Contributed Paper

Bird-community responses to habitat creation in a long-term, large-scale natural experiment

Robin C. Whytock (iD),[1]* Elisa Fuentes-Montemayor,[1] Kevin Watts,[2,1] Patanjaly Barbosa De Andrade,[3] Rory T. Whytock,[4] Paul French,[5] Nicholas A. Macgregor,[6]† and Kirsty J. Park[1]

[1]Biological & Environmental Sciences, Cottrell Building, University of Stirling, Stirling FK9 4LA, U.K.
[2]Forest Research, Alice Holt Lodge, Farnham GU10 4LH, U.K.
[3]Animal Biology Department, Federal University of Viçosa, Av. PH Rolfs 36570900, Viçosa/MG, Brazil
[4]5 Alloway Avenue, Kilmarnock, East Ayrshire KA3 7DB, U.K.
[5]Greenfield Bungalows, Easington, East Yorkshire HU12 0TZ, U.K.
[6]Natural England, Nobel House, 17 Smith Square, London SW1P 3JR, U.K.

Abstract: *Ecosystem function and resilience are compromised when habitats become fragmented due to land-use change. This has led to national and international conservation strategies aimed at restoring habitat extent and improving functional connectivity (i.e., maintaining dispersal processes). However, biodiversity responses to landscape-scale habitat creation and the relative importance of spatial and temporal scales are poorly understood, and there is disagreement over which conservation strategies should be prioritized. We used 160 years of historic post-agricultural woodland creation as a natural experiment to evaluate biodiversity responses to habitat creation in a landscape context. Birds were surveyed in 101 secondary, broadleaf woodlands aged 10–160 years with ≥80% canopy cover and in landscapes with 0-17% broadleaf woodland cover within 3000 m. We used piecewise structural equation modeling to examine the direct and indirect relationships between bird abundance and diversity, ecological continuity, patch characteristics, and landscape structure and quantified the relative conservation value of local and landscape scales for bird communities. Ecological continuity indirectly affected overall bird abundance and species richness through its effects on stand structure, but had a weaker influence (effect size near 0) on the abundance and diversity of species most closely associated with woodland habitats. This was probably because woodlands were rapidly colonized by woodland generalists in ≤10 years (minimum patch age) but were on average too young (median 50 years) to be colonized by woodland specialists. Local patch characteristics were relatively more important than landscape characteristics for bird communities. Based on our results, biodiversity responses to habitat creation depended on local- and landscape-scale factors that interacted across time and space. We suggest that there is a need for further studies that focus on habitat creation in a landscape context and that knowledge gained from studies of habitat fragmentation and loss should be used to inform habitat creation with caution because the outcomes are not necessarily reciprocal.*

Keywords: conservation planning, ecological network, forest, fragmentation, land-use change, reforestation, revegetation

Respuestas de la Comunidad de Aves a la Creación de Hábitat en un Experimento Natural a Largo Plazo y a Gran Escala

Resumen: *La función y la resiliencia de un ecosistema están en peligro cuando los hábitats se fragmentan por el cambio en el uso de suelo. Esto ha llevado a estrategias nacionales e internacionales enfocadas en la restauración de la extensión del hábitat y en la mejora de la conectividad funcional (es decir, mantener los procesos de dispersión). Sin embargo, las respuestas de la biodiversidad a la creación de hábitats a escala de*

345

paisaje y la importancia relativa de las escalas espaciales y temporales están pobremente entendidas, y existen desacuerdos sobre cuáles estrategias de conservación deberían ser prioridad. Utilizamos 160 años de creación de bosque post-agrícola como un experimento natural para evaluar las respuestas de la biodiversidad a la creación del hábitat en un contexto de paisaje. Se censaron aves en 101 bosques secundarios de hoja ancha con edades entre 10 y 160 años con una cobertura del dosel ≥ 80% y 0 – 17% de bosques de hoja ancha en el paisaje circundante (dentro de los primeros 3000 m). Utilizamos el modelado de ecuaciones estructurales por fragmentos para examinar las relaciones directas e indirectas entre la abundancia y diversidad de aves, la continuidad ecológica, las características del fragmento, y la estructura del paisaje y cuantificamos el valor relativo de conservación de las escalas locales y de paisaje para las comunidades de aves. La continuidad ecológica afectó indirectamente a la abundancia general y a la riqueza de especies de aves a través de sus efectos sobre la estructura de los árboles, pero la continuidad ecológica tuvo una influencia más débil (tamaño del efecto cercano a 0) sobre la abundancia y la diversidad de especies asociadas más cercanamente con los hábitats boscosos. Esto probablemente se debió a que los bosques fueron colonizados rápidamente por los generalistas de bosques en ≤10 años (edad mínima de los fragmentos) pero en general eran demasiado jóvenes (mediana de 50 años) para ser colonizados por los especialistas de bosques. Las características de los fragmentos locales fueron relativamente más importantes que las características del paisaje para las comunidades de aves. Con base en nuestros resultados, las respuestas de la biodiversidad a la creación de hábitats dependen de factores a escala local y de paisaje que interactuaron a lo largo del tiempo y el espacio. Sugerimos que hay una necesidad de estudios más a fondo que se enfoquen en la creación de hábitats en un contexto de paisajes y que el conocimiento obtenido de los estudios sobre la fragmentación y la pérdida del hábitat deberían usarse para informar a la creación de hábitats con precaución porque no son necesariamente recíprocos.

Palabras Clave: bosque, cambio en el uso de suelo, fragmentación, planificación de la conservación, red ecológica, reforestación, revegetación

Introduction

For landscapes to support biodiversity and ecosystem services in the long term, they need to function as coherent "ecological networks" (Lawton et al. 2010; Humphrey et al. 2015). Conceptually, these comprise a spatial network of core habitats areas, corridors, stepping-stones, and buffer zones. In combination, these local and landscape elements are expected to contribute to ecosystem function by increasing the persistence and movement of species across fragmented landscapes (e.g., Opdam et al. 2006; Lawton et al. 2010; Humphrey et al. 2015).

Based on principles derived from island biogeography and conservation planning (MacArthur & Wilson 1967; Diamond 1975), there is increasing interest in applying the ecological network concept to landscape-scale conservation (e.g., Hoctor et al. 2000; Jongman et al. 2011; Watts et al. 2016). However, the value of this concept as a conservation tool has been contested (Boitani et al. 2007), and there is disagreement over which elements should be prioritized. For example, should the focus be on actions to restore functional connectivity by creating habitat corridors or on actions to increase habitat quality or extent (e.g., Hodgson et al. 2011; Fahrig 2013; Hanski 2015)?

There are 2 main knowledge gaps that potentially impede efforts to design effective ecological networks. First, for most taxa, the relative ecological importance of local versus landscape-scale characteristics is poorly understood, which has led to uncertainty over where

to prioritize resources (Dolman et al. 2007; Humphrey et al. 2015). Second, understanding of biodiversity responses to landscape configuration is underpinned by studies of habitat loss (e.g., Villard et al. 1999; Vergara & Armesto 2009; Gibson et al. 2013) and it is unclear if the ecological consequences of removing habitat (i.e., fragmentation) and the outcomes of habitat creation are reciprocal (Munro et al. 2007; Naaf & Kolk 2015; Watts et al. 2016).

Addressing these knowledge gaps has been challenging, not least because the time lag between habitat creation and biodiversity responses can be tens to hundreds of years, and many taxa respond to landscape configuration at kilometer scales or more (Boitani et al. 2007; Haddad et al. 2015; Watts et al. 2016). Processes occurring over such long periods and large spatial scales are difficult to replicate (Watts et al. 2016); thus, controlled experiments designed to test the effects of alternate conservation actions remain rare (Haddad 2012; Jenerette & Shen 2012; Legrand et al. 2012).

Recently, natural (or mensurative) experiments have advanced understanding of landscape-scale ecological processes and patterns (McGarigal & Cushman 2002; Lindenmayer 2009; Watts et al. 2016). These seek to strike a balance between the rigidity of manipulative experiments and the relatively low control of observational studies (Watts et al. 2016). For example, Mortelliti and Lindenmayer (2015) used a longitudinal (16 years) natural experiment (Nanangroe, Australia) to evaluate the effects of landscape-scale matrix transformation on bird

communities. They used a random stratified design to control for factors that could influence the bird community independent of the changing matrix. Thus, the effects of matrix change could be untangled from the effects of other local and landscape characteristics (Mortelliti & Lindenmayer 2015), and results showed that matrix transformation in the form of forestry plantations can influence bird turnover rates in remnant native woodland.

Responses of bird communities to landscape configuration have received widespread attention (e.g., Bennett et al. 2004; Vergara & Armesto 2009; Galitsky & Lawler 2015). This is in part due to the taxon's high diversity and because landscape attributes, such as patch isolation and matrix composition, can inhibit some species' movements despite their ability to fly and apparent high mobility (e.g., Bélisle et al. 2001). This paradox raises questions about the biological and ecological mechanisms that govern dispersal (Stevens et al. 2014). Forest birds are particularly vulnerable to landscape change, and many species have declined globally as a result of deforestation, which has wider implications for ecosystem function (Şekercioğlu et al. 2004).

Existing evidence, primarily from studies of habitat loss, suggests that for forest birds there should be a focus on maintaining or creating large forest patches, and patch area consistently predicts avian diversity, occupancy, and turnover rates (e.g., Dolman et al. 2007; Bregman et al. 2014; Humphrey et al. 2015). Other factors such as vegetation structure, management practices (e.g., livestock grazing), and patch shape can also play an important role in determining the diversity of forest birds (Martin & McIntyre 2007; Munro et al. 2007). However, few studies (Vergara & Armesto 2009; Galitsky & Lawler 2015) have simultaneously examined the relative influence of these factors across multiple spatial and temporal scales.

In addition to maintaining gene flow, migration and dispersal processes, functional ecological networks should satisfy the reproductive, feeding, resting, and sheltering requirements of multiple taxa. However, conservation actions that benefit one species could disadvantage another. For example, restoring contiguous forest on grazing pasture will benefit forest species but is likely to be detrimental to species associated with grassland. Furthermore, even within a land-cover type, individual species can have opposing responses to environmental factors and landscape configuration (Law et al. 2014; Galitsky & Lawler 2015). Finding a balance between the needs of multiple taxa therefore presents a challenge, and biodiversity metrics such as species richness may not capture the diverse needs of different groups or individual species. To find a middle ground, species can be grouped objectively according to shared ecological traits. For example, French and Picozzi (2002) used hierarchical clustering to group breeding birds based on their feeding, breeding, and resting habitat requirements and assessed the relationship between these clusters and large-scale patterns of land use.

We moved beyond investigating biodiversity responses to landscape fragmentation and habitat loss and evaluated, in a natural experiment, biodiversity responses to habitat creation in a landscape context. We surveyed bird abundance and diversity in 101 agricultural woodlands that appeared on historic maps in the last 10–160 years (Watts et al. 2016). We used structural equation models (SEMs) and tested for the existence of direct and indirect causal relationships between patch characteristics, ecological continuity, and landscape structure based on a priori expectations (Supporting Information), which allowed us to tease apart interactions that operate across temporal and spatial scales. We also compared the relative importance of local versus landscape-scale characteristics for the purposes of informing conservation and policy.

Methods

Study Area and Site Selection

A detailed description of the methods we used for site selection, as part of the Woodland Creation and Ecological Networks (WrEN) project, is in Watts et al. (2016). In summary, broadleaf, secondary woodland patches >0.5 ha with ≥80% canopy cover were identified in lowland agricultural areas in central Scotland and central England (Supporting Information) from the National Forest Inventory for Great Britain data set (Forestry Commission 2013). Potential sites were systematically selected based on multiple local- (e.g., size and age) and landscape- (e.g., amount and degree of connectivity of surrounding woodland) level selection criteria.

A total of 101 woodlands were surveyed for birds. Woodlands were 10–160 years old, 0.5–31.89 ha in area (reflecting the size distribution in the landscape), in landscapes with 0–17% broadleaf woodland cover within 3000 m and within 7–1573 m from the nearest broadleaf woodland. Detailed information and summary statistics for all local and landscape variables are given in Supporting Information.

Bird Surveys

Breeding birds were surveyed using a reduced version of the common bird census method (Marchant et al. 1990). Sites were visited in 2015 on 3 occasions, once in April, May, and June, respectively. There was a minimum of 7 d between surveys. Based on national bird census data, bird population trends for most species of interest did not fluctuate significantly from the average in 2015 (British Trust for Ornithology 2016), suggesting that it was a representative year. Surveys began 30 min after sunrise and

usually ended by 1100 (no later than 1130). Woodland patch geometry varied considerably. To account for this, survey effort was standardized to 10 min per hectare per visit, and observers approached all areas of the patch within a minimum distance of 50 m to increase the probability of detecting territorial birds. Repeat visits were made by the same observer and patches of <1 ha were surveyed for a minimum of 10 min per visit. Further details on the bird-survey methods are given in Supporting Information.

Corvids (other than Eurasian Jay [*Garrulus glandarius*]) and raptors were excluded due to their large territories and, for some species, low detectability (e.g., Eurasian Sparrowhawk [*Accipiter nisus*]). Species with a distribution that did not include both of our study areas in Scotland and England (e.g., Nightingale *Luscinia megarhynchos*) were also excluded (Supporting Information). We included resident and migrant species in the analyses, and species were assigned to one of five functional groups (see Results) based on the classifications given in table 1 of French and Picozzi (2002), who used Euclidean distance and hierarchical clustering (Ward 1963) to group British birds based on their feeding, breeding, and resting habitat requirements. Each species belongs to a single cluster. Nomenclature follows the British Ornithologists' Union (2013).

Patch Characteristics and Landscape Data

Local patch characteristics (patch age, patch geometry, vegetation structure, and management practices) and landscape metrics (landscape composition and landscape configuration) were recorded during field surveys in 2013, 2014, and 2015 or estimated from the U.K. Land Cover Map 2007 (Morton et al. 2011) and National Forest Inventory data set (Forestry Commission 2013) using ArcMap *v*10.2 (ESRI 2013).

Landscape composition was quantified by calculating the percent cover of broadleaf woodland, any woodland, seminatural land cover (excluding woodland), and urban land cover surrounding the patch at 8 nested scales (GIS buffers): 100, 250, 500, 1000, 1500, 2000, 2500, and 3000 m. We limited the maximum buffer size to 3000 m to ensure spatial independence between sites as far as possible, and this was also considered ecologically appropriate based on knowledge of woodland-bird dispersal distances (Paradis et al. 1998).

To quantify landscape configuration, we calculated a connectivity index for broadleaf woodland (broadleaf woodland connectivity) based on the incidence function model (Hanski 1994; Moilanen & Hanski 2001).

Modeling Approach

Our 2 main aims were to disentangle the direct and indirect relationships between bird diversity and abundance,

local patch characteristics (i.e., metrics of ecological continuity, patch geometry, vegetation structure and management), and landscape metrics (habitat composition and configuration in the landscape) and to quantify the relative importance of local versus landscape scales. We therefore used piecewise SEMs (Lefcheck 2016), a multivariate technique that can be used to test whether a priori hypothesized direct and indirect causal relationships between variables are supported by the observed data, and to compare relative effect sizes between variables. A global conceptual model (metamodel) (Fig. 1) based on underlying theory and evidence was used to guide the construction of more narrow hypotheses for individual functional groups and total species richness (Supporting Information).

Before fitting SEMs, constituent generalized linear models (GLMs) were validated following Zuur et al. (2010). In some cases, variables were log transformed to achieve a normal error distribution (Supporting Information). Bivariate relationships were explored graphically to identify potential nonlinear relationships. No multicollinearity was detected in constituent GLMs with a variance-inflation-factor threshold of <5. Continuous predictor variables were mean centered and scaled by 1 SD, and binary predictor variables were transformed to have values of –1 and 1 so that their effect sizes were directly comparable with those of continuous predictors. For all landscape metrics, we preselected the most appropriate buffer size for inclusion in the SEM by creating GLMs for each metric, scale, and response combination and retained only the scale with the lowest corrected Akaike information criterion.

During SEM validation, missing paths were evaluated and either added to the model if they were considered causal (these were few and are indicated in Supporting Information) or allowed to freely covary. Shipley's test of directed separation (Fisher's C) was used to evaluate global SEM fit, where values of $p > 0.05$ indicated the model was supported by the observed data (although alternative models may also be valid). Predictions from SEMs were made with nonfocal predictors set at their median value. We used R statistical software (R Core Team 2015) for all analyses.

Results

A total of 8252 records of adult birds of 59 species were recorded. After applying selection criteria to exclude probable nonbreeders and species with a restricted range, 7791 records of adult birds (median = 59, range = 17–495 records per site) of 46 species (median = 13, range 5–26 species per site) were retained for analysis. The remaining species fell into 5 functional groups (Fig. 2). Those in the open, mixed, or general wood and scrub group, such as Eurasian Wren
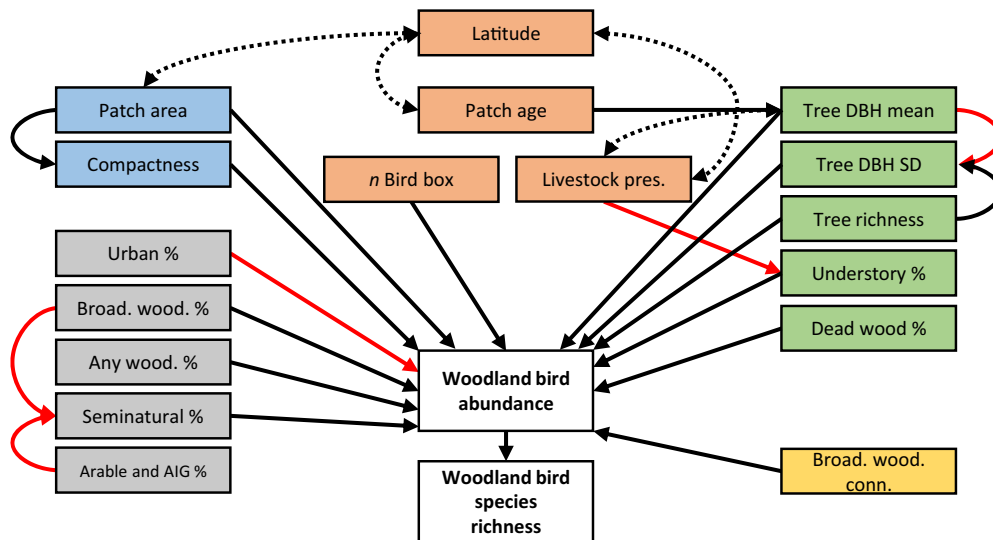
Figure 1. Metamodel used to guide construction of the structural equation model (SEM). Illustrated are the general hypothesized direct and indirect relationships (Supporting Information) between response variables (bird abundance and bird species richness) and metrics of patch geometry, vegetation structure, management practices, landscape composition, and landscape configuration (dashed arrows, hypothesized correlated relationships [based on knowledge of our study sites] that do not have a causal explanation; AIG, agriculturally improved grasslands). Final SEMs are given in Supporting Information.

(*Troglodytes troglodytes*) (96% of woodlands), Blue Tit (*Cyanistes caeruleus*) (90% of woodlands), and European Robin (*Erithacus rubecula*) (89% of woodlands) dominated. Chaffinch (*Fringilla coelebs*), a farmland seed eater, was detected in 98% of woodlands.

A complete analysis was conducted for each of the 5 functional groups. For brevity, only results for raw species richness and the 2 groups most strongly associated with woodland habitats (open, mixed, or general wood and scrub and broadleaf trees and hedgerows) are presented in the main text, but all results are given in Supporting Information. These 2 functional groups are also likely to be the main conservation focus of woodland creation. Goodness-of-fit statistics for all SEMs are given in Supporting Information, and in all cases the final models reproduced the data well (*p*> 0.05).

Total Species Richness

As expected, there was a strong positive relationship between total bird abundance and total bird species richness (Fig. 3a & Supporting Information). However, in contrast to expectations, abundance was not the only direct driver of species richness, and by evaluating missing paths we also identified significant direct relationships between species richness and local- (patch area) and landscape-scale (broadleaf woodland connectivity) variables (Fig. 3a).

Confirming our expectations, mean tree diameter at breast height was larger in older patches (Supporting Information), which in turn positively influenced total

bird species richness. Other than patch area, only tree species richness directly affected total bird abundance at the local scale.

Broadleaf woodland connectivity at 250 m had a positive, direct effect on species richness, but no other landscape-scale metric strongly affected total bird abundance or richness (Fig. 3a).

Broadleaf Trees and Hedgerows Functional Group

Only 2 of the 9 species expected in the broadleaf trees and hedgerows group were recorded in ≥20% of woodlands (Fig. 2), and 2 species with a geographic distribution that overlapped our 2 study areas were not detected, Wood Warbler (*Phylloscopus sibilatrix*) and Pied Flycatcher (*Ficedula hypoleuca*) (Balmer et al. 2013).

Unexpectedly, patch age and abundance of this group were not significantly related (Fig. 3b & Supporting Information). After evaluating missing paths, there was a direct negative relationship between patch size and species richness (controlling for abundance), although the effect was relatively small and unlikely to be ecologically relevant.

Livestock presence in the woodland reduced the group's relative abundance by approximately 61%, from an estimated mean of 5.41 (5.24–7.84 CI) to 2.12 (2.02–4.82 CI) adult birds recorded. In contrast to our original hypothesis, analysis of missing paths showed this effect was direct and not mediated by the negative effect of livestock presence on understory cover.
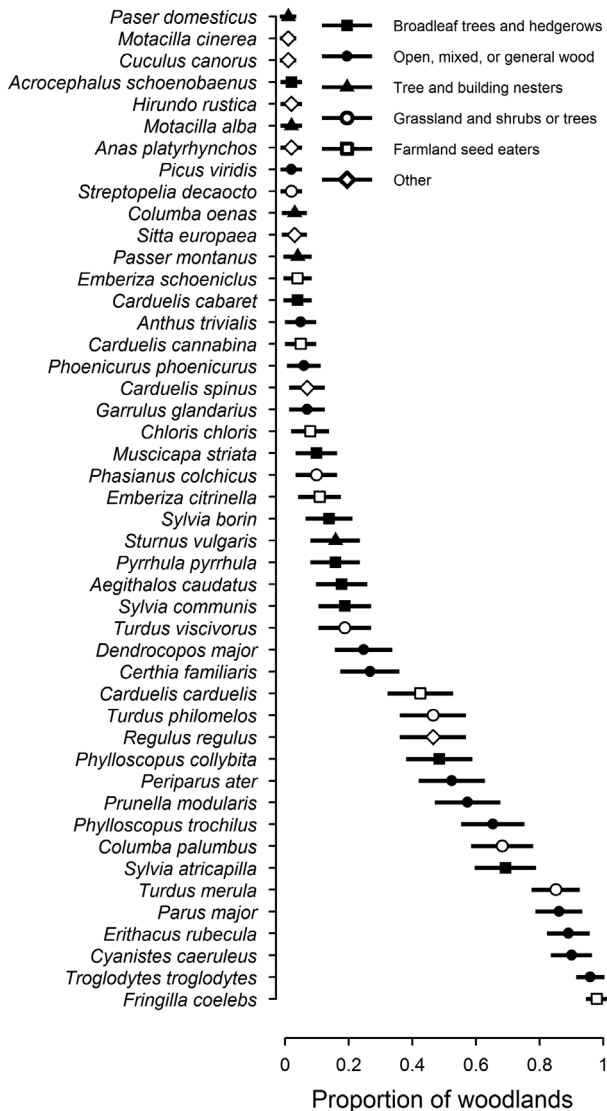
Figure 2. The proportion of woodlands (points and 95% confidence intervals [Eq. given in Supporting Information]) in which each species was recorded as probably breeding. Functional groups are from French and Picozzi (2002) (see Methods).

Also contradicting expectations, high proportions of broadleaf woodland in the landscape reduced rather than increased relative abundance. This effect was equivalent to a 4% reduction in abundance per 1% increase in the amount of broadleaf woodland surrounding the patch at 1000 m, from an estimated mean of 7.52 records of adult birds (6.3–11.53 CI) in woodlands with no surrounding broadleaf at 1000 m to 1.72 (1.32–5.56 CI) records with 20% broadleaf woodland at 1000 m.

Open, Mixed, or General Wood and Scrub Functional Group

All 13 species expected in the open, mixed, or general wood and scrub group were detected: 7 species in >40%

of woodlands and 9 in >20% of woodlands (Fig. 2). Results from the SEM (Fig. 3c & Supporting Information) were similar to the broadleaf trees and hedgerows group.

Ecological continuity had no detectable influence on abundance. Unexpectedly, after controlling for the positive area-abundance relationship, larger patches had lower species richness than smaller patches, although the effect was small relative to other variables. Livestock presence directly reduced relative abundance but not because of reduced understory cover.

At the landscape-scale, there was a direct positive relationship between species richness and the amount of any woodland in the landscape at 500 m, but other landscape metrics were of relatively low importance.

We also hypothesized that dead wood cover and the number of nest boxes in the woodland would have a positive effect on the relative abundance of this group, but we did not detect any significant relationships, and effect sizes for these predictors were small relative to other variables in the model.

Discussion

The strategic creation of ecological networks could mitigate the effects of past habitat loss and fragmentation by improving ecosystem function and resilience (Lawton et al. 2010; Humphrey et al. 2015). For most taxa, there are likely to be substantial time lags between habitat creation and species' responses (e.g., patch colonization), and it could take centuries for communities to fully reestablish. However, despite the theoretical importance of ecological continuity, its importance for biodiversity has rarely been measured at representative time scales, and its importance relative to other factors such as patch size is generally unknown (Munro et al. 2007; Humphrey et al. 2015). Here, ecological continuity (i.e., patch age) ranged from 10 to 160 years (median 50 years), and older woodlands with mature trees had higher total bird abundance and thus richness, supporting our hypothesis that older woodlands can support more individuals and species due to greater structural diversity.

Although ecological continuity was important for total species richness, it had little detectable influence on functional groups most closely associated with wooded habitats. Generalist woodland species in the open, mixed, or general wood and scrub group ($n = 13$ species) were found in a high proportion of study sites, and the lack of any strong direct or indirect relationships between patch age and this group's abundance or diversity suggests they can rapidly colonize post-agricultural woodlands, probably in ≤10 years. This agrees with results of short-term studies (≤25 years) of bird community responses to woodland creation in Australia (Kavanagh et al. 2007; Law et al. 2014) and the Scottish uplands (Savory 2016). In contrast to generalist species, those in the more
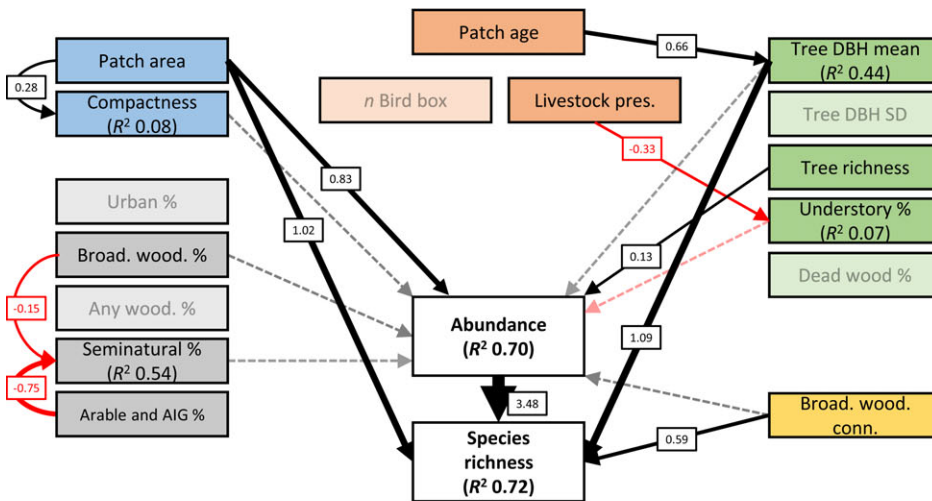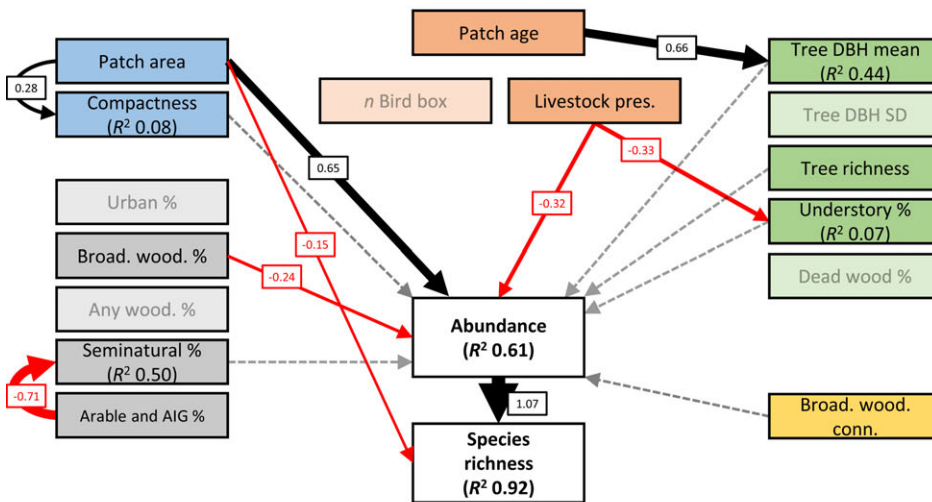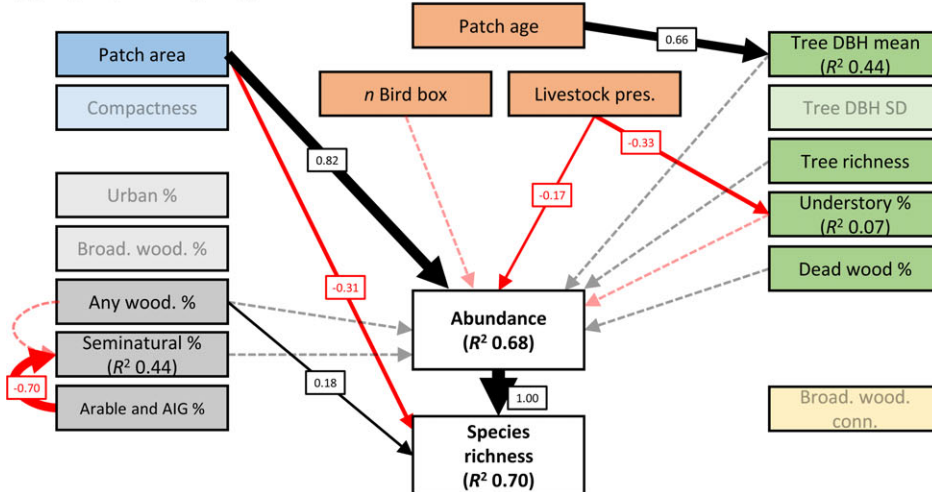
Figure 3. Structural equation model (SEM) path diagrams for (a) total bird species richness and (b, c) species richness and abundance of birds belonging to functional groups associated with woodland (arrows and number on arrows [standardized effect sizes], direction and relative magnitude of the relationship for significant variables, respectively; dashed arrows, nonsignificant relationships specified in the a priori model; gray shading, variable in the metamodel that was not in the SEM [Supporting Information]; AIG, agriculturally improved grassland). Coefficients of determination (R^2) are shown for all response variables and goodness-of-fit statistics are given in Supporting Information.

specialist broadleaf trees and hedgerows group were relatively scarce in our study sites. Although the reasons for this are unclear, we suggest that a combination of woodland age, size, and historic management practices inside the patch (e.g., livestock grazing) may have played a role in reducing woodland suitability for these species (Fuller et al. 2005; Dolman et al. 2007).

Several species of woodland birds have declined in the United Kingdom during the past 30 years, and others have increased, but reasons for these contrasting trends are unclear (Fuller et al. 2005). From 1995 to 2015, 9 of the 13 species belonging to the open, mixed, or general wood and scrub group increased, 3 did not change significantly, and one declined (British Trust for Ornithology 2016). During the same period, 5 species in the broadleaf trees and hedgerows group increased significantly, 2 did not change significantly, and 2 declined (British Trust for Ornithology 2016). All 3 declining species and the 2 species missing from our study areas (Pied Flycatcher and Wood Warbler) are long-distance migrants, and there is evidence that factors outside the breeding range are in part to blame for these declines (Vickery et al. 2014). For the remaining species that have increased or remained stable, some evidence suggests that population trends could be linked to higher overwinter survival rates due to a warming climate (Gregory et al. 2007). Based on our results, which show that post-agricultural woodlands provide highly favorable habitat for generalist woodland birds, we further suggest that the recent expansion of broadleaf woodland cover in the United Kingdom during the past 30 years (Harmer et al. 2015) may have contributed to population increases or stability. Although speculative, this gives some grounds for optimism, and conservation policies aimed at increasing broadleaf woodland cover can potentially have rapid, positive effects on woodland biodiversity. Nonetheless, some declining species have yet to benefit from expanding broadleaf woodland cover, and it is unclear just how long it will take for any benefits to be accrued.

Local, patch-level factors were generally more important than landscape characteristics. Patch area was consistently the most important predictor of bird abundance and thus species richness, which is a well-known relationship (Dolman 2012). However, the relative importance of patch area versus other important factors such as ecological continuity, management practices, vegetation structure, patch age, and landscape composition is unclear. This knowledge gap has made it difficult for land managers and policy makers to identify which of the many possible local and landscape-scale actions should be prioritized during woodland creation. Our results show that larger patches not only have higher abundance and thus species richness but also that this relationship is, in relative terms, almost twice as important as other local and landscape-scale metrics for bird communities in post-agricultural woodlands. We propose that, as a simple rule of thumb, patches larger than 5 ha should be created where possible (Supporting Information) (Bellamy et al. 1996; Dolman 2012) when the aim is to benefit generalist woodland bird communities, although much larger woodlands (i.e., >30 ha) may be required to benefit woodland specialists (Dolman 2012).

Secondary to patch area, livestock presence (an index of grazing pressure) within the woodland was consistently negative for the 2 functional groups of woodland birds, and the effect was strongest for the broadleaf trees and hedgerows group. We hypothesized that this negative relationship would be due to the effect of grazing on understory cover, but our results did not support this, and we found that livestock directly reduced bird abundance. This could be because our measure of understory cover did not reflect the structural needs of affected species or because disturbance from livestock has more of an effect than the structural impact of grazing. We suggest that both explanations are plausible, and further work is needed to disentangle their independent effects. Because livestock was present in approximately 18% of woodlands we studied (all in Scotland), reducing or removing grazing pressure could be an efficient way to increase woodland bird diversity in Great Britain. We also suggest that, where woodland exists for conservation purposes, livestock should be excluded unless grazing forms part of a well-defined conservation strategy (Pollock et al. 2005).

Our results also showed some unexpected relationships. For example, abundance of the broadleaf trees and hedgerows group declined when there were higher proportions of broadleaf woodland cover in the surrounding landscape. Our original hypothesis was based on the assumption that source populations would be larger in the presence of more woodland in the landscape and this would lead to higher abundance and richness in the focal patch. However, results instead suggest that when there is more broadleaf woodland in the landscape, this might draw individuals away from the relatively small isolated patches represented by our study sites. Perhaps, the perceived quality (as captured by patch age and measures of vegetation structure and size) and thus attractiveness of a patch is therefore relative to the amount and quality of other patches in the landscape (Stier & Osenberg 2010), but further work is required to test this hypothesis.

To achieve the best outcomes for biodiversity, there is a need for evidence-based habitat creation, which may involve using knowledge gained from studies of habitat fragmentation (i.e., habitat loss) to inform habitat creation efforts. However, biodiversity responses to habitat fragmentation and biodiversity responses to habitat created in a patchy configuration are not necessarily reciprocal. This is because time-dependent resources will likely persist for some time in remnant patches after fragmentation of the surrounding landscape has occurred (e.g., ancient woodland fragments), but in new habitat patches there are likely to be time lags between resource

development and subsequent colonization. Thus, remnant patches may retain species associated with long periods of ecological continuity until the patch eventually pays an extinction debt (Tilman et al. 1994), which could temporarily mask the importance of local and landscape-scale factors for colonization. We therefore suggest that lessons learned from studies of habitat fragmentation should only be used to inform habitat creation with caution, and there is a need for further work that specifically examines biodiversity responses to habitat creation in a landscape context.

Our results demonstrate that local and landscape-scale factors interact across time and space to determine the biodiversity outcomes of habitat creation, and factors at the local scale have relatively more effect on woodland bird communities than landscape characteristics. Policy makers and conservationists are often faced with the challenge of evaluating the outcomes of their actions, such as habitat creation. Although some taxa may respond rapidly to habitat creation (i.e., generalists), it could take centuries for specialist communities to fully reestablish. Thus, short-term assessments of biodiversity responses to conservation actions, such as the decadal time scales used to assess the conservation status of global biodiversity (e.g., Aichi biodiversity targets), could paint an overly pessimistic view of conservation actions. One must therefore be careful to acknowledge the existence of time lags between conservation actions and biodiversity responses when evaluating the efficacy of conservation efforts.

Acknowledgments

Supporting Information

Additional details of the bird-survey methods (Appendix S1), hypotheses underlying the metamodel (Appendix S2), descriptions and summary statistics for all variables (Appendix S3), SEM results (Appendix S4), map of the study sites (Appendix S5), and formula for calculating 95% confidence intervals in Fig. 2 (Appendix S6) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Literature Cited

Balmer D, Gillings S, Caffrey B, Swann B, Downie I, Fuller R. 2013. Bird atlas 2007–2011: the breeding and wintering birds of Britain and Ireland. British Trust for Ornithology, Thetford.

Bélisle M, Desrochers A, Fortin MJ. 2001. Influence of forest cover on the movements of forest birds: a homing experiment. Ecology **82:**1893–1904.

Bellamy PE, Hinsley SA, Newton I. 1996. Factors influencing bird species numbers in small woods in south-east England. Journal of Applied Ecology **33:**249–262.

Bennett AF, Hinsley SA, Bellamy PE, Swetnam RD, MacNally R. 2004. Do regional gradients in land-use influence richness, composition and turnover of bird assemblages in small woods? Biological Conservation **119:**191–206.

Boitani L, Falcucci A, Maiorano L, Rondinini C. 2007. Ecological networks as conceptual frameworks or operational tools in conservation. Conservation Biology **21:**1414–1422.

Bregman TP, Sekercioglu CH, Tobias JA. 2014. Global patterns and predictors of bird species responses to forest fragmentation: implications for ecosystem function and conservation. Biological Conservation **169:**372–383.

British Ornithologists' Union. 2013. The British list: a checklist of birds of Britain (8th edition). Ibis **155:**635–676.

British Trust for Ornithology (BTO). 2016. BTO/JNCC/RSPB breeding bird survey trends 2015—UK. BTO, Thetford. Available from https://www.bto.org/volunteer-surveys/bbs/latest-results/population-trends (accessed March 2017).

Diamond JM. 1975. The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. Biological Conservation **7:**129–146.

Dolman PM. 2012. Mechanisms and processes underlying landscape structure effects on bird populations. Pages 93–124 in Fuller RJ, editor. Birds and habitat: relationships in changing landscapes. Cambridge University Press, United Kingdom.

Dolman PM, Hinsley SA, Bellamy PE, Watts K. 2007. Woodland birds in patchy landscapes: the evidence base for strategic networks. Ibis **149:**146–160.

ESRI. 2013. ArcGIS v10.2. Environmental Systems Research Institute, Inc., Redlands, California.

Fahrig L. 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis. Journal of Biogeography **40:**1649–1663.

Forestry Commission. 2013. National Forest Inventory. Forestry Commission, Edinburgh. Available from http://www.forestry.gov.uk/inventory (accessed April 2015).

French DD, Picozzi N. 2002. Functional groups' of bird species, biodiversity and landscapes in Scotland. Journal of Biogeography **29:**231–259.

Fuller RJ, Noble DG, Smith KW, Vanhinsbergh D. 2005. Recent declines in populations of woodland birds in Britain. British Birds **98:**116–143.

Galitsky C, Lawler JJ. 2015. Relative influence of local and landscape factors on bird communities vary by species and functional group. Landscape Ecology **30:**287–299.

Gibson L, Lynam AJ, Bradshaw CJ, He F, Bickford DP, Woodruff DS, Bumrungsri S, Laurance WF. 2013. Near-complete extinction of native small mammal fauna 25 years after forest fragmentation. Science **341:**1508–1510.

Gregory RD, Vorisek P, Van Strien A, Gmelig Meyling AW, Jiguet F, Fornasari L, Reif J, Chylarecki P, Burfield IJ. 2007. Population trends of widespread woodland birds in Europe. Ibis **149:**78–97.

Haddad NM. 2012. Connecting ecology and conservation through experiment. Nature Methods **9:**794–795.

Haddad NM, et al. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Science Advances **1:**1–9.

Hanski I. 1994. A practical model of metapopulational dynamics. Journal of Animal Ecology **63:**151–162.

Hanski I. 2015. Habitat fragmentation and species richness. Journal of Biogeography **42:**989–993.

Harmer R, Watts K, Ray D. 2015. A hundred years of woodland restoration in Great Britain: changes in the drivers that influenced the increase in woodland cover. Pages 299–320 in Stanturf JA, editor. Restoration of boreal and temperate forests. 2nd edition. CRC Press, Boca Raton, Florida.

Hoctor TS, Carr MH, Zwick PD. 2000. Identifying a linked reserve system using a regional landscape approach: the Florida ecological network. Conservation Biology **14:**984–1000.

Hodgson JA, Moilanen A, Wintle BA, Thomas CD. 2011. Habitat area, quality and connectivity: striking the balance for efficient conservation. Journal of Applied Ecology **48:**148–152.

Humphrey JW, Watts K, Fuentes-Montemayor E, Macgregor NA, Peace AJ, Park KJ. 2015. What can studies of woodland fragmentation and creation tell us about ecological networks? A literature review and synthesis. Landscape Ecology **30:**21–50.

Jenerette GD, Shen W. 2012. Experimental landscape ecology. Landscape Ecology **27:**1237–1248.

Jongman RH, Bouwma IM, Griffioen A, Jones-Walters L, Van Doorn AM. 2011. The pan European ecological network: PEEN. Landscape Ecology **26:**311–326.

Kavanagh RP, Stanton MA, Herring MW. 2007. Eucalypt plantings on farms benefit woodland birds in south-eastern Australia. Austral Ecology **32:**635–650.

Law B, Chidel M, Brassil T, Turner G, Kathuria A. 2014. Trends in bird diversity over 12 years in response to large-scale eucalypt plantation establishment: implications for extensive carbon plantings. Forest Ecology and Management **322:**58–68.

Lawton JH, et al. 2010. Making space for nature: a review of England's wildlife sites and ecological network. DEFRA, London.

Lefcheck JS. 2016. piecewiseSEM: piecewise structural equation modelling in R for ecology, evolution, and systematics. Methods in Ecology and Evolution **7:**573–579.

Legrand D, et al. 2012. The metatron: an experimental system to study dispersal and metaecosystems for terrestrial organisms. Nature Methods **9:**828–833.

Lindenmayer DB. 2009. Large-scale landscape experiments: lessons from Tumut. Cambridge University Press, Cambridge, United Kingdom.

MacArthur RH, Wilson EO. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey.

Marchant JH, Hudson R, Carter SP, Whittington PA. 1990. Population trends in British breeding birds. British Trust for Ornithology, Tring.

Martin TG, McIntyre S. 2007. Impacts of livestock grazing and tree clearing on birds of woodland and riparian habitats. Conservation Biology **21:**504–514.

McGarigal K, Cushman SA. 2002. Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. Ecological Applications **12:**335–345.

Moilanen A, Hanski I. 2001. On the use of connectivity measures in spatial ecology. Oikos **95:**147–151.

Mortelliti A, Lindenmayer DB. 2015. Effects of landscape transformation on bird colonization and extinction patterns in a large-scale, long-term natural experiment. Conservation Biology **29:**1314–1326.

Morton D, Rowland C, Wood C, Meek L, Marston C, Smith G, Wadsworth R, Simpson IC. 2011. Final report for LCM 2007—the new UK land cover map. Countryside survey technical report 11/07. Centre for Ecology & Hydrology, Edinburgh.

Munro NT, Lindenmayer DB, Fischer J. 2007. Faunal response to revegetation in agricultural areas of Australia: a review. Ecological Management & Restoration **8:**199–207.

Naaf T, Kolk J. 2015. Colonization credit of post-agricultural forest patches in NE Germany remains 130–230 years after reforestation. Biological Conservation **182:**155–163.

Opdam P, Steingröver E, van Rooij S. 2006. Ecological networks: a spatial concept for multi-actor planning of sustainable landscapes. Landscape and Urban Planning **75:**322–332.

Paradis E, Baillie SR, Sutherland WJ, Gregory RD. 1998. Patterns of natal and breeding dispersal in birds. Journal of Animal Ecology **67:**518–536.

Pollock ML, Milner JM, Waterhouse A, Holland JP, Legg CJ. 2005. Impacts of livestock in regenerating upland birch woodlands in Scotland. Biological Conservation **123:**443–452.

R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Savory C. 2016. Colonisation by woodland birds at Carrifran Wildwood: the story so far. Scottish Birds **36:**135–149.

Şekercioğlu ÇH, Daily GC, Ehrlich PR. 2004. Ecosystem consequences of bird declines. Proceedings of the National Academy of Sciences of the United States of America **101:**18042–18047.

Stevens VM, et al. 2014. A comparative analysis of dispersal syndromes in terrestrial and semi-terrestrial animals. Ecology Letters **17:**1039–1052.

Stier AC, Osenberg CW. 2010. Propagule redirection: habitat availability reduces colonization and increases recruitment in reef fishes. Ecology **91:**2826–2832.

Tilman D, May RM, Lehman CL, Nowak MA. 1994. Habitat destruction and the extinction debt. Nature **371:**65–66.

Vergara PM, Armesto JJ. 2009. Responses of Chilean forest birds to anthropogenic habitat fragmentation across spatial scales. Landscape Ecology **24:**25–38.

Vickery JA, Ewing SR, Smith KW, Pain DJ, Bairlein F, Škorpilová J, Gregory RD. 2014. The decline of Afro-Palaearctic migrants and an assessment of potential causes. Ibis **156:**1–22.

Villard MA, Trzcinski MK, Merriam G. 1999. Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. Conservation Biology **13:**774–783.

Ward JH. 1963. Hierarchical grouping to optimize an objective function. Journal of the American Statistical Association **58:**236–244.

Watts K, Fuentes-Montemayor E, Macgregor NA, Peredo-Alvarez V, Ferryman M, Bellamy C, Brown N, Park KJ. 2016. Using historical woodland creation to construct a long-term, large-scale natural experiment: the WrEN project. Ecology and Evolution **6:**3012–3025.

Zuur AF, Ieno EN, Elphick CS. 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution **1:**3–14.