees for foraging and nesting.

Despite there being no significant difference in total bird density between rotations in Pre-thicket after correcting for natural population increase, second-rotation Pre-thicket did support significantly higher migrant bird density than first-rotation Pre-thicket. This likely reflects the fact that many migrant passerines to Ireland utilize shrubs for nesting or foraging (Fuller 1995, Snow & Perrins 1998, Robinson 2005), and the higher shrub cover in the second rotation increased the carrying capacity of this age class for such migrant species. However, some resident species, notably Sky Lark *Alauda arvensis* which is a species of conservation concern (Lynas *et al.* 2007), were recorded at lower density in second-rotation Pre-thicket than in the first rotation. Sky Lark requires open ground for nesting (Snow & Perrins 1998) and the increase in shrub cover may render second-rotation Pre-thicket less suitable than first-rotation Pre-thicket for this species. A similar mechanism may explain the lower densities of Meadow Pipit *Anthus pratensis* and Reed Bunting *Emberiza schoeniclus* in second-rotation Pre-thicket.

The indicator species for the three age classes in this study differed slightly from those of the three age classes in the first rotation (Wilson *et al.* 2006), but there was considerable overlap. This suggests that, although differences exist in both vegetation structure and the bird communities of a particular age class in different rotations, these differences are not fundamental enough to change their suitability to particular species. For example, Chaffinch was an indicator of Closed canopy forest in the first rotation and Thicket in the second, but it seems unlikely that this pattern is driven by fundamental differences in second-rotation forests. Chaffinch is a widespread generalist species and was also present at relatively high density in second-rotation Closed canopy.

Second-rotation forests differ from those of the first-rotation in their pre-planting state. While afforestation typically involves a change from open habitat to forest, second-rotation plantations replace recently harvested forests. Forestry activities can affect soils (Worrell & Hampson 1997), and the productivity of a site may increase in later rotations as a result of deposited organic matter (Fox 2000). Additionally, young stands of second-rotation forests may differ structurally from first-rotation stands because non-crop tree species have had more time to colonize both prior to and following clear felling (Cooper *et al.* 2008). Because changes in bird communities are often related to changes in vegetation (Cherkaoui *et al.* 2009, Nikolov 2009) we may, therefore, expect young second-rotation plantations to have a higher carrying capacity for birds than similarly-aged first-rotation plantations.

However, the greatest differences between rotations were found in later age classes when structural complexity was low in second-rotation forests, and differences in vegetation between rotations were small. In Closed canopy, differences between rotations were largely due to increases in two species, Coal Tit and Goldcrest and, when these species were removed, the difference in total density between rotations in Closed canopy was no longer significant (Fig. 5). Work is ongoing to test whether invertebrate abundance is different between rotations, and whether this can explain the difference in Coal Tit and Goldcrest density. Populations of both Coal Tit and Goldcrest are increasing in Ireland, perhaps as a consequence of increasing plantation forest cover, and so natural population increase in the time period between the first- and second-rotation fieldwork may also account for some of the difference. Finally, because different observers were used in the first- and second-rotation fieldwork and density estimations of Coal Tit and Goldcrest are particularly prone to observer differences, it is difficult to exclude completely an affect of observer on the densities of these species.

Bird density remained higher in second-rotation Thicket after the removal of Coal Tit and Goldcrest, despite a reduction in shrub and field cover in the second rotation. Some birds may utilize young plantation trees as tall shrubs (Loyn *et al.* 2007), and the slightly taller trees and higher canopy cover in the second rotation (Table 3) may, therefore, have provided more nesting and foraging opportunities. The increase in canopy cover in second-rotation Thicket may reflect a slight improvement in growth rates of the crop species in the second rotation. The higher densities of Robin and Chaffinch in second-rotation Thicket are difficult to explain as shrub and canopy cover were similar between rotations. Both are generalist species that thrive in a range of habitats, although Robin may benefit from brash piles in second-rotation forests left over after clear-felling (Snow & Perrins 1998).

Migrant birds are typically more vulnerable to decline than sedentary species (Heldbjerg & Fox 2008, Kirby *et al.* 2008). The higher density of migrants in second-rotation Pre-thicket therefore suggests that the increasing extent of second-rotation Pre-thicket in the landscape may be a positive development for such species, especially as some of the migrant species in this study have declined in other parts of their ranges (Hewson & Noble 2009). However, comparisons of densities recorded in different years must be interpreted with caution as breeding numbers of species such as Grasshopper Warbler are known to fluctuate from year to year (Snow & Perrins 1998).

Conclusion

Although species richness was similar between age classes, bird assemblages of Pre-thicket and Thicket forests were more even than those of Closed canopy forests, which were dominated by two or three common species. Migrant densities were low in Closed canopy forests, likely owing to the habitat preferences of these species. Pre-thicket, and to a lesser extent Thicket, supported species that are declining elsewhere. This study supports previous findings in illustrating the importance of Pre-thicket to the diversity of coniferous plantations.

Higher migrant bird density in second-rotation Pre-thicket is likely linked to increased shrub cover, while differences in other age classes between rotations may be due to differences in crop vegetation structure. Differences between Closed canopy forests may also have been partially affected by observer differences, but this is unlikely to have been the case in Pre-thicket or Thicket.

The species present at higher densities in the second rotation tended to be common species, which suggests that the future expansion of second-rotation forests will not affect all species equally. Notably, some species of conservation concern were also present at higher density in young second-rotation forests than in first-rotation forests, although one was present at lower density.

The future increase of second-rotation plantations may benefit bird communities up to the point of canopy closure. However, bird assemblages in the second rotation were broadly similar to the first rotation, and became more so as the forest cycle progressed. Management, targeted at the Closed canopy stage of the forest cycle and aiming to increase habitat heterogeneity, may help to decrease the dominance of a small number of species and enable plantations to benefit a wider range of species.

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. Dr Anne Oxbrough, Dr Linda Coote, Karen Moore, Dr Dan Chamberlain and three anonymous reviewers all made invaluable comments and suggestions on the manuscript.

ENDNOTE

a. The following NMS setup was used: random starting coordinates with 6 axes; maximum iterations = 500; 250 runs with real data; 250 runs with randomized data; stability criterion = 0.00000 with 10 iterations to evaluate stability; reduction in dimensionality at each cycle = 1 with initial step length 0.2.

REFERENCES

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

Askins, R.A., Zuckerberg, B. & Novak, L. 2007. Do the size and landscape context of forest openings influence the abundance and breeding success of shrubland songbirds in southern New England? *Forest Ecol. Manag.* **250:** 137–147.

Berg, A. 2002. Breeding birds in short-rotation coppices on farmland in central Sweden – the importance of *Salix* height and adjacent habitats. *Agri. Ecosyst. Environ.* **90:** 265–276.

Bibby, C.J., Phillips, B.N. & Seddon, A.J.E. 1985. Birds of restocked conifer plantations in Wales. *J. Appl. Ecol.* **22:** 619–633.

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

Brockerhoff, E., Jactel, H., Parrotta, J., Quine, C. & Sayer, J. 2008. Plantation forests and biodiversity: oxymoron or opportunity? *Biodivers. Conserv.* **17:** 925–951.

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

Burton, N.H.K. 2007. Influences of restock age and habitat patchiness on Tree Pipits *Anthus trivialis* breeding in Breckland pine plantations. *Ibis* **149:** 193–204.

Cherkaoui, I., Selmi, S., Boukhriss, J., Hamid, R.-I. & Mohammed, D. 2009. Factors affecting bird richness in a fragmented cork oak forest in Morocco. *Acta Oecol.* **35:** 197–205.

Christian, D.P., Hoffman, W., Hanowski, J.M., Niemi, G.J. & Beyea, J. 1998. Bird and mammal diversity on woody biomass plantations in North America. *Biomass & Bioenergy* **14:** 395–402.

Coombes, R.H., Crowe, O., Lauder, A., Lysaght, L., O'Brien, C., O'Halloran, J., O'Sullivan, O. & Tierney, T.D. 2009. *Countryside Bird Survey Report 1998–2007.* BirdWatch Ireland, Wicklow, Ireland.

Cooper, A., McCann, T. & Ridge, D. 2008. Vegetation development in second rotation Irish conifer plantations. *Forest Ecol. Manag.* **255:** 962–972.

Cronk, Q. & Ojeda, I. 2008. Bird-pollinated flowers in an evolutionary and molecular context. *J. Exp. Bot.* **59:** 715–727.

Cross, J.R. 1998. An outline and map of the potential natural vegetation of Ireland. *Appl. Veg. Sci.* **1:** 241–252.

Dettmers, R. 2003. Status and conservation of shrubland birds in the northeastern US. *Forest Ecol. Manag.* **185:** 81–93.

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.

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

Food and Agriculture Organisation of the United Nations 2007. *State of the World's Forests 2007.* FAO, 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

Forest Service. 2000. *Code of Best Forest Practice.* Forest Service, Wexford, Ireland.

Forest Service. 2007. *National Forest Inventory – Republic of Ireland.* Forest Service, Wexford, Ireland.

Fox, T.R. 2000. Sustained productivity in intensively managed forest plantations. *Forest Ecol. Manag.* **138:** 187–202.

Fuller, R.J. 1995. *Bird Life of Woodland and Forest.* Cambridge University Press, Cambridge, UK.

Fuller, R.J. & 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*: 93–99. Forestry Commission, Edinburgh, UK.

Fuller, R.J., Gaston, K.J. & Quine, C.P. 2007. Living on the edge: British and Irish woodland birds in a European context. *Ibis* **149:** 53–63.

Gómez, J.M. 2003. Spatial patterns in long-distance dispersal of *Quercus ilex* acorns by jays in a heterogeneous landscape. *Ecography* **26:** 573–584.

Gunnarsson, B., Heyman, E. & Vowles, T. 2009. Bird predation effects on bush canopy arthropods in suburban forests. *Forest Ecol. Manag.* **257:** 619–627.

Heldbjerg, H. & Fox, T. 2008. Long-term population declines in Danish trans-Saharan migrant birds. *Bird Study* **55:** 267–279.

Hewson, C.M. & Noble, D.G. 2009. Population trends of breeding birds in British woodlands over a 32-year period: relationships with food, habitat use and migratory behaviour. *Ibis* **151:** 464–486.

Humphrey, J.W., Ferris, F. & Quine, C.P. 2003. *Biodiversity in Britain's planted forests.* Forestry Commission, Edinburgh, UK.

Iremonger, S., O'Halloran, J., Kelly, D., Wilson, M., Smith, G., Gittings, T., Giller, P.S., Mitchell, F., Oxbrough, A., Coote, L., French, L., O' Donoghue, S., McKee, A., Pithon, J., O'Sullivan, A., Neville, P., O'Donnell, V., Cummins, V., Kelly, T. & Dowding, P. 2006. *Biodiversity in Irish plantation forests.* BioForest Project final synthesis report made to the EPA and COFORD.

Kelly, T.C. 2008. The origin of the avifauna of Ireland. *Ir. Nat. J.* **Spec. Suppl.:** 97–107.

Kirby, J.S., Stattersfield, A.J., Butchart, S.H.M., Evans, M.I., Grimmett, R.F.A., Jones, V.R., O'Sullivan, J., Tucker, G.M. & Newton, I. 2008. Key conservation issues for migratory land

and waterbird species on the world's major flyways. *Bird Conserv. Int.* **18:** S49–S73.

Loyn, R.H., McNabb, E.G., Macak, P. & Noble, P. 2007. Eucalypt plantations as habitat for birds on previously cleared farmland in south-eastern Australia. *Biol. Conserv.* **137:** 533–548.

Lynas, P., Newton, S.F. & Robinson, J.A. 2007. The status of birds in Ireland: an analysis of conservation concern 2008–2013. *Ir. Birds* **8:** 149–167.

Magurran, A.E. 2004. *Measuring Biological Diversity*. Blackwell Science Ltd, Oxford, UK.

Maicas, R. & Fernandez Haeger, J. 2004. Pine plantations as a breeding habitat for a hole-nesting bird species Crested Tit (*Parus cristatus*) in southern Spain. *Forest Ecol. Manag.* **195:** 267–278.

Martinez, I., Garcia, D. & Obeso, J.R. 2008. Differential seed dispersal patterns generated by a common assemblage of vertebrate frugivores in three fleshy-fruited trees. *Ecoscience* **15:** 189–199.

McCune, B. & Grace, J.B. 2002. *Analysis of Ecological Communities*. MjM Software Design, Gleneden Beach, OR.

McCune, B. & Mefford, M.J. 2006. *PC-ORD. Multivariate Analysis of Ecological Data*. MjM Software, Gleneden Beach, OR.

Mitchell, F.J.G. 1995. The dynamics of Irish post-glacial forests. In Pilcher, J.R. & Mac an tSaoir, S. (eds) *Wood, Trees and Forests in Ireland*. Royal Irish Academy, Dublin, Ireland.

Mortensen, H.S., Dupont, Y.L. & Olesen, J.M. 2008. A snake in paradise: disturbance of plant reproduction following extirpation of bird flower-visitors on Guam. *Biol. Conserv.* **141:** 2146–2154.

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. *Irish Forestry* **55:** 2–14.

Patterson, I.J., Ollason, J.G. & Doyle, P. 1995. Bird populations in upland spruce plantations in northern Britain. *Forest Ecol. Manag.* **79:** 107–131.

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.

Rackham, O. 2006. *Woodlands*. HarperCollins, London.

Robinson, R.A. 2005. *Birdfacts: Species Profiles of Birds Occurring in Britain and Ireland*. British Trust for Ornithology, Thetford, UK.

Santos, T., Telleria, J.L., Diaz, M. & Carbonell, R. 2006. Evaluating the benefits of CAP reforms: can afforestations restore bird diversity in Mediterranean Spain? *Basic Appl. Ecol.* **7:** 483–495.

Schieck, J. 1997. Biased detection of bird vocalizations affects comparisons of bird abundance among forested habitats. *Condor* **99:** 179–190.

Sekercioglu, C.H. 2006. Increasing awareness of avian ecological function. *TREE* **21:** 464–471.

Skoczylas, D.R., Muth, N.Z. & Niesenbaum, R.A. 2007. Contribution of insectivorous avifauna to top down control of *Lindera benzoin* herbivores at forest edge and interior habitats. *Acta Oecol.* **32:** 337–342.

Snow, D.W. & Perrins, C.M. 1998. *The Birds of the Western Palearctic*, concise edn. Oxford University Press, Oxford, UK.

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, 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., Irwin, S., Norriss, D.W., Newton, S.F., Collins, K., Kelly, T.C. & O'Halloran, J. 2009. The importance of pre-thicket conifer plantations for nesting Hen Harriers *Circus cyaneus* in Ireland. *Ibis* **151:** 332–343.

Worrell, R. & Hampson, A. 1997. The influence of some forest operations on the sustainable management of forest soils – a review. *Forestry* **70:** 61–85.

Yalden, D.W. & Carthy, R.I. 2004. The archaeological records of birds in Britain and Ireland compared: extinctions or failures to arrive? *Environ. Archaeol.* **9:** 123–126.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G. 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer Science+Business Media, New York.

(MS received 11 January 2010; revised MS accepted 23 March 2010)