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Changes in forest cover result in a shift in bird community composition

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Abstract

Determining the extent of land-use change that can be tolerated by wildlife communities is crucial for effective conservation management. Recent landscape-scale studies have found increasing evidence for critical threshold levels of forest cover, after which the existing communities of plants and animals are negatively impacted. This is particularly true when plantation forests replace native vegetation. We used large datasets (Irish Bird Atlas and Forest Inventory) and a novel method, Latent Dirichlet Allocation, to model changes in bird community composition along the existing forest cover gradient in Ireland and evaluated the degree of spatial overlap between birds of conservation concern and areas of recent afforestation. We found that as we approach 35% forest cover in the landscape one community of birds replaces another as the dominant community. The highest levels of recent afforestation overlapped with areas of high numbers of birds of conservation concern. This means that habitat change is occurring in the areas with highest bird diversity. This finding has policy implications for the design of land-use policies, such as those on afforestation and forest expansion. It can be used to ensure plantation forests are planted in the right place to minimise impact on biodiversity values; that is, practitioners need to consider the level of forest already present in an area as well as the level of biodiversity in the area when selecting areas for afforestation.

Introduction

The diversity of birds present in an area is shaped by a range of human activities, but the effect of land-use changes such as through forest cover levels, is arguably one of the most influential (Fuller 2012). While the effects of deforestation are well understood and established, the effects of forest creation or afforestation on biodiversity have not received the same level of attention, apart from a few exceptions such as reforestation in abandoned farmland in Eastern Europe (Taff *et al*., 2009) and the Conservation Reserve Programme in the US (Riffell, Scognamillo & Burger, 1993). Bucking the trend of a global decline in forest cover, the area of plantation forests is increasing by about 3 million hectares annually and now cover *c*. 290 million ha (about 3.5% of total forest cover worldwide) (FAO 2015). The specific impacts of plantation forests on biodiversity have been the focus of considerable research effort (Brockerhoff *et al*., 2008; Bremer & Farley, 2010; Pawson *et al*., 2005), and there is a growing body of evidence to show that the distribution of species and the composition of communities can be altered dramatically by afforestation (Fahrig, 2013; Dirzo *et al*., 2014).

The concept of ecological thresholds has been subject of considerable recent research (e.g. Andersen *et al*., 2009; Muradian 2010; Kelly *et al*., 2015; Ratajczak *et al*., 2012). Threshold effects arise when 'small changes in an environmental driver produce large responses in the ecosystem' (Groffman *et al*., 2006). There have been many well-documented examples of ecological thresholds, such as clear lakes turning turbid (e.g. Tátrai *et al*., 2014). Recent landscape–scale studies have found increasing evidence for critical threshold levels of forest cover; below these levels of forest cover the responses of species and communities to forest cover changes dramatically (Radford *et al*., 2018; Betts *et al*., 2007; Swift & Hannon, 2009; Maron *et al*., 2012). However, the applicability of thresholds in relation to species loss at landscape scales has been much debated; for example, Lindenmayer *et al.* (2005) suggest that community-level responses to thresholds are unlikely because of differences between species, whereas Radford *et al.* (2018) found strong threshold responses in species richness of birds in remnant woodland habitats.

Estimates of how much suitable habitat in the surrounding landscape is required for the persistence of individual species are notoriously difficult to calculate and can range widely from 20 to 75% (e.g. Margules & Nicholls, 1988; Soule & Sanjayan, 2010; Saetersdal *et al*., 2000; Miller *et al*., 2001). There are many contributing factors to biodiversity loss but habitat destruction due to land-use change is the predominant driver (Purvis *et al*., 2005; Sala, 1988; Jantz *et al*., 2015). Many species, populations or communities do not disappear immediately following landscape or habitat change: in grasslands, for example, plant species may remain for at least 70 years postchange (Helm *et al*., 2006; Cousins, 2009; Plue & Cousins, 2000).

The magnitude of habitat loss may also play a part in determining whether a time lag occurs, with a threshold suggested at around 10% remaining habitat, after which biodiversity loss becomes synchronised with the reduced habitat cover (Cousins, 2009).

Determining the extent to which increases in forest cover can be tolerated by open habitat bird communities is critical for conservation management of open habitat species. A study looking at afforestation on agricultural land in three States in North America, found that while the planting of new forest leads to a gain in populations of forest birds, farmland bird populations decrease, and at 10% forest cover there were net losses of bird densities (Matthews *et al.*, 2004). Research in Irish lowland farmland landscapes has shown that total forest cover of 30% at a scale of 2000 ha has no negative effect on bird diversity (Pithon *et al.*, 2013). However, at the time this study was conducted, it was not possible to investigate effects on bird communities at forest threshold levels above 30%. Changes in forest cover have been shown to affect individual species, for example, hen harrier (*Circus cyaneus*) (Wilson *et al.*, 1997). Ireland has undergone a period of significant afforestation with a rise in total forest cover from 1.2% to 11% between 1928 and 2017 (DAFM, 2018) and with recent afforestation, total forest cover in some areas is now as high as 64% (within areas of 100 km^2). Thus, the identification of a critical level, should it exist, is of considerable interest to conservation managers.

The location and intensity of future land-use change is important because certain regions are home to a disproportionately high number of endemic species or species of high conservation concern. The net effect of plantation forests on biodiversity is dependent on a range of factors including the nature of the plantation forest and of the preceding habitat (Graham et al., 2014). The establishment of plantation forests that replace native vegetation typically causes biodiversity losses locally, while plantations established on former agricultural, or otherwise degraded land, may provide significant opportunities for biodiversity conservation (Carnus *et al.*, 2006; Loyn *et al.*, 2007; Brockerhoff *et al.*, 2008; Pawson *et al.*, 2013) and deliver important ecosystem services (Winjum & Schroeder, 1997).

The aim of this study was to examine the relationship between current bird diversity and patterns of recent afforestation in Ireland. We focus on changes at the community level and use a clustering method to model changes in community composition along the existing forest cover gradient. We then investigate the extent to which the locations of recent afforestation overlap with the distribution of birds of conservation concern.

Materials and methods

Study area

Ireland is undergoing one of the highest rates of afforestation in Europe at present, with further expansion predicted. Forests currently cover 11% of Ireland, making it one of the least forested countries in Europe (DAFM, 2018). However, the government's aim is to increase forest cover to 18% by 2046, conditional on land and funding availability (DAFM, 2015). Until the early 1980s, the Irish state, with support from the EU, was responsible for almost all annual forest planting in Ireland, which was dominated by nonnative coniferous species on publicly owned peatland areas (Kearney, 2001). Nonnative conifers make up 70% of the Irish forest estate (DAFM, 2018).

Data

We used data from the most recent Bird Atlas for Britain and Ireland, which ran from November 2007 to July 2011 (Balmer *et al.*, 2013). An extensive network of volunteers surveyed bird communities during both winter and summer to collect the atlas data. The Irish National Grid formed the basis for selecting the sampling units in Ireland and full details of the survey methods and coverage are presented in Balmer *et al.*, (2013). Two field methods were used (*Balmer et al.*, 2013). The 'Roving Records' method gathered details on presence or absence of each bird species within 10 km x 10 km squares, and the 'Timed Tetrad Visit' (TTV) method was used to provide an estimate of the relative abundance of species within 2 km x 2 km squares and both are used in our analyses. The TTV survey method is a fixed effort survey requiring the observer to devote 2 h (1 h visit in early spring and another in late spring) to surveying a minimum of eight tetrads (2 km × 2 km squares) within their allocated 10-km square and to focus their survey effort within the major habitats present in that tetrad. By amalgamating the lists from eight surveyed tetrads, a species list for the 10-km square is produced based on a known field effort (see Figure S1 for more information on sampling effort). The Forest Inventory and Planning System (FIPS) was used to determine the distribution of forests between 2008 and 2012 (Forest Service, 1999). Both the forest and bird datasets were managed using ArcGIS–ArcMap® 10.2 and the per cent cover of forest was determined for the same 10 km x 10 km atlas squares and 2 km x 2 km atlas squares for which bird distribution and abundance data were available. A total of 80 breeding bird species were included in the analysis (Table 1).

Modelling community composition

We used a clustering method to model changes in community composition along the existing forest cover gradient in Ireland. We analysed distribution and abundance data (2 km x 2 km) for 80 breeding bird species with the multivariate model 'Latent Dirichlet Allocation' (LDA). We used the R code provided in the supplemental materials of Valle *et al.* (2008) as a basis for the analysis, carrying out the analysis with the 'topicmodels' package, v3.3 (Hornik & Grün 2011). The aim was to identify the distinct biological communities in this species-rich dataset. The advantage of LDA over other available multivariate approaches is that it can represent both gradual and abrupt transitions, whereas traditional clustering methods are better at representing abrupt transitions (Vale *et al.*, 2008). An important consideration in the LDA model construction is the

Table 1 List of all breeding species that were included in analyses

Species & habitat group	Latin name	Species & habitat group	Latin name
Blackbird (W)	*Turdus merula*	Mallard (F, B)	*Anas platyrhynchos*
Blackcap (F, W)	*Sylvia atricapilla*	Meadow pipit (F, B, U, W)	*Anthus pratensis*
Blue Tit (F, W)	*Cyanistes caeruleus*	Merlin (U, B, W)	*Falco columbarius*
Bullfinch (F, W)	*Pyrrhula pyrrhula*	Mistle thrush (F, W)	*Turdus viscivoru*
Buzzard (F, B, U, W)	*Buteo buteo*	Moorhen (F, B, U)	*Gallinula chloropus*
Chaffinch (F, W)	*Fringilla coelebs*	Peregrine (F, B, U)	*Falco peregrinus*
Chiffchaff (F, W)	*Phylloscopus collybita*	Pheasant (F, U, W)	*Phasianus colchicus*
Chough (F, U)	*Pyrrhocorax pyrrhocorax*	Pied wagtail (F)	*Motacilla alba*
Coal Tit (F, W)	*Parus ater*	Raven (F, B, U, W)	*Corvus corax*
Collared dove (F)	*Streptopelia decaocto*	Red grouse (U, B)	*Lagopus lagopus scoticus*
Common crossbill (W)	*Loxia curvirostra*	Redpoll (F, W)	*Carduelis flammea cabaret*
Common sandpiper (F, B, U)	*Actitis hypoleucos*	Reed bunting (F, B, U)	*Emberiza schoeniclus*
Coot (F)	*Fulica atra*	Robin (F, W)	*Erithacus rubecula*
Cuckoo (F, B, U)	*Cuculus canorus*	Rock dove (F)	*Columba livia*
Curlew (F, B, U)	*Numenius arquata*	Rock pipit	*Anthus petrosus*
Dipper (U)	*Cinclus cinclus*	Rook (F, B, U)	*Corvus frugilegus*
Dunlin (B, U)	*Calidris alpina*	Sand martin (F)	*Riparia riparia*
Dunnock (F, W)	*Prunella modularis*	Sedge warbler (F, B, U)	*Acrocephalus schoenobaenus*
Goldcrest (W)	*Regulus regulus*	Siskin (W)	*Carduelis spinus*
Goldfinch (F, B)	*Carduelis carduelis*	Skylark (F, B, U)	*Alauda arvensis*
Grasshopper warbler (F, B, U)	*Locustella naevia*	Snipe (F, B, U)	*Gallinago gallinago*
Great crested grebe (F)	*Podiceps cristatus*	Song thrush (F, W)	*Turdus philomelos*
Great tit (F, W)	*Parus major*	Sparrowhawk (F, W)	*Accipiter nisus*
Greenfinch (F, B, W)	*Carduelis chloris*	Spotted flycatcher (F, W)	*Musciapa striata*
Grey heron (F, U)	*Ardea cinerea*	Starling (F, W)	*Sturnus vulgaris*
Grey wagtail (F)	*Motacilla cinerea*	Stock dove (F)	*Columba oenas*
Hen harrier (F, B, U, W)	*Circus cyaneus*	Stonechat (F, B, U)	*Saxicola torquata*
Hooded crow (F, B, U, W)	*Corvus cornix*	Swallow (F, B, U)	*Hirundo rustica*
House martin (F)	*Delichon urbicum*	Swift (F, U)	*Apus apus*
House sparrow (F)	*Passer domesticus*	Teal (F, B)	*Anas crecca*
Jackdaw (F, B, U, W)	*Corvus monedula*	Tree sparrow (F)	*Passer montanus*
Jay (W)	*Garrulus glandarius*	Treecreeper (W)	*Certhia familiaris*
Kestrel (F, B, U)	*Falco tinnunculus*	Tufted duck (F)	*Aythya fuligula*
Kingfisher (F)	*Alcedo atthis*	Water rail (F)	*Rallus aquaticus*
Lapwing (F, B)	*Vanellus vanellus*	Wheatear (U)	*Oenanthe oenanthe*
Linnet (F, W)	*Carduelis cannabina*	Whitethroat (U, W)	*Sylvia communis*
Little egret (F)	*Egretta garzetta*	Willow warbler (F, B, U)	*Phylloscopus trochilus*
Little grebe (F)	*Tachybaptus ruficollis*	Woodpigeon (F, W)	*Columba palumbus*
Long-tailed tit (F, W)	*Aegithalos caudatus*	Wren (F, B, U, W)	*Troglodytes troglodytes*
Magpie (F, B, U, W)	*Pica pica*	Yellowhammer (F)	*Emberiza citrinella*

B, Raised bog birds; F, lowland farmland birds; U, upland birds; W, woodland/scrub birds.

number of component communities inputted. Similar to most clustering methods (Jain, 2009) the number of component communities must be specified *a priori*. We decided this by fitting multiple LDA models and varying the number of component communities from 2 to 10; and chose the best model based on Akaike Information Criterion (AIC).

Each 2 x 2 km square was categorised by the amount of forest it contained. We pooled all the data to provide one abundance record at each forest cover level (the highest count for each species) so that the data for our analysis consisted of a synthesised table of counts for each species for each level of forest cover. This amounted to 101 sampling units (0 to 100% forest cover) and 80 species. We manually checked a subset of the data to ensure that there was not a bias in the distribution of forest cover. For example, for the lowest forest cover sampling units (1–11) the highest abundance of meadow pipit occurs in seven different 10 km x 10 km atlas squares distributed right around the country and in the highest forest cover sampling units (91–101) the highest abundance in the seven meadow pipit occupied squares were distributed throughout the country in five separate 10 km x 10 km squares.

We then fitted the dataset with LDA, the outputs of which reveal the components or species within each community and the relative abundances of the species within those communities (Vale *et al.*, 2008). The model then estimates the relative abundance of the predetermined component communities for each level of forest cover (101 sampling units; 0 to 100%

forest cover) and the results are a visual interpretation or graph of this shift in community dynamics.

Recent afforestation and species distribution overlap

The distributions of all species listed as Red and Amber on the Birds of Conservation Concern in Ireland (Colhoun & Cummins, 2013) and all Annex 1 species that breed in Ireland were mapped. Suitable data for a total of 44 species were available and were recorded as presence data in the 868 10 km × 10 km Bird Atlas squares that comprise the Republic of Ireland (using Irish Transverse Mercator (ITM) coordinates). We evaluated the degree of spatial overlap or co-occurrence between each of the 44 species and the level of recent (2008–2012) afforestation over all atlas squares with a simple tabulation; the % of occupied squares in which recent planting has occurred.

The levels of both existing (pre-2008) forest cover and recent afforestation within the atlas squares were scored from 0 (zero planting) up to 5 (highest planting). The groupings were determined in ArcGIS using Jenks (Jenks 1977) optimal–break classification algorithm, which is a statistical method used to identify natural breaks in the data.

Maps were produced to visually assess the distribution patterns of species with occurrence of afforestation. Species were grouped together on the basis of their habitat associations as defined within the Group Species Action Plans-national plans detailing habitats that encompass threatened species and the associated necessary conservation plans (BirdWatch Ireland 2011). Only species groups that utilise habitats likely to be affected by afforestation were selected; lowland farmland, upland, raised bog and woodland/scrub. We tested whether the overlap between bird distributions and recent afforestation differed among the habitat associated groups with the use of Kruskal–Wallis tests and used Spearman's rank correlation tests to assess whether the number of species present in a 10 km x 10 km square was correlated to recent afforestation levels.

Results

Based on AIC we found the optimal number of component bird communities to be two (Table 2). The first component community (CC1) was dominated by passerines with the top three species, chaffinch, wren and willow warbler equally abundant (each comprising 7% of the total community) and making up 21% of the community. Rooks were the dominant species in the second component community (CC2), and together with starling and jackdaw made up 35% of the community. In the absence of any forest cover, community 2 was dominant but steadily decreased in dominance as forest cover increased (Fig. 1). At 35% forest cover both communities are equally abundant in the landscape but at higher forest cover levels community 1 steadily increased in abundance and after 90% forest cover community 2 was no longer present (although individual members of the community may still be present).

Table 2 Output of LDA model with the ten most abundant characteristic species for each component community

Community 1	Community 2
Chaffinch (0.07)	Rook (0.16)
Wren (0.07)	Starling (0.11)
Willow warbler (0.07)	Jackdaw (0.08)
Robin (0.06)	Wood pigeon (0.08)
Blackbird (0.05)	Sand martin (0.06)
Coal tit (0.05)	Swallow (0.05)
Swallow (0.04)	House sparrow (0.04)
Goldcrest (0.04)	House martin (0.04)
Wood pigeon (0.04)	Mallard (0.03)
Meadow pipit (0.03)	Linnet (0.03)

The total proportion of individuals that each species contributes to each community is in brackets.
Community 2 is dominant where there is little or no forest cover. Community 1 becomes dominant with increasing forest cover.

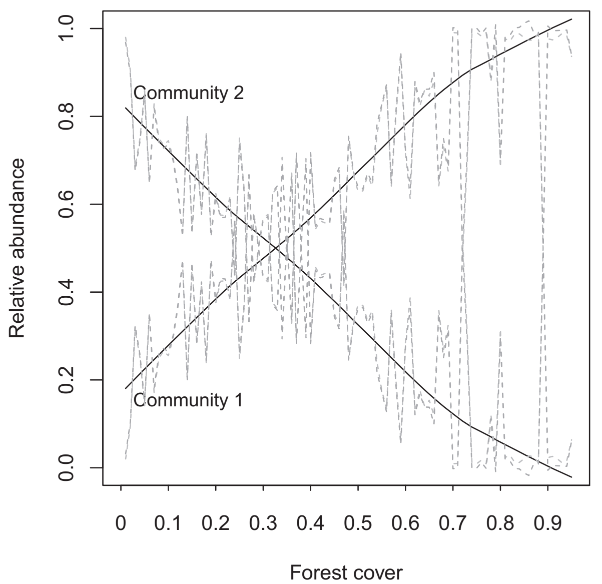

Figure 1 Relative abundance of each bird-community component along a gradient of increasing forest cover. The two black lines (loess smoother added) represent the two-component communities (see Table 2) and the grey dashed lines represent 95% confidence intervals. Afforestation index starts at zero and increases to 100% forest cover within a 2 x 2 km squares.

Between 2008 and 2012 an additional 38 610 ha of new forest was planted, increasing total forest area nationally by 5.5% up to 731 652 ha. New forests were planted in 72% (n = 672) of the 10 km x 10 km squares throughout Ireland, with 12% of squares (n = 102/868) being planted with more than 105 ha (>1% of the square), that is, the top two quantiles of planting intensity during this period (Fig. 2). The overlap of recent afforestation with the distributions of the 44-bird species of conservation concern ranged from 6% of the occupied atlas squares experiencing recent afforestation in the case of twite

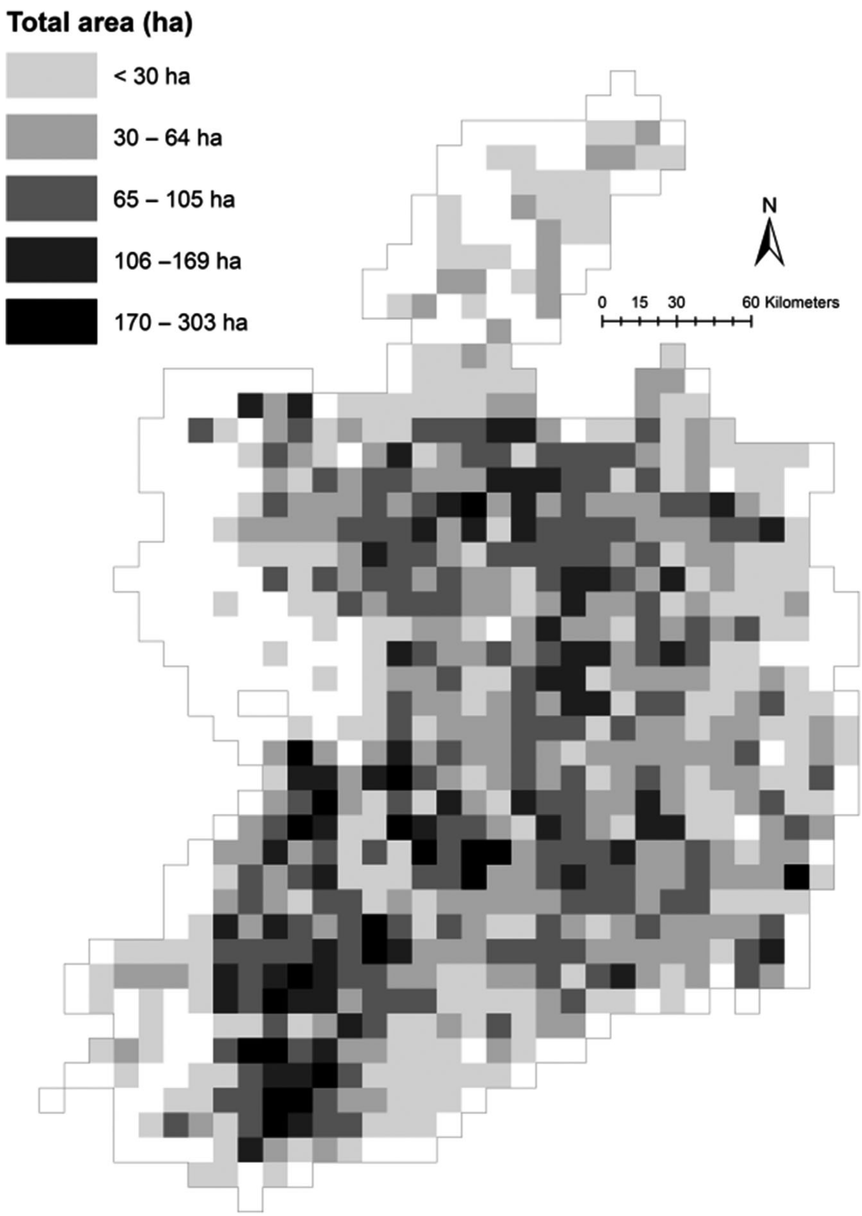

Figure 2 Total recent afforestation area (ha) in the Republic of Ireland, 2008–2012. The levels of both existing (pre-2008) forest cover and recent afforestation within the atlas squares were scored from 0 (zero planting) up to 5 (highest planting). The groupings were determined in ArcGIS using Jenks (Jenks 1977) optimal–break classification algorithm.

(*Linaria flavirostris*), to 94% in the case of both hen harrier (*Circus cyaneus*) and quail (*Coturnix coturnix*). For 26 bird species of conservation concern, at least 80% of their distribution (i.e. occupied 10 km x 10 km squares) had been impacted by recent afforestation (Table 3), with very high levels of afforestation (score 4 or 5;> 105ha) overlapping with 10% of the distribution of 13 species. There was no overlap between the distributions of five bird species; twite, golden plover (*Pluvialis apricaria*), ring ouzel (*Turdus torquatus*), red kite (*Milvus milvus*) and dunlin (*Calidris alpine)* and the areas of highest recent afforestation. The greatest overlap with the areas of highest planting was recorded for the hen harrier (17% of 10 km x 10 km squares), barn owl (*Tyto alba*) and curlew (*Numenius arquata*) (14% of 10 km x 10 km squares).

The amount of overlap with recent afforestation differed significantly among the habitat associated groups (Kruskal–Wallis chi–square = 16.13, d.f. = 3, P–value < 0.01). For example, higher proportions of woodland/scrub birds (0.73) and lowland farmland (0.57) birds had high overlap (more than 80% of their distribution) with recent afforestation, compared with upland (0.19) and raised bog (0.27) birds. Species richness in 10 km x 10 km squares was positively related to the level of

Table 3 The overlap between the distribution of 44 bird species of conservation concern (atlas squares occupied) and recent afforestation (2008–2012)

Species	No. of occupied squares	% occupied squares planted	% occupied squares planted > 105 ha	Habitat group
Barn Owl	249	93	14	F
Chough	167	46	4	F, U
Common Sandpiper	163	61	3	B
Corncrake	43	51	2	F
Curlew	64	84	14	F, U, B
Dunlin	19	47	0	U
Goldcrest	780	84	11	W
Golden Plover	27	33	0	F, U
Great Spotted Woodpecker	27	85	7	W
Greenfinch	790	83	11	F, W
Grey Wagtail	649	88	11	F
Hen Harrier	142	94	17	F, U, B, W
House Martin	795	84	11	
House Sparrow	825	81	10	
Kestrel	768	81	10	F
Lapwing	206	75	8	F, B
Linnet	804	80	10	F, W
Meadow Pipit	831	78	10	F, U, B, W
Merlin	110	75	9	U, B, W
Mistle Thrush	752	87	11	F, W
Peregrine	330	71	6	U
Quail	18	94	11	F
Red Grouse	70	70	6	U, B
Red Kite	12	83	0	F, W
Redshank	68	72	13	F, B
Reed Warbler	25	92	8	
Ring Ouzel	12	42	0	U
Robin	841	80	10	F, W
Sand Martin	682	83	10	
Skylark	737	76	10	F, U, B
Snipe	306	81	12	F, U, B
Sparrowhawk	662	85	11	F, W
Spotted Flycatcher	598	88	12	W
Starling	842	80	10	F
Stock Dove	252	91	10	F, W
Stonechat	655	76	10	F, U, B
Swallow	855	79	10	F
Tree Sparrow	141	81	4	F
Twite	18	6	0	F, U
Wheatear	332	58	5	U
Whinchat	34	79	6	F, U
Wood Warbler	10	90	0	W
Woodcock	128	93	12	W
Yellowhammer	309	88	7	F

Grey box highlights species with >80% of their occupied squares recently planted and more than 10% of their occupied squares planted with >105 ha (highest planting level between 2008 and 2012).

B, Raised bog birds; F, lowland farmland birds; U, upland birds; W, woodland/scrub birds.

recent afforestation for lowland farmland birds ($r_s(866) = 0.2$, $P < 0.01$) and for woodland/scrub birds ($r_s(866) = 0.37$, $P < 0.01$), but negatively related to the level of recent afforestation for upland birds ($r_s(866) = -0.22$, $P < 0.01$), with no statistically significant relation between level of afforestation and species richness of raised bog birds ($r_s(866) = -0.02$, $P = 0.57$).

Discussion

We demonstrate that along the existing forest cover gradient in Ireland a switch in community composition happens when forest cover approaches 35% of the land area. At approximately 10% forest cover community 2 (dominant species include rooks, starling and jackdaw) represents about 75% of the birds present at a site. At approximately 60% forest cover community 1 (dominated by passerines including chaffinch, wren and willow warbler) is 80% dominant and at 90% forest cover community 2 is completely absent. Our results do not support a threshold response but rather a gradual replacement of one community with another. Previous research suggested that total forest cover of up to 30% at a scale of 2000 ha has no negative effect on bird diversity in typical Irish lowland farmland landscapes (Pithon *et al.*, 2013), whereas we show that by adding just 5% more forest cover into the landscape we reach a landscape composition at which one community replaces another as the dominant community.

The composition of bird species within communities can change without systematic declines in species diversity (Dornelas *et al.*, 2014). However, our knowledge on how alterations in species composition in a community lead to changes in the ecological functions performed is still limited. Specialist birds are thought to be more adversely affected by anthropogenic disturbances when compared to more generalist species (Clavel *et al.*, 2011). However, recent research has shown that within Europe the more common birds are generally declining faster than less abundant species and that this may be a significant issue as declines in these species can have much greater impact in terms of ecosystem function and services which they provide (Inger *et al.*, 2014). In our study, as forest cover increases beyond 35% of the landscape the avian communities are less likely to include species such as rook, starling, jackdaw, swallow or house sparrow. Exactly how these changes in community composition will affect ecological functioning is unknown. Currently, rooks, starlings, jackdaws and swallows are amongst the most abundant species recorded in Ireland (Crowe *et al*., 2011). House sparrows are a species of conservation concern that have recently increased in numbers in Ireland, in contrast to declines throughout the UK and Europe (*Crowe et al*., 2011). A limitation of this model is that it does not take into account imperfect detection, that is, variable detectability of species. However, the data suggest this may not be such an issue, for example, coal tits (Periparus ater) are a species considered to have relatively low detectability (Graham *et al.*, 2014) but the two highest max counts for this species are in tetrads of 53% and 86% forest cover. This is counter to the expected results if variable detectability was a major issue. Nevertheless, this uncertainty should be accounted for when performing more formal statistical tests. Thus, our results have uncovered clear spatial patterns in the distribution of bird communities along a forest cover gradient but follow up analyses that account for the multiple factors that influence distribution should confirm whether forest cover is driving the shifts we have detected.

The highest levels of recent afforestation overlapped with areas where the highest species richness for lowland farmland birds and for woodland/scrub birds was observed. This is at the centre of the conservation issue: areas prioritised for afforestation have coincided with regions where the highest species richness of threatened birds occurs. While our results show correlation and not causation, that is, we cannot infer that species with high overlap with recently afforested areas are at risk because of this land-use change, this does warrant further study as independent lines of evidence suggest that many open habitat bird species may be disadvantaged by afforestation. This and the effect of pre-2008 planting will be explored further in a follow-up paper. The 44 species of conservation concern identified in this study represents 35% (44/127) of all threatened bird species in Ireland (Colhoun & Cummins, 2013). These species may be particularly vulnerable to any future land cover changes. For example, the breeding range of the curlew has contracted by more than 70% in the last 21 years and during the 2008–2012 period afforestation has occurred over 84% of their range (10 km x 10 km squares). Declines of curlew in the UK have been linked with land-use changes in the uplands (principally afforestation), with predation by foxes *Vulpes vulpes* the most likely mechanism for the observed effect (Douglas *et al.*, 2013).

In Ireland, ecological sustainability is an important component of forest policy (DAFF 2010). However, currently, most planting is carried out by private landowners whereas in the past planting was largely undertaken by State bodies. It is likely that future planting areas will be relatively small, scattered blocks of forest on mostly marginal land or open habitats (Pithon *et al.*, 2013). This scenario potentially carries the greatest risk for open habitat birds due to the greater fragmentation of open habitats. Although afforestation in Ireland is controlled, many areas of biodiversity importance receive no formal protection or designated status. Forest expansion relies on applications by landowners and thus cannot be 'directed' into preselected areas. For example, most seminatural grasslands in Ireland lack formal nature conservation designations that preclude afforestation (Buscardo *et al.*, 2008) and not all vulnerable species are limited to Natura 2000 (protected) sites.

There is also an increasing potential for land-use management to increase the resilience of avian populations to climate change (Vos *et al.*, 2012; Lawton *et al.*, 2010). Thus, there is a demand for knowledge on the impacts of future climate change on species and ecological function, but this information is of little use in the absence of supporting data on the impacts of land-use change. We may see bird species exhibiting range-shifts contrary to those expected in response to climate change because of their use of human-modified aspects of the landscape (Hockey *et al.*, 2011). The next step would be to compare the relative importance of increasing afforestation and climate change in driving future population change of these species and to also explore the potential for afforestation to moderate likely future population declines resulting from climate change. Models such as the ones used in the current study, could be used to guide future management, particularly if they can incorporate dispersal information (Renwick *et al.*, 2008).

Conclusions

Our findings that the composition of bird communities changes along a forest cover gradient and that there is a high degree of spatial overlap between the distribution of species of concern with areas that have high rates of recent afforestation, raises the issue of afforestation as a threat to bird species in Ireland. These findings indicate that habitat conversion to forestry may be an important driver of change in bird communities. The ability to assess whether species assemblages are expanding or contracting in dominance is essential for managing and forecasting plantation forest locations and associated conservation issues. Considerable challenges to obtain quantitative predictions for the resultant effects of forest expansion on species and ecosystems remain, but we have increasingly sophisticated sets of data and tools for understanding and managing this change. Studies such as this are vital to tease out correlative relationships into ecological predictions and to link expected effects of forest cover change to both communities and individual species. Finding the best locations for future planting in terms of bird conservation requires detailed research into the level of land-use change tolerated by individual species and communities in conjunction with other threats.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. The percentage of the total tetrads (2 km x 2 km squares) surveyed within each county (n = 28) in the Republic of Ireland.