Factors affecting the bird diversity of planted and semi-natural oak forests in Ireland

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Capsule In Ireland, which has relatively low diversity of bird species, commercially mature plantation oak forests (aged 72–151 years old) have similar bird diversity to typical semi-natural oak woodlands, and higher bird diversity than over-browsed semi-natural oak woodland, with bird diversity related to habitat complexity.

Aims To investigate whether oak plantations can support comparable bird assemblages to semi-natural oak woodlands, and to assess if high levels of ungulate browsing and grazing impact on the quality of semi-natural oak woodland habitat for birds.

Methods Bird and vegetation surveys were conducted in commercially mature oak plantations ($n = 4$), semi-natural oak woodlands ($n = 10$) and intensively browsed semi-natural oak woodland ($n = 4$). Species richness, total bird density, warbler density and density of parids were compared between oak forest types. Variation in bird communities between sites was investigated using ordination, and relationships between bird and vegetation metrics were assessed using general linear models.

Results Bird diversity in plantation oak and the semi-natural forests subject to low levels of ungulate browsing, was similar, with no difference in species richness, total bird density or density of warbler and density of parids. However, browsed semi-natural oak woods had lower species richness than either of the other two study site types, and lower density of warblers than oak plantations. These observed differences in bird communities appear to be a result of browsing mediated differences in habitat complexity between the forest types.

Conclusions Plantation forests of native tree species may support comparable bird communities to semi-natural woodlands in areas that lack forest specialists. Bird diversity in woodlands subject to high levels of browsing and grazing is likely to be limited, unless ungulate populations and their access to these woodlands are managed to promote the development of a more complex understorey.

Although it was once extensively forested, Ireland's forest cover today, at 11% of land area, is one of the lowest in the EU (FAO 2011). Before extensive deforestation, Ireland was largely covered in *Ulmus-Quercus* (elm and oak) woodland (Mitchell & Ryan 1997) but today such semi-natural forests are rare in Ireland, covering less than 1.5% of the country (Forest Service 2007). Ireland is conspicuously lacking in forest specialist birds even when compared to the bird assemblages of forests in Britain, where there are far fewer forest specialists than on mainland Europe

(Fuller *et al.* 2007). This is probably due to a combination of Ireland's geographical location as an island at the western extremes of Europe (Fuller *et al.* 2007), and the paucity of forest cover in Ireland over the last few centuries (O'Halloran & Kelly 2012). However, Ireland had the highest afforestation rate in Europe between 1990 and 2007, despite not always achieving the ambitious targets set by government policy (Malone 1998, COFORD Council 2009). As a result, 87% of the forest cover in Ireland is composed of plantations, in which approximately 97% of the trees are conifers, with broadleaf plantations currently accounting for just 0.3% of Ireland's land cover (Forest Service 2007). However, broadleaf planting has increased substantially in the last decade, from 15% of

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new plantings in 1994–98 to 36% in the period 2009–12 (Forest Service 2012).

The ongoing expansion of plantation forest cover in Ireland and many other European countries (FAO 2007), in combination with a decline in woodland bird species throughout the continent (Fuller *et al.* 2005, Gregory *et al.* 2007), mean that assessments of the bird communities supported by plantation forests are timely (Sweeney *et al.* 2010a). This is particularly true in Ireland where plantations are potentially of greater local conservation importance than in regions where forest cover is dominated by native woodlands (Berndt *et al.* 2008, Bremer & Farley 2010). The benefits of plantation forests for biodiversity may be affected by a number of factors including the species of tree planted and various aspects of plantation management (Stephens & Wagner 2007, Brockerhoff *et al.* 2008, Bremer & Farley 2010). While many studies have shown that plantations of exotic species can contribute to the conservation of biodiversity (Humphrey *et al.* 2000, Berndt *et al.* 2008, Pawson *et al.* 2009, Wilson *et al.* 2009), native species are generally considered preferable for biodiversity conservation because of their higher value as habitat for native species (Brockerhoff *et al.* 2008, Bremer & Farley 2010). Several studies have noted that oak trees (*Quercus robur & Q. petraea*) have the highest number of associated canopy invertebrates of any tree in Britain (Southwood *et al.* 1982, Kennedy & Southwood 1984, Southwood 1996) with beneficial impacts for forest species that rely on invertebrates (Whittingham *et al.* 2001). For example, oaks were found to be preferentially selected for foraging by breeding Chaffinches (when not cited in the text, species names are listed in Table 1), with broods located near oaks experiencing greater fledgling success (Whittingham *et al.* 2001).

However, the contribution of any forest to the conservation of biodiversity can be affected by factors other than the species of tree contained within a forest, such as grazing and browsing by herbivores. Deer abundance is increasing in Europe (Gill 1990, Ward 2005, Loe *et al.* 2009, Apollonio *et al.* 2010) and they can exert a considerable influence on the vegetation structure of woodlands (Gill & Beardall 2001, Perrin *et al.* 2006, Newson *et al.* 2012) and on ecosystem functioning (Newson *et al.* 2012). Excessive grazing (herbivory in ground and herb layers of vegetation) and browsing (foraging of vegetation in shrub and understorey layers) can impact negatively on woodland habitat complexity by decreasing the cover

and suppressing the development of shrubs, climbers, seedlings and saplings, as well as vegetation in the ground and herb layers (Putman *et al.* 1989, Gill & Beardall 2001, Stockton *et al.* 2005, Gill 2006, Holt *et al.* 2013). These impacts (hereon referred to collectively as 'browsing') can have cascading impacts on the biodiversity of birds (Martin & Joron 2003, Allombert *et al.* 2005a, Gill & Fuller 2007, Newson *et al.* 2012) and other taxa (Putman *et al.* 1989, Baines *et al.* 1994, Allombert *et al.* 2005b). The impact of deer browsing on woodland understorey vegetation can affect birds through loss of nest sites, increased vulnerability to nest predation and changes in food supply (Martin & Joron 2003). Numerous studies have shown that the abundance of a wide range of invertebrates can be reduced by ungulate browsing (Putman *et al.* 1989, González-Megías *et al.* 2004, Allombert *et al.* 2005b), including *Lepidoptera* larvae which are of considerable importance to several species of birds during the breeding season (Baines *et al.* 1994).

The main aim of this study was to evaluate whether oak plantation forests can support similar bird communities to those of semi-natural oak woodlands in Ireland. We also wished to assess the extent to which variation in the bird communities of semi-natural woodlands was related to intensive browsing by ungulates, and to elucidate the influence of forest vegetation structure on the bird diversity of oak forests.

METHODS

Bird assemblage and habitat data were collected from 14 semi-natural oak forests and four commercially mature oak plantations (ranging in age from 72 to 151 years) in Ireland (Fig. 1). Of these 14 semi-natural oak woodlands, four sites were located in one area around Killarney in County Kerry and are subject to atypically intensive browsing by wild populations of Sika (*Cervus nippon*) and Red (*Cervus elaphus*) deer (Higgins *et al.* 2001). The other ten semi-natural woodlands and the oak plantations experience variable levels of browsing by ungulates but at levels far below that of the intensively grazed oak semi-natural woodlands. We use the term 'semi-natural forest' because it is difficult to confirm if these forest have not been modified by human activity as some stage. A selection criterion for these sites was that they were shown as being present on maps from the 1840s.

Vegetation variables were estimated visually at each of six point-count locations at each site. Variables recorded were canopy height (m), canopy cover including

Table 1. Bird species recorded in each of the oak forest types, their average population densities (no. ha^{-1} ± standard error), the detection group (DG) to which each was assigned and Pearson's *r* correlation coefficients with axes 1 and 2 of the NMDS ordination. Species with no Pearson's *r* correlation coefficients were recorded at fewer than 5% of the study sites and were excluded from the NMDS analysis.

Species	Scientific name	DG	Semi-natural oak	Browsed semi-natural oak	Plantation oak	*r* Axis 1	*r* Axis 2
Blackbird	*Turdus merula*	1	2.80 ± 0.57	0.42 ± 0.17	1.50 ± 0.49	0.04	−0.38
Blackcap	*Sylvia atricapilla*	1	1.30 ± 0.34	0.63 ± 0.13	2.76 ± 0.40	−0.59	0.22
Blue Tit	*Cyanistes caeruleus*	4	5.93 ± 0.98	11.6 ± 5.74	9.95 ± 3.08	−0.21	−0.74
Bullfinch	*Pyrrhula pyrrhula*	3	0.04 ± 0.03	0.15 ± 0.04	0.22 ± 0.07	−0.36	0.07
Buzzard	*Buteo buteo*	1	0	0	0.06 ± 0.05	–	–
Chaffinch	*Fringilla coelebs*	3	3.12 ± 0.40	2.91 ± 0.63	1.77 ± 0.43	0.56	−0.41
Chiffchaff	*Phylloscopus collybita*	1	0.86 ± 0.23	0	2.31 ± 0.98	−0.38	−0.07
Coal Tit	*Periparus ater*	4	6.41 ± 1.18	7.54 ± 2.21	8.15 ± 2.10	−0.27	−0.72
Cuckoo	*Cuculus canorus*	3	0.07 ± 0.05	0	0	0.38	0.01
Dunnock	*Prunella modularis*	2	0.09 ± 0.04	0	0.53 ± 0.25	−0.55	−0.06
Garden Warbler	*Sylvia borin*	1	0.04 ± 0.04	0	0	–	–
Goldcrest	*Regulus regulus*	4	7.19 ± 0.85	6.10 ± 3.65	1.07 ± 0.36	0.43	−0.68
Grasshopper Warbler	*Locustella naevia*	1	0.02 ± 0.02	0	0	–	–
Great Tit	*Parus major*	3	0.61 ± 0.10	0.73 ± 0.17	0.81 ± 0.27	−0.04	−0.70
Hooded Crow	*Corvus cornix*	1	0.02 ± 0.02	0	0.06 ± 0.05	−0.25	−0.13
Jackdaw	*Corvus monedula*	1	0.02 ± 0.02	0	0.07 ± 0.06	−0.08	−0.25
Jay	*Garrulus glandarius*	2	0.37 ± 0.12	0.08 ± 0.07	0.52 ± 0.35	−0.25	0.10
Lesser Redpoll	*Carduelis cabaret*	3	0.01 ± 0.01	0	0	–	–
Longtailed Tit	*Aegithalos caudatus*	4	1.32 ± 0.51	0.18 ± 0.16	0.57 ± 0.49	0.37	−0.18
Magpie	*Pica pica*	1	0.36 ± 0.13	0	0.15 ± 0.07	0.10	−0.09
Mistle Thrush	*Turdus viscivorus*	1	0.16 ± 0.04	0	0.13 ± 0.06	−0.01	0.21
Pheasant	*Phasianus colchicus*	1	0.12 ± 0.05	0.15 ± 0.08	0.22 ± 0.13	−0.15	0.50
Raven	*Corvus corax*	1	0	0	0	–	–
Robin	*Erithacus rubecula*	2	5.49 ± 0.45	4.41 ± 1.09	2.64 ± 0.36	0.52	0.09
Rook	*Corvus frugilegus*	1	0.02 ± 0.02	0	0	–	–
Siskin	*Carduelis spinus*	3	0.06 ± 0.02	0	0	0.51	0.21
Song Thrush	*Turdus philomelos*	1	1.24 ± 0.18	0.27 ± 0.15	0.92 ± 0.19	0.09	−0.43
Sparrowhawk	*Accipiter nisus*	2	0.12 ± 0.07	0	0	0.01	−0.20
Spotted Flycatcher	*Muscicapa striata*	2	0.08 ± 0.05	0.36 ± 0.18	0.08 ± 0.07	0.15	−0.31
Stock Dove	*Columba oenas*	1	0.06 ± 0.06	0	0	–	–
Swallow	*Hirundo rustica*	1	0.02 ± 0.02	0.08 ± 0.07	0	0.37	0.16
Treecreeper	*Certhia familiaris*	2	0.68 ± 0.12	0.36 ± 0.22	0.20 ± 0.10	0.44	−0.32
Whitethroat	*Sylvia communis*	1	0.01 ± 0.01	0	0	–	–
Willow Warbler	*Phylloscopus trochilus*	1	0.81 ± 0.36	0.71 ± 0.12	0.78 ± 0.39	0.06	0.20
Wood Pigeon	*Columba palumbus*	1	1.07 ± 0.20	0.08 ± 0.07	1.89 ± 0.76	−0.30	−0.24
Wren	*Troglodytes troglodytes*	1	4.23 ± 0.65	1.71 ± 0.41	5.23 ± 0.92	−0.37	−0.38

understorey cover (%), percentage shrub cover (woody vegetation between 0.5 and 2 m in height) and percentage ground vegetation cover (0.5 m in height or less). Measurements from individual point locations were averaged to generate site means. The same methodologies for measuring vegetation were used in all sites, and all observers trained with one another and took part in measurements by multiple observers at the same sites (in these and other forest sites) to ensure that the simple measures of vegetation structure recorded were repeatable between observers.

Birds communities were sampled at six point locations in each study site using point-count methodology (Bibby *et al.* 2000) as in other similar surveys (Sim *et al.* 2005, Wilson *et al.* 2006, Sweeney *et al.* 2010c) with each

point count conducted for five minutes. Surveys of the plantations and the browsed semi-natural oak forests were carried out in the summer of 2011, and of the semi-natural oak forests in the summers of 2007 and 2008. Data were collected at each site over two visits, one in May/early June and the second in June/early July, between the hours of 07:00 and 18:00 by the same observer. One morning and one afternoon survey were conducted at each site, in order to cover the relatively large number of sites. During each five minute count, the species and behaviour of all birds detected within 100 m of the observer were recorded. Absolute distances of birds from the observer were estimated, and accuracy of estimates in the field was improved using combinations of range-finding
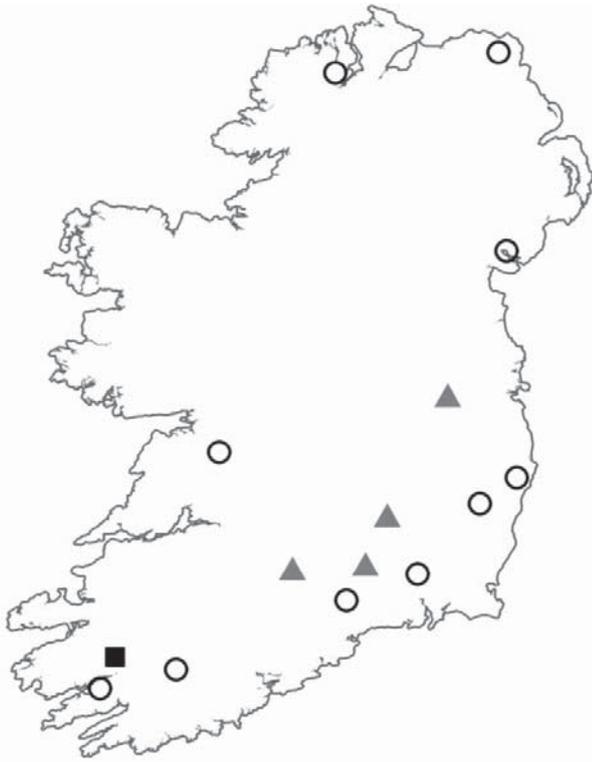
Figure 1. Map of Ireland showing the location of the ten semi-natural oak forests (open circles), four oak plantation forests (grey triangles) and the four grazed semi-natural oak forests (black square, only one symbol is displayed for the four semi-natural sites as they were located close together).

binoculars, detailed field maps and aerial photos. Surveys were carried out by three different experienced observers, with two observers collecting data in 2007–2008 and a third observer collecting data in 2011. Year of data collection was included in analyses to ensure there was no observer bias. Bird surveys were not conducted in winds greater than Beaufort scale 4 or in heavy or persistent rain. Clusters of birds of the same species were recorded as having a maximum number of two individuals to reduce the influence of family parties with fledglings on density estimates. All observations except those of birds only observed flying overhead were included in the analyses, because the presence of overflying birds could not be assumed to indicate an association with that habitat.

Distance (version 5.0) software was used to derive individual species densities from field observations (Buckland *et al.* 2001) collected during point counts, with the distributions of distances at which birds were recorded being used to derive detection functions.

Each species was assigned to one of four detection groups based on aspects of the ecology and behaviour likely to influence species' detectability (Table 1), with separate detection functions generated for each of the four species' groups. Species were assigned to such detection groups because *Distance* requires approximately 60 bird detections to generate reliable detection functions and several species were recorded too seldom to generate species specific detection functions. Analysis assumed that counts were of clusters of birds for distance analyses and Akaike information criterion (AIC) was used to select between four models for fitting of the detection functions: Uniform + Cosine, Uniform + Polynomial, Half normal + Hermite and Hazard-rate + Cosine (Buckland *et al.* 2001). Species richness, total bird density, density of warbler and density of parids were calculated for each study site. Warblers and tits were combined on the basis of broad intra-family similarities in nesting substrate – the three parid species are the most common hole-nesters in Ireland and so potentially affected by availability of old trees and standing deadwood, while the warblers all nest on or near the ground (and so potentially affected by ground and shrub cover, and therefore by grazing levels). Species richness was calculated as the cumulative number of species recorded over both visits in each site. Species richness values presented here should not be interpreted as the total number of bird species present in each site, but rather should be treated as standardized measures of bird diversity that enable comparison between site types.

Generalized linear models were used to test for differences in the recorded vegetation variables between forest types. We used an information theoretic model averaging framework based on Akaike's information criterion corrected for small sample sizes (AIC_c) to model relationships between vegetation variables between forest types. As forest type was collinear with each of the vegetation variables, generalized linear models assuming Gaussian and Poisson distributions for densities and species richness, respectively, with forest type as the single response variable, were run to calculate the residuals from these models. The remaining variation in the data was then analysed using generalized linear models using a Gaussian distribution to identify how much residual variation in species richness, total bird density and density of warbler and parids was related to the recorded vegetation variables. Variables included in each analysis were canopy cover and height, shrub
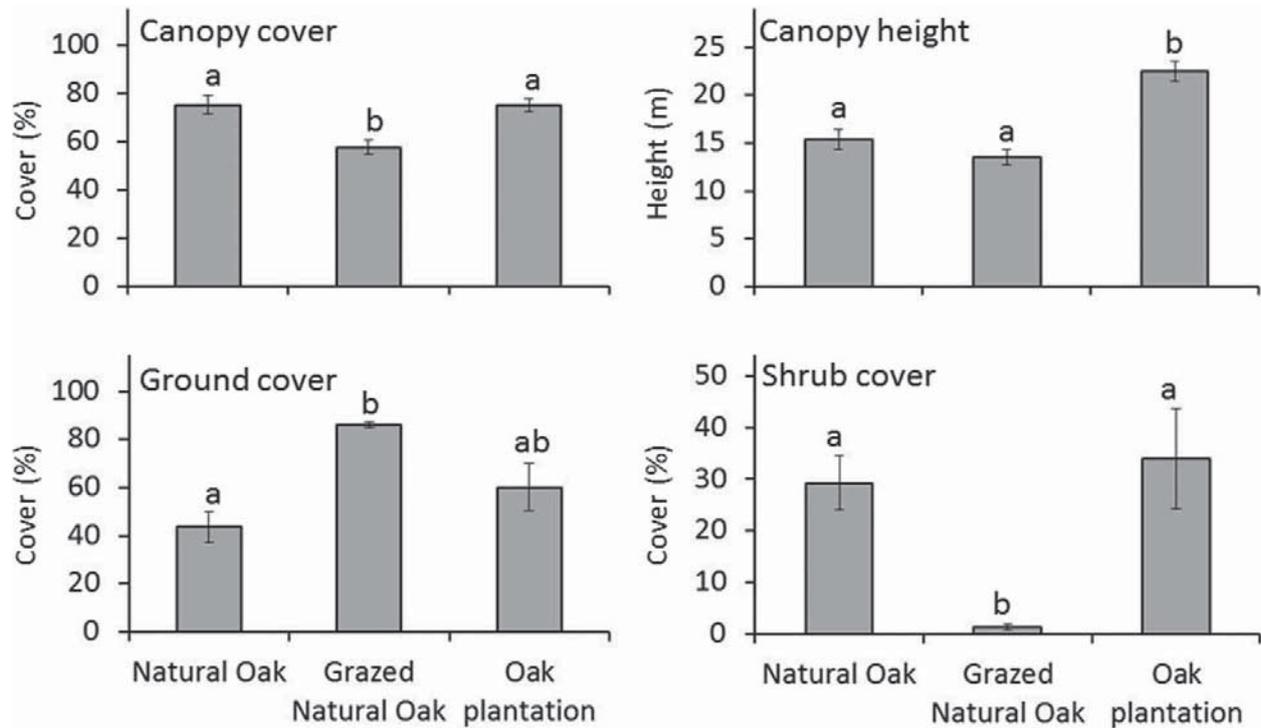
Figure 2. The mean (± standard error) canopy cover, canopy height, ground cover and shrub cover in each of the oak forest types. Lowercase letters above error bars refer to homogenous subsets indicated by general linear models.

cover, ground cover and survey year. Top models were assessed based on AIC$_c$. To determine the most important explanatory variables in the GLMs, we applied model averaging (Burnham & Anderson 2002) using the dredge function in the R library MuMIn (Bartoń 2009). Residuals from final models were tested for normality and homogeneity of variance using Kolmogorov–Smirnov and Levene's test, respectively.

Redundancy analyses (RDAs) with a forward selection procedure using the results of a Monte Carlo permutation test of 4999 random permutations with the R package *Packfor* (Dray *et al.* 2007) and variance partitioning using the *Vegan* package (Oksanen *et al.* 2010) were conducted in order to assess if bird community structure was confounded by geographic location. A variable matrix of two-dimensional coordinates *x* and *y* was completed by adding all terms of the cubic regression: $(x + y) \times (x + y) \times (x + y)$ following Legendre (1990) to account for non-linear patch and gap elements of spatial variation in bird assemblages. Non-metric multi-dimensional scaling (NMDS) analysis with Sørensen distance measures was carried out in PC-ORD (version 6; MjM Software, Gleneden Beach, Oregon, USA), to determine

between site patterns in the bird community assemblages, to investigate if the bird communities differed between the three site types. All species recorded at fewer than 5% of the study sites were excluded from this analysis.

RESULTS

Percentage canopy cover and shrub cover were significantly lower in the browsed semi-natural oak forests than in the other two forest types (Fig. 2, Table 2). Canopy height was significantly taller in the oak plantations than in the other two oak forest types (Fig. 2, Table 2). While ground cover was greater in the browsed semi-natural oak forests relative to the semi-natural oak forests, there was no significant difference in ground cover between the oak plantations and the other two forest types (Fig. 2, Table 2).

There was no significant difference in total bird density or the density of parids (Blue Tit, Coal Tit and Great Tit) between the three forest types. The density of warblers (Blackcap, Chiffchaff, Grasshopper Warbler, Garden Warbler, Whitethroat and Willow Warbler) was lower in the browsed semi-natural oak

Table 2. Results of generalized linear models assessing the difference in: canopy cover and height; ground and shrub cover; total species density and richness; and parid density and warbler density, between the three types of oak forest. Note that both warbler density and shrub cover were square root transformed prior to analyses to meet assumptions of the tests. Note that total species richness model used a Poisson distribution.

Vegetation variable	Forest type	Estimate ± se	t	P
Canopy cover	Semi-natural oak	75.3 ± 3.57	21.1	<0.0001
	Browsed semi-natural oak	−17.6 ± 6.69	−2.6	0.02
	Plantation oak	−0.16 ± 6.69	−0.02	0.98
Canopy height	Semi-natural oak	15.4 ± 0.93	16.6	<0.0001
	Browsed semi-natural oak	−1.87 ± 1.73	−1.1	0.30
	Plantation oak	7.13 ± 1.72	4.1	0.0009
Shrub cover	Semi-natural oak	2.21 ± 0.14	16.0	<0.0001
	Browsed semi-natural oak	−1.23 ± 0.26	−4.8	0.0002
	Plantation oak	0.12 ± 0.26	0.5	0.66
Ground cover	Semi-natural oak	43.8 ± 6.12	7.1	<0.0001
	Browsed semi-natural oak	42.3 ± 11.55	3.7	0.0023
	Plantation oak	16.5 ± 11.55	1.4	0.17
Total bird density	Semi-natural oak	44.9 ± 4.97	9.0	<0.0001
	Browsed semi-natural oak	−6.27 ± 9.29	−0.7	0.51
	Plantation oak	−2.20 ± 9.29	−0.2	0.82
Total species richness	Semi-natural oak	2.93 ± 0.07	40.1	<0.0001
	Browsed semi-natural oak	−0.36 ± 0.16	−2.3	0.02
	Plantation oak	−0.10 ± 0.15	−0.7	0.50
Warbler density	Semi-natural oak	1.63 ± 0.20	8.3	<0.0001
	Browsed semi-natural oak	−0.47 ± 0.37	−1.3	0.22
	Plantation oak	0.71 ± 0.37	1.9	0.07
Parid density	Semi-natural oak	12.9 ± 3.17	4.1	0.0009
	Browsed semi-natural oak	6.97 ± 5.93	1.2	0.26
	Plantation oak	5.96 ± 5.93	1.0	0.33

forests than in the oak plantations, but there was no difference in warbler density between the semi-natural oak forests and the other forest types. Species richness was lower in the browsed semi-natural oak forests than in the other forest types (Fig. 3, Table 2).

Multimodel inference from the generalized linear models, conducted on the residual variation from the models with forest type as the only explanatory factor, showed that there was a difference in the relative importance of the vegetation variables in modelling species richness, total bird density, warbler density and density of parids (Table 3). Canopy cover was the best predictor of residual variation in species richness and total bird density, although this relationship was much weaker for total bird density, with the remaining vegetation variables being of lower relative importance (Table 3). Although canopy cover was the most important variable in models of residual density of parids (relative variable importance (RVI) of 0.36),

none of the explanatory variables of this model had high importance values and the null model was the top model. Shrub cover (RVI of 0.35) had the highest relative importance value for modelled residual variation of warbler density. However, as with the parid density model, all of the vegetation variables of this model had relatively low variable importance values and the null model was the top model.

NMDS analyses showed that bird communities of both the semi-natural and the browsed semi-natural oak forests were heterogeneous and somewhat different to those of oak plantations, with these two groups of sites separated on axis 1 but not on axis 2 (Fig. 4). Axes 1 and 2 explained 6% and 82% of the variation in bird assemblages at all sites, respectively. Canopy height and shrub cover were negatively correlated with axis one scores of the NMDS ordination (strongly and weakly, respectively) as were the bird species Wren, Blackcap, Chiffchaff and Dunnock, indicating that
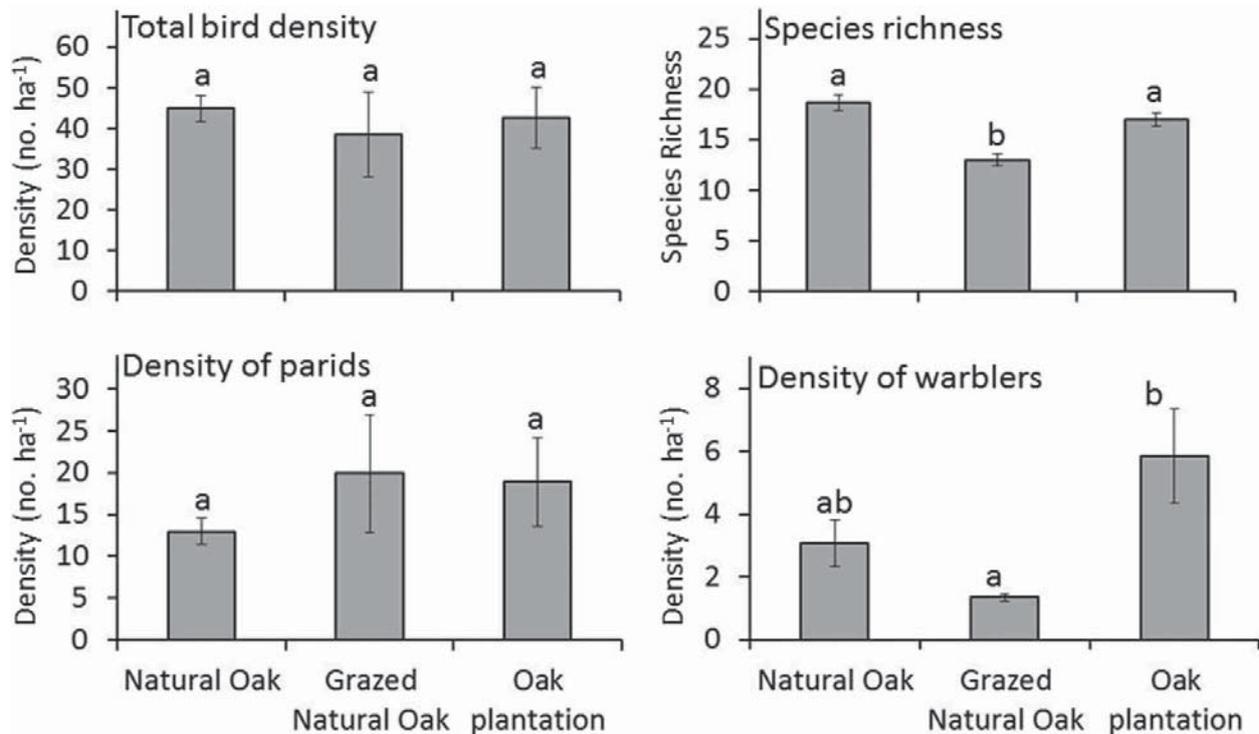
Figure 3. Mean (± standard error) total density of birds, bird species richness, density of parids and density of warblers, in each of the oak forest types. Lowercase letters above error bars refer to homogenous subsets indicated by general linear models.

Table 3. Explanatory variable parameter estimates, standard errors (±se) and significance values of each of the top models, and the RVI from the model averaging, from the general linear models demonstrating the relationship of measured environmental variables on the bird species richness and density of all birds, parid and warbler species in the three types of oak forest. For both warbler and parid density, the null model was the top model. Note warbler density was square root transformed prior to analyses to meet assumptions of the test.

	Total density			Total species richness		
Explanatory variable	Estimate ± se	P	RVI	Estimate ± se	P	RVI
Intercept	14.09 ± 19.5	0.48	–	−1.13 ± 0.62	0.085	–
Canopy cover	0.41 ± 0.27	0.152	0.46	0.016 ± 0.01	0.083	0.72
Canopy height			0.21			0.37
Shrub cover			0.11			0.17
Ground cover			0.23			0.28

these species were associated with sites with higher taller canopy and greater amounts of shrub cover. Species with positive correlations with axis one included Gold Crest, Chaffinch, Siskin, Treecreeper and Robin, indicating that these species were associated with sites with lower canopy height and levels of shrub cover (Fig. 4). Although axis two explained more of the variation in community assemblage, somewhat surprisingly, none of the vegetation variables were significantly related to axis two scores (Table 4). However, Blackcap, Siskin, Mistle Thrush and Pheasant were positively correlated

to axis 2 of the ordination and Blue Tit, Great Tit, Coal tit and Gold Crest were negatively correlated with axis 2 of the ordination. Forward selection procedures from the RDAs indicated that geographical location did not account for any of the observed differences in bird communities.

DISCUSSION

The bird diversity of oak plantations compared favourably to that of semi-natural oak forests, with no
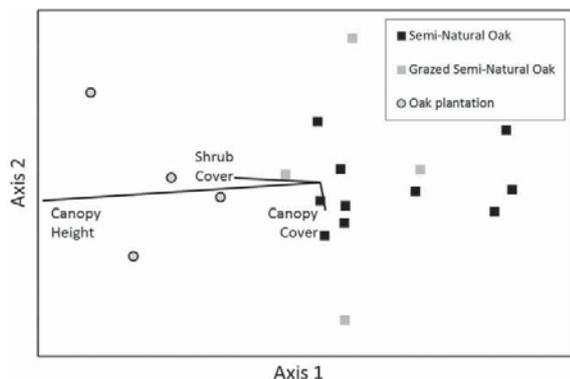
Figure 4. NMDS ordination plot of bird community data from the three types of oak forest, including the vectors of the explanatory variables, canopy cover, canopy height and shrub cover that the variation in bird assemblages were related to. Final stress from two-dimensional solution = 12.9, final instability = 0.00042. Axes 1 and 2 explain 6% and 82% of the variation in the data set, respectively.

Table 4. Correlations between axis 1 and axis 2 site scores with each of the vegetation variables from the NMDS analyses, showing the relationships between the bird communities of site types and vegetation variables. Axes 1 and 2 explain 6% and 82% of the variation in the data set, respectively.

Vegetation variable	Axis 1		Axis 2	
	r	P	r	P
Canopy cover	0.02	0.48	−0.29	0.12
Canopy height	−0.67	0.001	−0.24	0.41
Shrub cover	−0.39	0.057	0.13	0.47
Ground cover	−0.16	0.26	−0.09	0.49

difference in species richness, total bird density, warbler density or density of parids between these forest types. The browsed semi-natural oak forests, however, had lower bird species richness than either of the other two forest types and lower density of warbler species than the oak plantations. These observed differences in bird communities appear to be related to variation in habitat structural complexity, as has been shown by several previous studies in Ireland (Wilson *et al.* 2006, Sweeney *et al.* 2010a, 2010c, Wilson *et al.* 2010), Britain (Gill & Fuller 2007, Quine *et al.* 2007) and elsewhere (Cherkaoui *et al.* 2009, Nikolov 2009).

The bird communities of the semi-natural oak forests and oak plantations compare very favourably to previous studies in Irish semi-natural forests (Batten 1976, Wilson 1977, Nairn & Farrelly 1991). The mean species richness in both semi-natural oak forests (18.7 ± 0.8) and oak plantations (17.0 ± 0.6) in this study were comparable to the mean species richness of

the semi-natural forests in previous studies, which ranged from 18.6 to 21.0 (Batten 1976, Wilson 1977, Nairn & Farrelly 1991). Comparisons of bird densities between our study and these previous studies are impracticable, because we used *Distance* sampling to correct for the influence of distance from the observer on detectability, while these studies did not.

The oak plantations included in this study supported very similar bird communities to the semi-natural oak forests, demonstrating that plantation forests of native species can support comparable bird communities to semi-natural woodlands in areas such as Ireland where the generalist bird fauna lacks forest specialists. The role of plantations in the conservation of forest biodiversity has been debated extensively (Stephens & Wagner 2007, Brockerhoff *et al.* 2008, Bremer & Farley 2010, Coote *et al.* 2012, Pawson *et al.* 2013). However, the lower levels of biodiversity commonly reported in plantation forests (Lindenmayer & Hobbs 2004, Barlow *et al.* 2007, Lantschner *et al.* 2009, Sweeney *et al.* 2010a) may, in part, be due to the fact that most of these plantations are composed of exotic species. It is evident from our results that the oak plantations and semi-natural oak forests supported bird communities with similar species richness, total density and density of typical woodland groups such as parids and warblers. The diversity of bird species recorded in the oak plantations here (an average of 17.0 species per site) is higher than has been previously been typically found by studies of bird communities in Irish conifer plantation forests. For example, Sweeney *et al.* (2010d) reported average species richness values of between 11.0 and 14.5 species in commercially mature Norway spruce (*Picea abies*) and Norway spruce/Scots pine mix plantations, respectively. Studies in plantations of Ireland's most widely planted tree species, Sitka spruce (*P. sitchensis*) also found lower bird diversity than the oak plantations of this study, with averages of 12.6 (Wilson *et al.* 2006) and 12.3 (Sweeney *et al.* 2010c) species per site. The bird communities of closed canopy conifer plantations in Ireland tend to be dominated by relatively few generalist bird species, particularly Coal Tit, Goldcrest and Chaffinch, and typically support few (if any) bird species of conservation concern (Wilson *et al.* 2006, Sweeney *et al.* 2010c). It therefore appears that, at least in regions without forest specialist species, plantations of native tree species (but not of exotic conifers) can support comparably diverse bird communities, with similar species composition, to those of semi-natural woodlands.

There were significant differences in bird diversity among the semi-natural oak forests we studied, with semi-natural oak forests subjected to intensive browsing by deer having significantly lower species richness than the other two forest types. The strongest relationship between warbler density and the measured vegetation variables was a positive association with shrub cover, which suggests that the lower density of warblers in the browsed sites was due to the browsing by deer. Using a deer exclosure experimental design in Britain, Gill & Fuller (2007) showed that the browsing by deer on shrub and understorey vegetation significantly reduced the density of shrub-associated species such as Blackcap, Chiffchaff, Garden Warbler and Dunnock. Similarly, large increases in deer browsing pressure in Wytham Woods in England resulted in decreased shrub cover and reductions in the numbers of bird species associated with low vegetation, especially warblers (Perrins & Overall 2001). High levels of shading from canopy cover can potentially confound the impacts of browsing on woodland vegetation structure, because both shading and browsing have similar effects in reducing understorey vegetation (Gill & Fuller 2007). However, the amounts of both canopy cover and shrub cover in browsed semi-natural oak forests were lower than the other two forest types. In fact, canopy cover was positively related to species richness, total bird density and density of parids. It is therefore likely that the development of shrub and understorey vegetation in browsed native oak forests was suppressed by deer rather than by shading. Despite a low amount of canopy cover in the browsed oak forests, the lack of understorey vegetation in these forests was presumably a result of high levels of ungulate browsing. The high amount of canopy cover in the oak plantations was due to the high density at which crop trees were planted.

Somewhat surprisingly, densities of parids in the oak plantations sites were comparable to those in the semi-natural oak forests. Populations of cavity-nesting species in plantations can be limited by the lack of old, cavity-rich trees, due to the fact that trees are typically harvested before partial and complete tree death can give rise to an abundance of cavities (Newton 1994). By the time they are 100 years old, less than 1% of oak trees have developed cavities or hollows (Ranius *et al.* 2009). The similarity in densities of parids between the oak plantations and semi-natural oak forests we studied may be due to the management history of these sites. The vast majority of forests in Ireland have been subjected to harvesting of wood for timber and fuel,

and low densities of cavities may result from historic exploitation of older trees (Sweeney *et al.* 2010b). Another contributing factor may be the historical absence of woodpeckers, which have only recently recolonized Ireland after an absence of several centuries (McDevitt *et al.* 2011) and were absent from all of our study sites. Although hollows in trees are created naturally over time by the shedding of large branches (Ranius *et al.* 2009), mechanical excavation by woodpeckers can increase the availability of nest sites for non-excavating hole-nesting species (Wesołowski 2007).

Despite lower species richness and warbler densities in the browsed oak semi-natural forests than in our other study sites, the bird communities of these woodlands, as indicated by NMDS ordination, were very similar to those of the other semi-natural oak forests. Although the oak plantations sites were somewhat separate from the semi-natural oak forest sites in ordination space, this separation was on axis 1, which explained just 6% of the variation in bird communities between all sites. Axis 1 scores were significantly negatively correlated with canopy height and shrub cover as were the shrub-associated species, Blackcap, Wren, Chiffchaff and Dunnock. The canopy associated bird species Gold Crest, Chaffinch, Siskin and Treecreeper were positively correlated with axis 1 of the ordination as was canopy cover, albeit weakly. There was no separation between the forest types on axis 2, which accounted for 82% of variation between sites, indicating that the bird assemblages of the three types of oak forests were broadly similar to one another. However, parids and Goldcrest were negatively correlated with axis 2 of the ordination, which was associated with canopy cover. These results from the ordination indicate, similar to the models on total density, species richness and density of warbler species and parid density, that what little variation there was between bird assemblages was related to aspects of the forest vegetation structure, and in particular, shrub cover and canopy height.

This study demonstrates that plantation forests of native tree species can support bird communities comparable to those of semi-natural woodlands in a region with a generalist bird fauna lacking forest specialists. This finding is highly relevant as plantation forest cover is expanding across the world and in particular in Europe, at the same time that populations of forest birds are declining (Fuller *et al.*, 2005, Gregory *et al.*, 2007). While the planting of native tree species in plantations is increasing in countries such as

Ireland, exotic conifers continue to dominate new plantings. As the ability of exotic conifer plantations to support forest birds is generally less than that of plantations composed of native species (Sweeney et al. 2010a), the planting of native tree species in future afforestation and reforestation schemes should be promoted to enhance biodiversity, particularly for birds.

Populations of deer are increasing throughout temperate Europe, with deleterious effects on woodland birds as a result of browsing mediated differences in vegetation complexity. We found that the diversity of bird communities in plantation and semi-natural forests is strongly related to habitat complexity, in agreement with many other studies in Ireland (Roycroft et al. 2008, Sweeney et al. 2010a, 2010d, Wilson et al. 2010) as well as other parts of Europe (Bibby et al. 1989, Barbaro et al. 2005, Gill & Fuller 2007, Cherkaoui et al. 2009). Therefore, the suitability of heavily browsed semi-natural oak forests for several bird species can be improved through management aimed at promoting the development of a more complex understorey. This would require steps to facilitate a reduction in the browsing of these woodlands by ungulate species, through increased management of their density within such landscapes.

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