



Bird and small mammal community composition and abundance in upland open habitats and early conifer forests

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Abstract

Anthropogenic land-use change, such as commercial afforestation, is a significant driver of shifts in ecological communities and species abundance. In this study, the consequences of afforestation of upland habitats for two distinct animal groups, birds and small mammals, were examined by comparing open moorland, early pre-thicket conifer forests (2–4 years post-replanting) and late pre-thicket conifer forests (6–8 years post-replanting) across 24 upland study sites in Ireland. Field data were collected using bird point counts, live trapping of small mammals and detailed vegetation surveys. A total of 17 bird species and four small mammal species were detected. Both groups showed contrasting patterns of abundance between moorland and pre-thicket forests, with bird density being higher in moorland, while small mammal abundance was higher in pre-thicket forests. Bird diversity was lowest in moorland and highest in late pre-thicket forests, while small mammal diversity was highest in moorland and lowest in late pre-thicket forests. Our study shows that afforestation can alter the abundance and community composition of bird and small mammal populations and that the consequences of land-use change associated with afforestation in upland areas vary across different taxa. Our findings have important implications for forest management practices and conservation of upland habitats and species.

Keywords Afforestation · Biodiversity · Birds · Conifer forest · Prey · Small mammals

Introduction

Land-use change is an important driver of shifts in species composition and abundance (Sala et al. 2000; Jetz et al. 2007). As much as 60% of land-use change occurs as a direct result of human activities (Song et al. 2018) and manifests through a range of mechanisms having positive, neutral, or negative impacts on biodiversity. Understanding the impacts of land-use change and the creation of new habitats, such as urban areas (Ortega-Álvarez and MacGregor-Fors 2009; Reis et al. 2012), agricultural lands (Reidsma et al. 2006) and

commercial forests (Graham et al. 2013), on biodiversity and ecosystems is crucial to inform conservation efforts.

As in many parts of Europe, anthropogenic land-use change has reshaped the landscape of Ireland for millennia. Widespread deforestation occurred since the Mesolithic period (Preece et al. 1986), with forest cover falling to less than 1% by the turn of the twentieth century (Cross 1987). Total forest cover has since increased to its current level of 11% in the Republic of Ireland (DAFM 2018), driven by government policy and commercial afforestation, with a target of 18% forest cover by 2046 (DAFM 2014). Much of this afforestation has occurred on land unsuitable for intensive agriculture in upland areas, with 39% of forests planted on peatlands comprising mostly of monospecific, even-aged plantations (DAFM 2018). The replacement of natural and semi-natural open habitats with forests impacts significantly on species whose ecology is closely linked to the preceding open habitats, including species of conservation concern (Thompson et al. 1988; Stillman and Brown 1994; Douglas et al. 2014). The transition from semi-natural habitat to commercial forest reduces the availability of key resources for foraging, breeding and predator avoidance which may ultimately result

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in population decline. For example, non-native Sitka spruce (*Picea sitchensis*) forests in Ireland have significantly fewer species and lower densities of birds of conservation concern than peatland habitats, highlighting the potential for commercial afforestation to significantly affect bird communities in upland areas (Armstrong and van Hensbergen 1995; Graham et al. 2017). An understanding of the impact of this new habitat on the ecology of upland communities is required to underpin conservation ecology and sustainable forest management.

Birds are an important component of forest ecosystems and are useful indicators of biodiversity due to the ease with which they can be surveyed and their responsiveness to environmental change (Furness et al. 1993; Venier and Pearce 2004; Fraixedas et al. 2020). The change in land use from open to forested habitats can have varied effects on bird communities and is largely dependent on the specific vegetative composition of the preceding habitat (Graham et al. 2017; Castano-Villa et al. 2019). Where open habitats are converted to forest, there is a transition from open-habitat specialists to scrub specialists and then generalist forest bird species (Sweeney et al. 2010). Previous research on the impact of afforestation on birds has looked at the influence of prior land use (Graham et al. 2017), forest age (Sweeney et al. 2010) and tree composition (Irwin et al. 2014). However, there remains a gap in our knowledge of bird community composition and density during the open pre-thicket planted forest stage when compared with preceding open habitats such as moorland. As young upland forest accounts for nearly 18% of forest cover in Ireland (DAFM 2018), with afforestation due to increase further in the coming decades, gaining an understanding of the changes to bird density and community composition in the initial stages of afforestation is a crucial first step to identify conservation priorities and potential wider ecosystem effects.

Small mammals are also integral components of forest ecosystems, being important herbivores and omnivores, as well as a key prey resource for mammalian and avian predators (Olofsson et al. 2004; Twining et al. 2019). It is therefore important to understand the influence of forest planting on small mammal communities. However, much of the previous research in this field has taken place in North America (Sullivan and Sullivan 1982; Fisher and Wilkinson 2005; Craig et al. 2006; Sullivan and Sullivan 2012), and this remains a largely unexplored topic in a European, and particularly in an Irish, context. Consequently, there is a requirement for a greater understanding of small mammal communities of young, upland conifer forests, and how they differ from those of preceding open habitats.

Together, bird and small mammal communities in upland areas provide an important food resource for many apex predators, including birds of prey (Redpath 1991; Fernández-Bellon and Lusby 2011; Nota et al. 2019). Thus, understanding the capacity for forest habitats to provide prey resources is

crucial for the development of appropriate conservation and management decisions aimed at supporting birds of prey. Certainly, commercial forests harbour potential prey species and offer foraging opportunities, particularly during the early growth stages prior to canopy closure. For example, hen harrier (*Circus cyaneus*) and merlin (*Falco columbarius*), species typically associated with open upland landscapes, often occupy planted upland areas where there is an absence of more suitable habitat (Petty 1996; Wilson et al. 2009; Lusby et al. 2017). However, the capacity for these habitats to support suitable prey populations is not yet fully understood and may be critical to the long-term persistence of these vulnerable upland birds of prey.

The turnover of bird and small mammal communities associated with the conversion of open upland areas to forest habitats is related to changes in structural habitat features that provide food and shelter (Ecke et al. 2001; Wilson et al. 2010; Gasperini et al. 2016). Furthermore, there is evidence that bird and small mammal communities change in response to further structural habitat changes that occur as forests age (Staines et al. 1987; Sullivan et al. 2000; Sweeney et al. 2010). Typically, conifer forests are harvested by clear-felling and then replanted shortly thereafter. The post clear-felling woody debris (brush) that remains in replanted areas during the early stages of the second and subsequent forest cycles enhances structural complexity and can provide habitat for birds and small mammals (Kirkland 1990; Sweeney et al. 2010). Despite the strong relationship between bird and small mammal abundance and structural complexity, few studies have investigated the potential role of woody debris in providing habitat for birds and small mammals during the early growth stages of commercial forests (Seibold et al. 2015).

This study set out to assess the composition and abundance of birds and small mammals in early upland second rotation pre-thicket conifer forests compared with open upland moorland. Particular focus was given to the conservation implications for the predators that rely upon these animals as prey.

Methods

The abundance of birds and small mammals was investigated in three different upland habitats in the Republic of Ireland between April and July 2018: (i) heather/grass moorland (hereafter referred to as 'moorland'); (ii) early second rotation pre-thicket conifer forests (aged 2–4 years post-replanting; hereafter referred to as 'early pre-thicket forests'); and (iii) late second rotation pre-thicket conifer forests (aged 6–8 years post-replanting; hereafter referred to as 'late pre-thicket forests'). Moorland sites were dominated by heather (*Calluna* and *Erica* spp.) and grasses (primarily *Molinia*). Forest sites were largely comprised of Sitka spruce, with lodgepole pine (*Pinus contorta*) and larch (*Larix* spp.) at lower densities. The

age classes of forests were calculated based on time since planting, relative to 2018, as defined in a database of forest planting provided by the Irish commercial forestry operator, Coillte.

Eight study areas were selected, based on the availability of focal habitats and brash management strategy (windrowing, i.e. lines of discarded material, heaped in rows by harvesting machinery) within forest patches. Each study area contained three study sites (one of each habitat), giving a total of 24 sites (Fig. 1). Study areas were separated by an average of 71.5 ± 43.1 km. Study sites averaged 12.6 ± 3.1 ha in size, were separated by an average of 1.30 ± 0.63 km within study areas and were located on average 350 ± 62 m above sea level.

Bird surveys

Non-raptorial bird species (i.e. putative prey) abundance was quantified at each site using point counts (Bibby et al. 2000). Three points with a detection radius of 100 m were randomly generated at each study site, avoiding overlap. Two count surveys were carried out at each point, the first count period from mid-April to mid-May 2018 (early-mid breeding season; $n = 72$) and the second count period from mid-May to late

June 2018 (mid-late breeding season; $n = 72$) (see Dettmers et al. 1999; Drapeau et al. 1999). Surveys were carried out between 1 hour after dawn and 12:00 and lasted 10 minutes, following a 1-minute settlement period. The survey schedule for areas, sites and points was randomised with the stipulation that all three sites within a study area were surveyed on the same morning. All bird surveys were conducted in suitable weather conditions, with no persistent rain, good visibility and calm winds ($< \text{Beaufort scale } 4$). Birds were detected both visually and by sound (song, calling, alarming). The same observer undertook all bird surveys. The distance from the observer to detected bird(s) was measured using an Eyoyo® rangefinder, and the species, number of individuals, behaviour and the direction of the detection relative to North were recorded. Only those birds deemed to be actively using the site (i.e. foraging, nesting or perching) were included in the analyses. Flocks greater than five individuals were excluded from analyses to minimise over-inflation of densities arising from transient flocks (Sweeney et al. 2010).

Small mammal surveys

Small mammals were surveyed at each site using live trapping (Gurnell and Flowerdew 2006) in June and July 2018. Two parallel, linear transects, each a minimum of 10 m from the edge of the site (i.e. boundary of forest coup/where moorland meets other land uses), measuring 90 m and separated from each other by approximately 50 m, were established in each study site. Transects in moorland were established perpendicular to the site edge. Transects in forest sites were established in direct proximity to windrows. Each transect consisted of 10 trapping stations spaced approximately 10 m apart (± 1 m). Each trapping station consisted of two live-capture small mammal traps, one Heslinga trap and one Longworth trap (Chitty and Kempson 1949), giving a total of 40 traps per study site. Paired traps at each station were placed within 1 m of each other and orientated in opposite directions along the transect. The alignment of specific trap models was randomised across all stations. Traps were angled downward to enable drainage of any moisture and were covered with vegetation to prevent overheating from direct sunlight. Traps were baited with peanuts, apple and dried mealworms and straw was provided as bedding. Trap chambers were fitted with shrew holes (11-mm diameter) to prevent retention of the protected pygmy shrew (*Sorex minutus*).

All sites in each study area were surveyed simultaneously. Traps were deployed without pre-baiting on the evening of day one, checked at approximately 08:00 and 20:00 on days two and three and checked and removed at 08:00 on day four, giving five 12-hour trap events for every site (Sullivan et al. 2017). Fresh bait was added to traps each evening while bedding was replaced after periods of rainfall. Both bedding and bait were replaced in traps where a small mammal had been



Fig. 1 Location of eight study areas in Ireland

caught. Captured animals were identified to species, aged (adult/juvenile), sexed (male/female), weighed (to the nearest 0.1 g using a digital scales), their breeding condition recorded (breeding/non-breeding) and photographed. Previously uncaptured individuals were given a unique combination of fur clips to facilitate subsequent identification. For recaptured individuals, the unique fur clip pattern was noted along with age, sex, breeding condition and weight (Gurnell and Flowerdew 2006).

The area in which this study was undertaken covered the distribution of two invasive small mammal species in Ireland: the bank vole (*Myodes glareolus*) and the greater white-toothed shrew (*Crocidura russula*). The native wood mouse (*Apodemus sylvaticus*) and pygmy shrew also occur in this area (McDevitt et al. 2014).

Small mammal vegetation surveys

Vegetation surveys were undertaken at each site on the morning of days two and three of small mammal surveys. These surveys were carried out at trap stations three and eight on each transect (20% of trap stations) to account for possible variation in vegetation characteristics along the length of the transect (Fig. 2). Vegetation cover was visually estimated for each plant species/group, to the nearest 5% (Hoffmann et al. 2010) in each of three 1-m² quadrats. Vegetation was subsequently grouped according to structural similarities: bare ground and moss; gorse and bramble; grasses and forbs; heather and bilberry; rushes and woodrush; and ferns. Maximum vegetation height was recorded within a 5-cm radius of the corner of each quadrat. Visual obstruction readings (VORs) were taken to obtain an index of vegetation density by placing a Robel pole (Robel et al. 1970) in the centre of the middle quadrat. The lowest number visible on the Robel pole was recorded at three observation heights (0.5 m, 0.8 m, 1 m) at each of three distances (2 m, 3 m, 4 m) away from the Robel pole, along a straight line (adapted from Evrard and Bacon 1998). The direction that VOR measurements were taken followed the line of least slope, as determined in the field, to mitigate impacts of slope on VOR measurements.

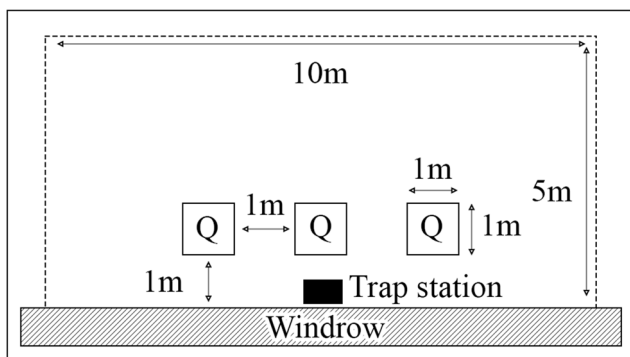


Fig. 2 Vegetation survey plots within study sites

The distance from the trap station to the five nearest trees was recorded to the nearest centimetre (Happold and Happold 1987). The heights of these trees were visually estimated and categorised within half-metre categories, and the tree species was also recorded. A 5 × 10 m plot was marked out with the innermost edge parallel to the windrow and with the trap station at the centre. The number of planted trees (i.e. tree density), tree stumps (> 50 cm diameter) and upturned tree root masses and logs (> 50 cm diameter) were counted within these larger plots (Carey and Harrington 2001; Fuller et al. 2004). Total coarse woody debris (CWD) was calculated as the sum of logs + stumps + root masses (Fuller et al. 2004).

Brash structure was assessed by measuring brash pile width and height at the point of the trap station, thus allowing an estimation of brash volume (Hardy 1996).

Data analysis

Bird observations were grouped into four distance bands (0–40 m, 41–60 m, 61–80 m and 81–100 m) to facilitate the fitting of distance functions and, hence, the calculation of density estimates. A minimum of 60 detections are required to produce a reliable detection function, and so it was not possible to construct individual detection functions for each species/habitat combination (Buckland et al. 2001). Therefore, bird species were grouped into three categories based on typical species-specific habitat associations: all bird species; open-country species; and scrub species (Nairn and O'Halloran 2012) (Table 1). As information on the detectability of individual species is scarce, birds with similar ecologies were assumed to have similar detection rates. Densities were calculated for all species in each habitat; for open-country species in moorland and early pre-thicket forests; and for scrub species in early and late pre-thicket forests. It was not possible to calculate densities of open-country species in late pre-thicket forests nor scrub species in moorland due to insufficient numbers of bird detections. Six species were not assigned to a group as five of these species are typically associated with post-thicket forests, while one species, the ring-necked pheasant (*Phasianus colchicus*), is associated with both open and scrub habitats. Akaike's information criterion (AIC) was used to select the best fitting detection function between five models: half-normal/cosine, hazard-rate/cosine, uniform/cosine, uniform/polynomial and half-normal/Hermite (Sweeney et al. 2010; Broekema and Overdyck 2012). Densities were calculated at each point for each count period and the maximum of these two values was taken as the density at that point. Differences in bird densities between habitats and species groups were investigated using general linear mixed effects models (GLMMs), with bird density as the response variable, habitat as the fixed factor and site as the random factor.

Table 1 Bird species included in analyses with associated Irish conservation status (Colhoun and Cummins 2013), habitats within which they were detected (M = moorland, E = early pre-thicket forest, L = late pre-thicket forest) and habitat group (Nairn and O'Halloran 2012)

Common name	Latin name	Conservation status	Habitats detected	Habitat group
Meadow pipit	<i>Anthus pratensis</i>	Red-listed	M/E/L	Open
Skylark	<i>Alauda arvensis</i>	Amber-listed	M	Open
Red grouse	<i>Lagopus lagopus</i>	Red-listed	M	Open
Blackbird	<i>Turdus merula</i>	Green-listed	L	Scrub
Blackcap	<i>Sylvia atricapilla</i>	Green-listed	L	Scrub
Dunnock	<i>Prunella modularis</i>	Green-listed	E/L	Scrub
Common whitethroat	<i>Sylvia communis</i>	Green-listed	E/L	Scrub
Reed bunting	<i>Emberiza schoeniclus</i>	Green-listed	E	Scrub
Robin	<i>Erithacus rubecula</i>	Amber-listed	E/L	Scrub
Willow warbler	<i>Phylloscopus trochilus</i>	Green-listed	M/E/L	Scrub
Wren	<i>Troglodytes troglodytes</i>	Green-listed	M/E/L	Scrub
Blue tit	<i>Cyanistes caeruleus</i>	Green-listed	L	NA
Chaffinch	<i>Fringilla coelebs</i>	Green-listed	M/E/L	NA
Coal tit	<i>Periparus ater</i>	Green-listed	L	NA
Goldcrest	<i>Regulus regulus</i>	Amber-listed	L	NA
Lesser redpoll	<i>Acanthis cabaret</i>	Green-listed	L	NA
Ring-necked pheasant	<i>Phasianus colchicus</i>	Green-listed	E/L	NA

Six species were generalists and therefore were not grouped into either open or scrub habitat categories

The minimum number of individual small mammals alive (MNA) within each site was used as an index of small mammal abundance (Gurnell and Flowerdew 2006) as too few small mammals were captured to support population estimation via more complex capture-recapture methods.

Zero-inflated negative binomial mixed effects models were constructed to explore differences between habitats. A discrete model was not constructed for greater white-toothed shrew due to the low number of captures across all habitats ($n = 27$). A suite of models were constructed including MNA of (i) all species, (ii) bank vole and (iii) wood mouse as the response variables, with habitat as the fixed factor and habitat nested within study area and surveyor ($n = 5$) as random factors. Models were compared to their null alternatives (i.e. with no explanatory variables) using AIC; the model with the lowest AIC value was considered to be the best performing model. Two discrete principal component analysis (PCA) processes were applied to habitat data; one captured all ground vegetation data while the other was comprised of tree data. All variables were standardised, with $\bar{x} = 0$ and $\sigma = 1$. It was not possible to incorporate habitat components in more complex models, primarily due to overspecification (i.e. non-Hessian matrix) errors in models with ≥ 2 variables and issues with model convergence. Thus, PCAs were only used to describe the vegetative composition of each habitat in the context of the simpler model, above.

Species diversity of both birds and small mammals was assessed using the inverse of the Simpson's diversity index. This index is suitable for assessing species diversity where sample sizes are small and indicates the probability that two

individuals drawn randomly from a sample belong to the same species (Magurran 2004). In addition, Simpson's diversity index accounts for both species richness and abundance. Simpson's diversity was calculated separately for each bird survey period (first and second).

Data were processed and analysed using ArcGIS 10.4.1 (ESRI 2011), distance (Thomas et al. 2010) and R version 3.5.1 (R Core Team 2018), including packages *caret* (Kuhn 2018), *ggplot2* (Wickham 2016), *glmmTMB* (Brooks et al. 2017), *lme4* (Bates et al. 2015) and *vegan* (Oksanen et al. 2018). The datasets generated and analysed during the current study are available at <https://doi.org/10.5281/zenodo.4526285>.

Results

Bird communities

Thirty-five bird species were recorded during this study. Seventeen species were included in the analyses as these were deemed to be utilising the habitat in which they were recorded. Of these 17 bird species, six were detected in moorland, nine were detected in early pre-thicket forests and 14 were detected in late pre-thicket forests. Moorland held the highest proportion of species of conservation concern, with one of the six species being amber-listed and two being red-listed (Table 1). Just one red-listed species and two amber-listed species were recorded in pre-thicket forest habitats.

There were significant differences in bird densities across the three habitats when considering all bird species together. Bird density was significantly higher in moorland (8.23 ± 0.43 birds/ha⁻¹) than in either early pre-thicket forests (3.41 ± 0.42 birds/ha⁻¹; $P < 0.01$) or late pre-thicket forests (6.49 ± 0.41 birds/ha⁻¹; $P < 0.05$). Early pre-thicket forests had significantly lower bird densities than late pre-thicket forests ($P < 0.01$). Densities of open-country birds were significantly higher in moorland (8.15 ± 0.45 birds/ha⁻¹) compared with early pre-thicket forests (2.74 ± 0.39 birds/ha⁻¹; $P < 0.01$). Densities of scrub species were significantly lower in early pre-thicket forests (0.88 ± 0.20 birds/ha⁻¹) than in late pre-thicket forests (5.23 ± 0.45 birds/ha⁻¹; $P < 0.01$; Fig. 3). Full model outputs are shown in Table 2.

Across both count periods (i.e. early and late), moorland held the lowest bird diversity ($I = 0.23 \pm 0.07$ and $I = 0.08 \pm 0.03$, respectively), followed by early pre-thicket forests ($I = 0.43 \pm 0.12$ and $I = 0.37 \pm 0.09$, respectively) and late pre-thicket forests ($I = 0.69 \pm 0.03$ and $I = 0.62 \pm 0.05$).

Small mammal communities

Two hundred and thirty-seven individual small mammals of three species were recorded from 351 captures, including 114 recaptures, across 4,760 12-hour trap events. The bank vole was the most frequently recorded species, with 152 individuals captured (64.1%). Fifty-eight individual wood mice (24.5%) and 27 greater white-toothed shrews (11.4%) were also captured (Table 3). Small mammal diversity was highest in moorland (0.42 ± 0.14), followed by early pre-thicket forests (0.41 ± 0.09) and late pre-thicket forests (0.20 ± 0.08).

Ground vegetation PC1 had positive associations with gorse and bramble and taller and denser vegetation, as seen in late pre-thicket forests, with a negative association with bare ground and moss that characterised moorland sites

(Table 4; Fig. 4a). Ground vegetation PC2 showed a positive association with heather and bilberry cover (i.e. late pre-thicket forests and moorland) and a negative association with grasses and forbs (i.e. early pre-thicket forests; Table 4, Fig. 4a). Tree vegetation PC1 had a positive association with the number of trees, tree height and brash volume and a negative association with greater distance between trees, describing early and late pre-thicket forest sites (Table 5; Fig. 4b). Tree PC2 had positive associations with canopy cover and a negative association with course woody debris, separating late and early pre-thicket forest (Table 5; Fig. 4b).

Habitat models showed that total small mammal abundance was significantly higher in early pre-thicket forests compared with both moorland (2.33 ± 0.71 ; $P < 0.01$) and late pre-thicket forests (1.42 ± 0.67 ; $P < 0.05$; Table 3). There was no significant difference between total small mammal abundance in moorland and late pre-thicket forests ($P > 0.05$). Bank vole abundance was significantly higher in early pre-thicket forests compared with both moorland (2.03 ± 0.56 ; $P < 0.001$) and late pre-thicket forests (1.34 ± 0.56 ; $P < 0.05$). There was no significant difference in bank vole abundance between moorland and late pre-thicket forests ($P > 0.05$). Wood mouse abundance was significantly higher in both early pre-thicket forests (3.06 ± 1.20 ; $P < 0.05$) and late pre-thicket forests (2.54 ± 0.97 ; $P < 0.01$) than in moorland. There was no difference between early and late pre-thicket forests ($P > 0.05$). Full model outputs are shown in Table 2.

Discussion

Our results showed contrasting patterns in the abundances of birds and small mammals between moorland, early pre-thicket forests and late pre-thicket forests. Our findings suggest that the transition from moorland to pre-thicket habitats increased

Fig. 3 Mean (\pm SE) density for three groups of bird species, grouped according to typical habitat associations (see Table 1), in moorland, early pre-thicket forests and late pre-thicket forests

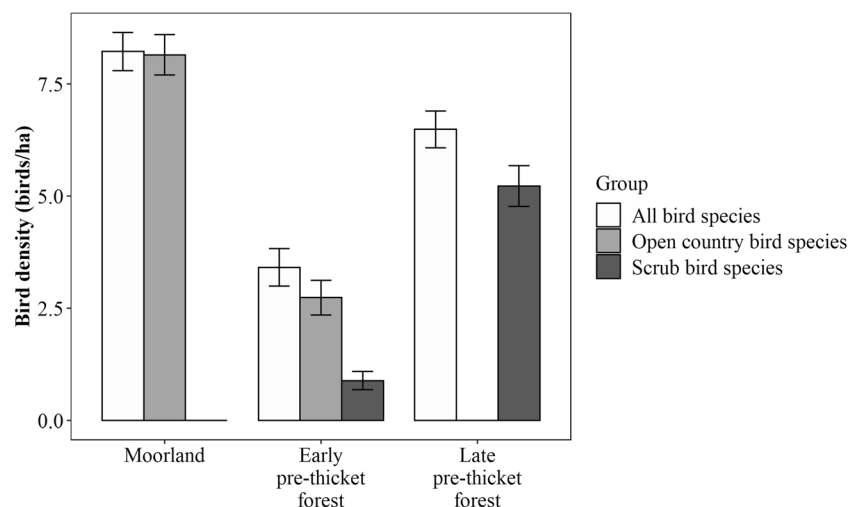


Table 2 Top models for avian-focussed GLMMs (a–c; n = number of density estimates) and mammal-focussed zero-inflated negative binomial mixed effects models (d–f; n = number of site capture site totals)

Model	n	Fixed effects	$\beta \pm SE$	p
(a) All bird species density	71	Early pre-thicket forests	-4.82 ± 0.59	< 0.001
		Late pre-thicket forests	-1.74 ± 0.59	< 0.05
(b) Open bird species density	47	Early pre-thicket forests	-5.36 ± 0.54	< 0.001
(c) Scrub bird species density	48	Early pre-thicket forests	-4.34 ± 0.40	< 0.001
(d) All small mammal habitat model	72	Early pre-thicket	2.33 ± 0.71	< 0.01
		Late pre-thicket	0.90 ± 0.54	0.09
(e) Bank vole habitat model	24	Early pre-thicket	2.03 ± 0.56	< 0.001
		Late pre-thicket	0.69 ± 0.46	0.14
(f) Wood mouse habitat model	24	Early pre-thicket	3.06 ± 1.20	< 0.05
		Late pre-thicket	2.54 ± 0.97	< 0.01

Parameter coefficients (β) with standard errors and probability (p) values are given

shrub vegetation complexity, altering the suitability of these areas for different bird groups. Specifically, the change from moorland to pre-thicket forests resulted in a reduction of open-country bird species and an increase in scrub-dwelling bird species. The observed differences are mediated by the increase in the complexity of shrub vegetation as moorlands are displaced by commercial forests (Sweeney et al. 2010; Graham et al. 2017; Burton et al. 2018). By contrast, small mammal species diversity was lowest in pre-thicket forests, but overall abundance was highest, primarily driven by bank voles. The increased cover, vegetation density and complexity afforded by windrowed pre-thicket second rotation forests appear to be beneficial in supporting higher densities of small mammals.

Bird communities in open moorland and young forests

Although the effect of afforestation on bird communities has been a focus of research attention in recent years (Graham et al. 2017; Burton et al. 2018; Castano-Villa et al. 2019), this is the first fine-scale study to compare bird communities across different ages of the pre-thicket stage of second rotation upland forests with moorland. Although meadow pipits, a red-

listed species in Ireland (Colhoun and Cummins 2013), were recorded in pre-thicket forests, they occurred at much lower densities than in moorland. Skylark and red grouse (*Lagopus lagopus*), which were both recorded in moorland and are also of high conservation priority (Colhoun and Cummins 2013), were entirely absent from pre-thicket forests (Table 1). Open moorland therefore supports a greater abundance of birds of conservation priority, with afforestation leading to the replacement of these threatened open-habitat bird species with lower densities of a wider variety of species that are currently of less conservation priority. These results have considerable implications for current forest management and future afforestation, with new forests continually replacing the habitat of threatened species, further contributing to their ongoing declines.

Similar effects of afforestation on open-habitat bird communities have been reported in other parts of northern Europe where a greater abundance of common generalist species is found in young forest habitats, replacing the open-habitat bird assemblage of less common and more specialist bird species (Moss et al. 1979; Thompson et al. 1988; Calladine et al. 2013). The lower abundance, and in some cases absence, of open-habitat specialists recorded in young forests in this study reflects the specific habitat requirements of these species during the breeding season (Vanhinsberg and Chamberlain

Table 3 Total number of captures of three small mammal species recorded across three habitats

	Habitat					
	Moorland		Early pre-thicket forest		Late pre-thicket forest	
Bank vole	21 (14)	a	95 (21)	A, B	36 (18)	b
Wood mouse	2 (0)	c, d	30 (6)	C	26 (10)	D
Greater white-toothed shrew	7 (2)		18 (6)		2 (0)	
Captures per trap event	0.04		0.14		0.08	
Total	30 (16)	e	143 (33)	E, F	64 (28)	f

Letters denote significant differences ($p < 0.05$) where UPPER > lower. The number of individuals re-trapped is shown in parentheses. The number of captures per trap event (excluding false triggers) is also shown to ease comparison between studies

Table 4 Principal component (PC) axes loadings capturing ground vegetation variation at small mammal survey sites

Vegetation variable	Principal components (variation explained)	
	PC1 (33.3%)	PC2 (24.5%)
Bare ground and moss	−0.567	−0.146
Ferns	0.446	−0.116
Gorse and brambles	0.747	0.067
Grasses and forbs	0.006	−0.873
Heather and bilberry	−0.153	0.943
Rushes and woodrush	0.075	−0.515
Vegetation height	0.948	0.054
Visual obstruction reading	0.811	0.068

Those loadings that explain the greatest proportion of variation within each of the retained PCs are in bold and the percentage variation explained by each PC is given. Vegetation variables are listed alphabetically

2001). Though these species may persist for short periods in first rotation pre-thicket forests due to the retention of suitable habitat features (Wilson et al. 2006), this is not the case with subsequent rotations. Second rotation pre-thicket forests therefore appear to be suboptimal habitats for several open-country bird species of conservation concern.

Within young forest sites, there was a shift in bird communities from open to scrub species with increasing forest age, related to the increase in the complexity of shrub vegetation layers over time (Wilson et al. 2006; Sweeney et al. 2010). Similar patterns have been observed in commercial forests in other parts of northern Europe (Patterson et al. 1995). Bird density and diversity also increased from early to late pre-thicket forests, likely driven by increased habitat suitability for a wider variety of generalist scrub habitat bird species (Quine et al. 2007).

Results from the current study suggest that the presence of woody debris (brash) may benefit scrub bird species, particularly during the initial growth stages post-planting (early pre-thicket forest stage). Brash adds structural complexity necessary for these bird species to a habitat otherwise bereft of such complexity (Kirkland 1990; Sweeney et al. 2010). The higher abundance of scrub species in the later pre-thicket stage is likely the result of increased shrub vegetation complexity as the forests develop (Wilson et al. 2010; Calladine et al. 2013). In a study of bird species richness in pre-thicket plantation forests and open moorland in Scotland, Calladine et al. (2013) reported lower bird species richness in pre-thicket Sitka spruce forests compared with adjacent open moorland. The observed difference was found to be mediated by differences in the extent of shrub cover, demonstrating the importance of vegetation complexity in providing resources for bird communities (Wilson et al. 2010; Calladine et al. 2013), further evidence of which is provided by the current study.

Small mammal communities in open moorland and young forests

In contrast to the negative impact observed on open-country bird species, land-use change from open habitat to pre-thicket forest appears to benefit small mammals. More small mammals were captured in early pre-thicket forests than in either of the other habitats. The abundance of grasses and forbs in young forest sites appears to be particularly suitable for bank voles, in clear contrast to the denser, taller and gorse- and bramble-dominated old forest sites where bank voles were less abundant. The trend seen in this study whereby small mammals reach higher densities soon after clearcutting, followed by a decrease in abundance, has also been demonstrated in other studies where vegetation community and structural changes caused by clearcutting resulted in enhanced habitat quality for small mammal species (Kirkland 1990; Fisher and Wilkinson 2005; Gasperini et al. 2016). The lower abundance of small mammals in moorland compared with pre-thicket forests observed in this study reflects the lower suitability of moorland as a habitat for those small mammals in Ireland. Within young forest sites, brash in the form of windrows provides small mammals with suitable runways and cover (Carter 1993; Fisher and Wilkinson 2005) and is associated with increased small mammal abundance (Fauteux et al. 2012; Gasperini et al. 2016). Small mammals showed a positive association with both the presence of brash and brash volume in the current study, likely due to the provision of food resources (Gunderson 1959; Bowman et al. 2000; Kaminski et al. 2007). The most frequently captured small mammal species across all sites in this study was the bank vole, making up 64% of all individuals captured. Although bank voles were captured in moorland in this study, their numbers were significantly lower than in pre-thicket forests, likely due to the absence of dense vegetation cover in moorland (Mazurkiewicz 1994; Hayden and Harrington 2000). Pre-thicket forest is known to be an important habitat for the species in Ireland (Smiddy and Sleeman 1994) and elsewhere in their range (Savola et al. 2013).

While the abundance of bank voles was significantly higher in early pre-thicket compared with late pre-thicket forests, the numbers of wood mice did not differ between pre-thicket forests of different ages. The differing effects of increasing forest age on bank voles and wood mice can be explained by vegetation differences between forest ages and comparative habitat requirements of both species. As forests age, dense herbaceous ground cover of grasses and forbs, important for both species, decreases, while shrub cover, important for wood mice, increases (Loy and Boitani 1984; Dickman and Doncaster 1987). Therefore, while the vegetation remains suitable for wood mice throughout this period, it becomes less suitable for bank voles.

Fig. 4 Principal component (PC) score (\pm SD) biplots for **a** ground vegetation and **b** tree vegetation

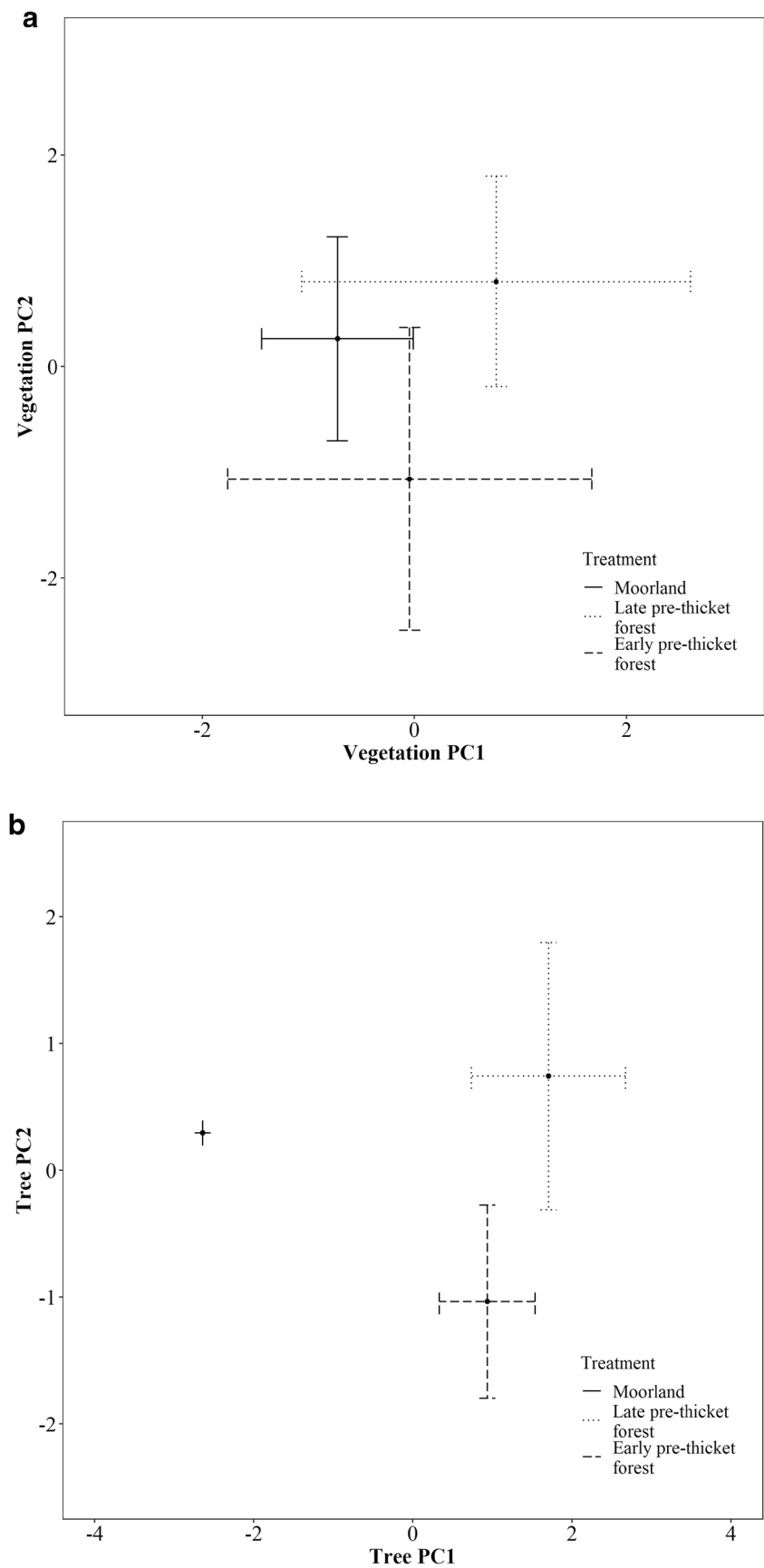


Table 5 Principal component (PC) axes loadings capturing tree vegetation variation at small mammal survey sites

Tree variable	Principal components (variation explained)	
	PC1 (69.6%)	PC2 (19.3%)
Brash volume	0.866	−0.094
Canopy cover	0.688	0.669
Course woody debris	0.602	−0.760
Distance to nearest tree	−0.935	0.199
Number of trees	0.934	−0.001
Tree height	0.919	0.289

Those loadings that explain the greatest proportion of variation within each of the retained PCs are in bold and the percentage variation explained by each PC is given. Tree variables are listed alphabetically

Greater white-toothed shrews were also captured during this study. This species was unintentionally introduced into Ireland around 2004 and their range is predicted to expand to cover the whole of Ireland by 2050 (Tosh et al. 2008; McDevitt et al. 2014). Greater white-toothed shrews displace native pygmy shrews from the invaded range, with habitats such as peatlands and woodlands thought to be the only possible refugia for the pygmy shrews (McDevitt et al. 2014). The current study revealed that greater white-toothed shrews have spread further west in south Limerick than had been previously recorded (National Biodiversity Data Centre 2019) and that they are capable of inhabiting upland moorlands (400 m asl). This suggests that peatlands may not be effective refugia habitat for the native pygmy shrew as they were previously thought to be. However, a number of pygmy shrews were temporarily captured in one late pre-thicket forest within the core range of the greater white-toothed shrew. This is the first evidence that pygmy shrews are able to persist within the core range of the invasive greater white-toothed shrew (in this case, greater white-toothed shrews have been present for at least 6 years (McDevitt et al. 2014)). These findings warrant further research as the identification of potential refugia habitats for the pygmy shrew and the potential coexistence of both species in relatively close proximity have important implications for pygmy shrew conservation in Ireland.

Implications for predators

Studying prey communities enables a deeper understanding of the underlying mechanisms of observed impacts of land-use change on predators. The bird and small mammal species that are the focus of this study are prey for a wide range of upland predators, including some of conservation concern. The results from this study indicate that the shift in land use from moorland to forest habitat leads to lower prey abundance for those predators that rely primarily on birds, such as hen harrier

and merlin (Fernández-Bellon and Lusby 2011; Irwin et al. 2012). For example, decreased prey abundance and accessibility in pre-thicket forests has been suggested as a contributing factor to lower breeding outputs of hen harriers nesting in landscapes with a high proportion of pre-thicket forests (Wilson et al. 2012).

Conversely, the shift from open to forested habitats may increase the abundance of preferred small mammal prey of predators such as the short-eared owl (*Asio flammeus*) and pine marten (*Martes martes*) (Glue 1977; Lynch and McCann 2007; Twining et al. 2019). However, this increased prey abundance may only be temporary as bird and small mammal abundances change with increasing forest age beyond the pre-thicket stage (Sweeney et al. 2010; Savola et al. 2013). Such shifts in prey abundances could have additional important ecological consequences. For example, increases in small mammals in upland forests may lead to increased abundance of mammalian predators, such as pine marten, potentially leading to increased rates of predation on the nests of declining ground-nesting birds, such as the hen harrier.

Conclusions

An understanding of the bird and small mammal communities in upland open moorland and commercial conifer forests has important applications in forest management, policy development and conservation science. The results of our study show how the bird and small mammal populations of open habitats and young forests in the uplands differ, and that the consequences of land-use change associated with afforestation are taxa specific. This study demonstrates the important ecological benefits of retained brash to provide essential cover for small mammals and nest sites for scrub bird species. Where planting follows clear-felling, the retention of brash can enhance the suitability of young forests for birds and small mammals by providing appropriate habitat and is an important tool in the management of forests as habitats for wildlife.

The results further demonstrate that open habitats, such as moorland, hold higher densities of bird prey, and therefore conservation management strategies should focus on the preservation and restoration of these habitats. Strategic deforestation, selective clear-felling to promoting age diversity and habitat restoration could support increased numbers of open-habitat birds, which are important prey species for threatened predators such as hen harrier and merlin. Our findings demonstrate the importance of preserving remaining open natural and semi-natural habitats in order to protect the specialist open-habitat bird species that rely upon them. In addition to leaving sites of conservation value unplanted, efforts should also be made to remove self-seeded conifer trees from open areas that originate from nearby plantations in order to

preserve the suitability of these habitats for open-habitat species. In addition, open habitats of high biodiversity value require identification and mapping in order to inform afforestation policies in these habitats, thereby protecting vulnerable and threatened open-habitat specialists. Additional research will expand our understanding of bird and small mammal ecology in response to land-use change and the wider ecosystem consequences of further forest expansion. Of particular importance in this regard will be long-term studies of prey abundance under different forest management strategies in tandem with habitat restoration studies and the knock-on effects on foraging success of key predator species.

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Declarations

Ethical approval All applicable international, national and institutional guidelines for the care and use of animals were followed. All small mammal trapping was in accordance with the ethical standards of the University College Cork's Animal Experimentation Ethics Committee, where the study was conducted.

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