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Do non-native conifer plantations provide benefits for a native forest specialist, the wood ant *Formica lugubris*?



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ABSTRACT

Recent increases in plantation forestry are starting to reverse the global decline in forest cover, in some areas of the world. Britain has practiced afforestation, primarily with non-native conifers, for over a century. It is unclear whether these new plantations have the potential to support native forest species.

We quantify afforestation across the North York Moors National Park, UK, deriving a chronology of afforestation from historic maps at six time points from 1854 to 2013. We map the location of current wood ant (*Formica lugubris*) nests and set their distribution in the context of historic forest cover. We use these nest locations and the features of the habitat in which they occur to model the suitability of recently established conifer plantations for wood ants using MaxEnt. We determine whether non-native conifers offer suitable habitat for a forest specialist species, and assess the lag between establishment of conifer plantations and colonisation by wood ants from historic woodland fragments.

Forest cover increased by 229% over 160 years and is now dominated by non-native conifer plantations. Our survey data show that current wood ant populations extend hundreds of metres from where forest was in the past, demonstrating geographical population expansions into newly formed forest, comprised of non-native conifer plantations. Both our data and model reveal that the recently planted non-native conifer plantations are a suitable habitat for this forest specialist species. Our model reveals that *Formica lugubris* has not yet spread through all available suitable habitat due to very poor dispersal ability, displaying a severe lag behind the availability of habitat.

Managers should not assume that unoccupied habitat is unsuitable nor should they expect to see immediate colonisation of plantations. Future forest creation should be targeted close to existing forests to facilitate colonisation of forest specialists.

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1. Introduction

Forest cover worldwide has undergone massive decreases in the past 300 years due to conversion of forested land into cropland (Ramankutty and Foley, 1999). In South America, Africa and Oceania this trend is still ongoing; all showed further decreases in forest area between 2000 and 2010 (FAO, 2010). In contrast, historical deforestation in Europe is in the process of being reversed and forest cover is now increasing, with a combination of natural expansion of forests and afforestation, the planting of forests on previously un-forested land (FAO, 2010). Afforestation in Great Britain provides a prime example of this trend, because forest cover was at a minimum of 5% in 1900 (Mason, 2007) and has since

recovered to the current figure of 13% (Forestry Commission, 2013a). During the first half of the twentieth century, British forestry policy was focussed on the creation of large plantations of fast-growing non-native conifer species for commercial objectives (Quine et al., 2013). These plantations account for the major increase in forest cover within Britain. In the latter half of the twentieth century, forest policy gradually shifted to encompass a broader range of objectives for forests and to emphasize the importance of native species (Forestry Commission, 2011; Quine et al., 2013). However, the legacy of afforestation with non-native conifers is still evident in Britain, for example, the non-native Sitka spruce, *Picea sitchensis*, is now the most common tree species in British forests (Forestry Commission, 2013a).

Creation of non-native conifer plantations on previously un-forested land gradually results in a flora and fauna more representative of a forest ecosystem (Ratcliffe, 1986). The loss of species

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specific to the land prior to afforestation has been extensively documented as a negative effect of afforestation (Moore and Allen, 1999; Thompson et al., 1988 and references therein). However, on the plus side, the progression towards a forest ecosystem offers potential benefits to forest-dependent species, if the conifer plantations offer similar habitats to native woodland. Although planted forests exhibit lower biodiversity than natural forests in South East Asia (Fitzherbert et al., 2008; Kanowski et al., 2005), the situation in Britain is less straightforward; there can be lower species richness or diversity in conifer plantations than mixed or broadleaved woodland (Fahy and Gormally, 1998; Pedley et al., 2014), whereas the reverse can also be observed (Day et al., 1993), or there may be no difference between the habitats (Bibby et al., 1985; Fuller et al., 2008; Pedley et al., 2014). However, the scales over which these studies were conducted were too narrow to determine whether there is a general direction of change. The only study on a sufficiently large scale to quantify country-wide patterns was the Forestry Commission's Biodiversity Assessment Project, which found no difference in species richness between native and non-native stands (Quine and Humphrey, 2010) and concluded that plantations made a significant contribution to the maintenance of woodland biodiversity (Humphrey et al., 2003). General studies measuring biodiversity or species richness, though of great value, do not inform about the status of individual populations within non-native conifer plantations; the presence of a species within a plantation does not necessarily mean there is a healthy breeding population utilising that habitat, and this must be confirmed with more in depth studies.

Historic deforestation has left the forest cover of the UK highly fragmented (Peterken, 1993). Fragmentation of a landscape has detrimental effects on populations dependent on those fragments, increasing local extinctions and inbreeding (Templeton et al., 1990; Wilcox and Murphy, 1985). Connection of fragments of native woodland by conifer plantations has the potential to defragment the landscape, if forest specialists can utilise this new plantation habitat. Non-native conifer plantations have been shown to increase the connectivity of previously isolated populations in the red squirrel, *Sciurus vulgaris* (Hale et al., 2001) and the wood ant *Formica aquilonia* (Vanhala et al., 2014). While this is a welcome and positive effect of non-native conifers, it is not clear from these studies whether such plantations provide a valuable habitat in their own right or if they merely represent a matrix that facilitates dispersal of forest specialists.

Species' responses to ecological change are known to be slow. It can take over a century for fragmentation and isolation of a population to result in extinction (Vellend et al., 2006), a phenomenon known as extinction debt (Tilman et al., 1994). The current distribution of a species in a recently changed landscape is therefore not expected to be in equilibrium. Species composition of plantations change throughout their development cycle, with the oldest stands being the most species rich (Brunet et al., 2011; Moss et al., 1979) and with a community structure more similar to natural woodland than earlier stages (Humphrey et al., 2000). As plantations progress beyond their first rotation, there are also opportunities for management to enhance plantation forest, in terms of its conservation potential (Nature Conservancy Council, 1986). Opportunities have been taken to improve management in Britain, with emphasis now on benefitting biodiversity as well as a range of other considerations (Forestry Commission, 2011). Presence of a given species in a section of habitat depends both on the suitability of the habitat for that species and the species' ability to disperse to that habitat (Saunders et al., 1991). We may therefore expect that plantations which are a long way from historic fragments of forest will have fewer of the species that are characteristic of forest habitat (Wallace and Good, 1995). This mismatch between the numbers of species a newly formed habitat is capable of supporting and

the number currently found there can be termed colonisation lag. If the effect of creating large areas of conifer plantations is to be properly understood, the speed at which organisms colonise this new habitat must be assessed.

We chose the wood ant *Formica lugubris* as our study species. It is a member of the mound-building red wood ants of the *Formica rufa* group, common across the temperate and boreal forests of Europe and Asia (Goropashnaya et al., 2004). Nests can be as high as 1 m and consist of various components of dead vegetation, depending on the type of forest in which they occur. The ants are dependent on forest cover because the majority of the food coming into the nest is honeydew from aphids, tended by ants on the trees (Rosengren and Sundström, 1991). Wood ants are keystone species in woodland ecosystems, with effects on the community structure of local invertebrates as well as providing a food source for predators (Hughes and Broome, 2007). Nest construction results in modification of soil structure, increasing porosity (Frouz and Jilková, 2008) and accumulation of food and detritus makes nests hotspots of nutrient exchange (Domisch et al., 2009). Nests support high levels of biodiversity, including many species that are dependent on the nests as habitat (Härkönen and Sorvari, 2014; Parmentier et al., 2014). In the UK, *F. lugubris* exhibits budding dispersal (Hughes, 2006), whereby a newly mated queen moves a short distance from her natal nest to form a new nest with a subset of the workers from the natal nest. Short distance dispersers are particularly susceptible to the negative effects of habitat fragmentation, such as local extinctions and inbreeding (Templeton et al., 1990; Wilcox and Murphy, 1985). Potential connection of historic fragments by afforestation, effectively defragmenting the landscape, would mean that *F. lugubris* might benefit greatly if it can make use of planted forests and overcome historic fragmentation. Due to its role as a keystone woodland species and promoter of biodiversity through nest building, *F. lugubris* has a positive role in the woodlands in which it is found.

Here we combine mapped populations of the wood ant *F. lugubris*, historic forest cover data and habitat suitability modelling over the landscape of the North York Moors National Park to answer the following questions:

1. How has recent afforestation impacted the forest cover of our study landscape?
2. Do non-native conifer plantations offer suitable habitat for *F. lugubris*?
3. What degree of lag is there between establishment of non-native conifer plantations and their colonisation by this forest specialist species?

This information will help us to understand the role that non-native conifer plantations currently have in providing suitable habitat for a woodland specialist species. It will provide new insights into the time taken to occupy these plantations and will clarify whether habitat suitability and/or ability to disperse limit occupancy of these new forest habitats.

2. Materials and methods

The study area comprises the southern half of the North York Moors National Park, in the north east of England, UK (Fig. 1). We assess forest cover in all 1:10,000 Ordnance Survey grid squares that cover some area of the National Park in an area cornered by the Lat/Long coordinates 54.3916, –1.3073 (North West) and 54.2110, –0.4695 (South East). The area of the study area within the National Park is 934 km². This landscape, as with many upland areas in Britain, has been extensively planted with non-native conifer plantations over the last century. It is also home

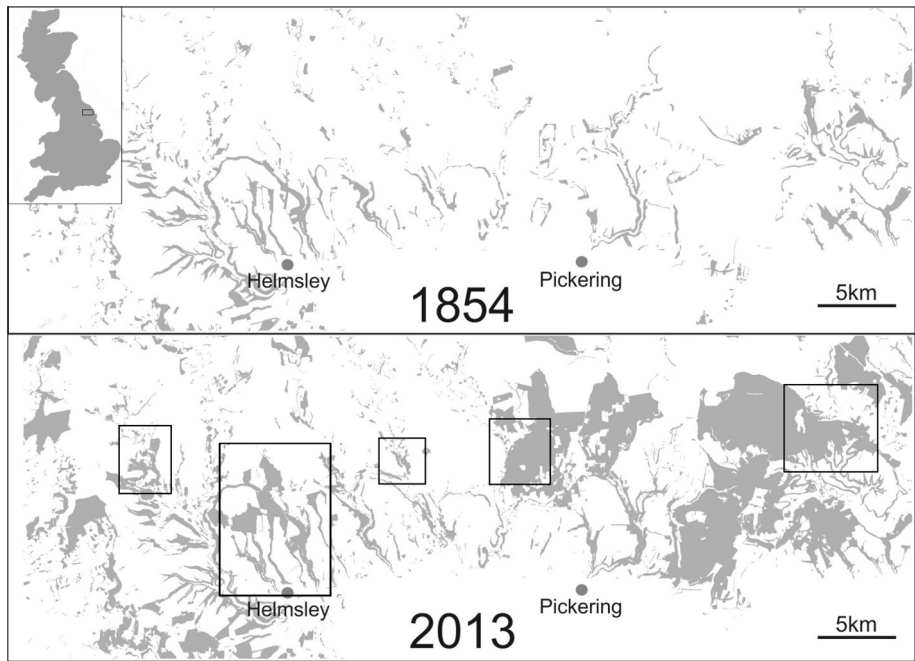


Fig. 1. Forest cover changes between 1854 and 2013; the grey polygons show forest cover at the time points stated on each map. The insert shows the location of the study landscape within Britain. Boxes in the lower panel show the location of wood ant populations displayed in Fig. 2 and enclose the land for which the estimates of area around current ant populations are provided in Table 1.

to wood ant populations, each based around ancient woodland fragments next to which plantation forest has been established. Historic records exist on the presence of ant nests within each of the mapped ant populations (Yarrow, 1955), pre-dating the establishment of conifer plantations, though without any detail on the area those populations cover or numbers of nests within those populations. This change in the forested landscape occupied by wood ants allows us to examine the potential benefit of non-native conifer plantations on the expansion of this forest specialist species. The Forestry Commission manages 60% of the forest area across this landscape, enabling us to access data from the extensive Forestry Commission sub-compartment database for use in modelling the suitability of non-native conifer forest as wood ant habitat. The sub-compartment database contains the current distribution of Forestry Commission forests, as well as data on the age and species composition of each plantation block as well as a number of other variables.

The plantations throughout the study landscape contain over 40 tree species as well as mixed stands, but the most common species are Sitka spruce, *P. sitchensis* (22.2% of land area), Scots pine, *Pinus sylvestris* (15.5% of land area), Japanese larch, *Larix kaempferi* (8.6% of land area) and Hybrid larch, *Larix x leptolepis* (4.8% of land area). In terms of age, approximately one third of plantations are 30 years old or younger (28.4% of land area), a further third are 31–60 years old (32.1% of land area), and the remainder are either older than 60 years (15.7% of land area) or undefined (23.8% of land area).

2.1. Creating a chronology of forest cover change

We manually produced forest cover data by creating polygons around forests depicted on historic maps in ArcMap 10.1. We obtained four maps from the county series 1:10,560 (© Crown Copyright 2014. An Ordnance Survey/EDINA supplied service) dated for the study area in question to 1854, 1894–5, 1914 and 1952. We also obtained two maps from the National Grid 1:10,000 series (© Crown Copyright 2014. An Ordnance Survey/EDINA supplied service) from 1976 to 1981 and 2013.

Changes in forest cover were assessed both across the whole study area and in a restricted area incorporating all land within 1 km of current ant population edges (Table 1, Figs. 1 and 2).

Repeatability of the method to obtain forest cover data from historical maps was assessed by repetition of the manual creation of forest cover estimates in 10 randomly assigned 1 km × 1 km squares across the landscape. This was repeated by the first author then again by an independent assessor who had not previously been involved in the work. The forest cover of the 10 areas was re-mapped for the 1894, 1952 and 2013 maps, giving a total of 30 re-mapped areas. Estimates of forest area per square showed a strong correlation between the original and when remapped by the first author (Pearson’s correlation, $r = 0.995$, Fig. S1). Estimates of forest area per square were also strongly correlated between the original data and when remapped by an independent assessor (Pearson’s correlation, $r = 0.986$, Fig. S1).

2.2. Mapping populations of the study species and their spread

Sites within the study area with historic population records (Yarrow, 1955) were surveyed for *F. lugubris* population

Table 1
Forest area and percentage increase in forest cover since 1854 at different time points for both the landscape as a whole (Fig. 1) and a reduced area extending 1 km in each compass direction from the edges of each ant population (Fig. 2).

Time of map	Whole study site		Area around current ant populations	
	Area of forest (km ²)	Percentage increase since 1854	Area of forest (km ²)	Percentage increase since 1854
1854	73.08	–	17.84	–
1894	93.78	28.3	20.70	16.0
1914	95.12	30.2	20.82	16.7
1952	130.24	78.2	29.44	65.1
1976	230.60	215.6	46.78	162.2
2013	240.75	229.5	49.05	175.0

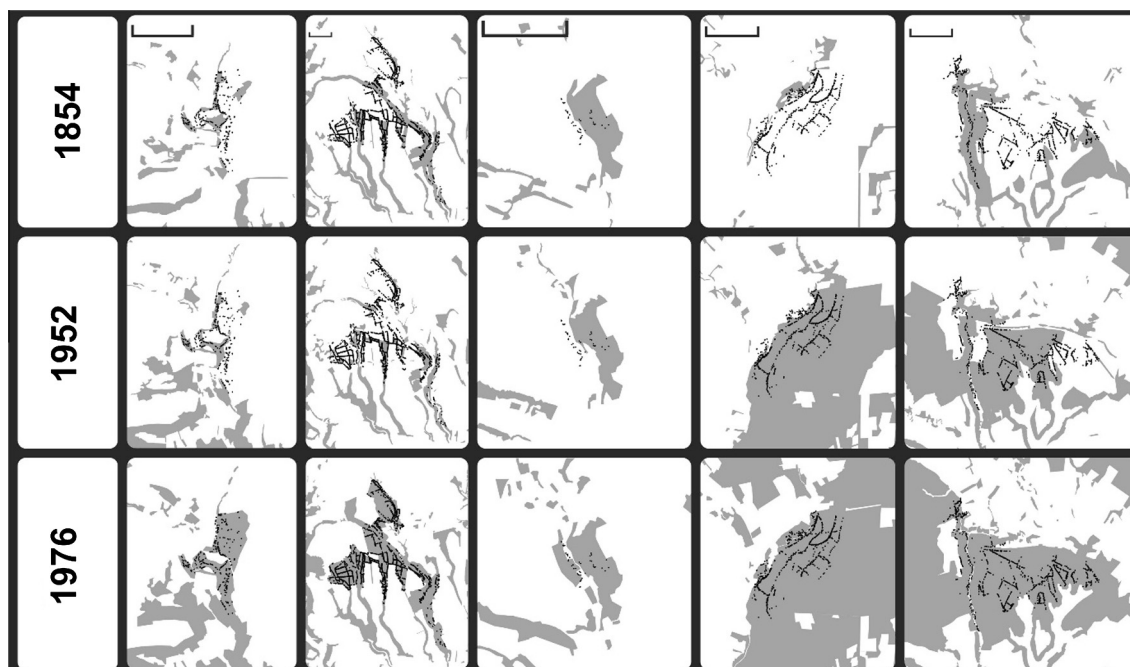


Fig. 2. The changes in forest cover over time for areas within 1 km of the current *F. lugubris* population boundaries. Each column represents a different population, with their relative location depicted in Fig. 1. Grey polygons are forest cover at the dates on the left hand side. Points are the locations of *F. lugubris* nests in 2013. The scale bar in the upper left of each column is 1 km wide. The dates chosen represent the start point of forest cover for the study in 1854 and the two major periods of afforestation, in 1952 and 1976. Numbers of nests per population, mapped in 2013, left to right: 400, 2938, 48, 856, and 1264.

persistence in 2011. These populations, along with large areas of forest currently unoccupied by wood ants, were re-surveyed during January and February 2013 to assess the geographic area colonised by the wood ant nests. During initial surveys we noted that most nests appeared to be close to the forest edge in plantations. In order to establish whether there was a relationship between distance to the forest edge and the location of wood ant nests, fourteen blocks of plantation forest were mapped during April 2013. These fourteen initial transect blocks were mature plantation at least 150 m wide and with a slope of less than 30° above horizontal, spread throughout four populations of *F. lugubris* across the study landscape. Each transect block consisted of 15 transect lines, each extending 75 m into the forest from an edge, separated by 5 m intervals. Transect lines of this length were chosen as this ensures sufficient penetration into plantation woodland to be under very dense canopy. Blocks of woodland are rarely greater than 150 m in width without some form of break, so transect lines longer than 75 m would merely result in being closer to another track or path than the point from which the transect began. Nest locations were recorded using a Garmin eTrex H handheld GPS device and their distance to the path measured. Initial transect results revealed that 78.5% of nests are found within 10 m of forest edges adjacent to paths (total 121 nests, Fig. S2).

To assess the accuracy of detection of wood ant nests using the methodology above, a subsample of six transect blocks was repeated by an independent assessor not involved in the original mapping work. There was 96% agreement between original and repeated surveys (55 vs 53 nests total). The difference between surveys was due to two small nests being overlooked by the second survey; no additional nest locations were found.

Our initial transect blocks confirmed that most *F. lugubris* are found in the first 10 m from a plantation edge (see above), therefore we only mapped the first 10 m from each edge into plantations. We conducted 10 m long transects into the plantations, spaced by 5 m, along every edge of the forest in which ants were found. Edges were defined as tracks or rides through the forest

which were wide enough to cause a gap in the canopy, including all external edges of the forest and the perimeter of felled areas. Internal edges between different plantation blocks without any form of track in between them were not included in the survey. Due to the importance of sunlight in the thermoregulation of wood ant nests (Chen and Robinson, 2014; Kadochová and Frouz, 2014), the higher solar radiation available at the margins of plantations makes *F. lugubris* an edge specialist. In contrast, natural or naturalised woodland has a much lower density of trees, which allows greater penetration of sunlight at ground level. Consequently, in natural/naturalised woodland there is no reason to expect such a strong relationship with the forest edge. We therefore decided to map natural/naturalised areas using transect lines that extended all the way through the woodland, spaced by 5 m. Five populations were mapped using these transect based methods between April and July 2013 (Fig. 2).

Our null hypothesis was that there has been no expansion of wood ant nests into non-native conifer plantations and our prediction therefore is that there should be no difference in the distance of current nest locations to the nearest forest cover at various points in the past; because wood ants are forest specialists they will always have been within forest. The Kruskal–Wallis test with multiple comparisons was used to test the difference between distances from current wood ant nest locations to the nearest forest cover was at various times in the past (Fig. 4), using the Kruskal function in the agricolae package of R (de Mendiburu, 2009; R Core Team, 2015).

2.3. Habitat suitability modelling

Suitability of the forest habitat across the landscape was modelled using the maximum entropy modelling software MaxEnt version 3.3.3 k (Phillips et al., 2006). MaxEnt uses spatial habitat data and the presence of the ant nest locations to assess the characteristics of the habitat in which nests are found. The habitat characteristics of ant nest locations are compared with the habitat

characteristics at pseudo-absence points i.e. locations in the habitat in which there are not ant nests. Habitat suitability was modelled in all of the areas on the landscape managed by the Forestry Commission, as that allowed us to use the extensive data of the sub-compartment database (<http://www.forestry.gov.uk/datadownload>) to include more relevant variables than would have otherwise been possible. As only 60% of the forested land in the study area is owned by the Forestry Commission, this approach led to a reduction in the number of nest locations that could be included from 5506 to 3811 before further data preparation (see below), a number which is nevertheless more substantial than many datasets used in such models. To create the modelled area, a layer of all non-forest areas around each of the five ant populations, such as tracks, roads and open ground, was manually created from published maps of the area and our survey data in ArcGIS 10.1, including the edges of forest from which transects were started in order to map ant populations. A buffer of 25 m into forests was then applied to the layer of non-forest areas and edges to allow for the 10 m transect distance plus some inaccuracy of the GPS device used to map nests. The Forestry Commission land within this buffered layer was the modelled area used. Sampling bias is known to be a problem in MaxEnt modelling (Elith et al., 2011), however for our data, sampling effort was even across the modelled area, therefore bias files are not required.

The variables included in the model, all rasters at 10 m resolution, were as follows: distance to forest cover in 1854, primary tree genus, slope of the ground, hillshade (a measure of the shadiness of the landscape that essentially takes into account aspect and the height of the sun at a given position on the globe), mean percentage of conifers within 50 m, mean percentage of broadleaves within 50 m, mean percentage of open land within 50 m and four variables for the mean percentage of different age classes of forest within 50 m (Table S1). The age classes were: under 20 years, 20–30 years, 31–80 years and over 80 years, based on the summary of age classes of woodland in Franklin et al. (2002). All genera used in the 'primary tree genus' variable were represented by at least five sub-compartments within the modelled area. Genera occurring in fewer than 5 sub-compartments were binned as 'other broadleaves' or 'other conifers'. The mean percentage of open ground within 50 m has a minimum value of 15% because all sub-compartments are assumed by the Forestry Commission to have at least 15% open ground incorporated into them, to allow for rides and tracks between plantation blocks. Slope and hillshade were calculated from a digital elevation model (© Crown Copyright 2014. An Ordnance Survey/EDINA supplied service) using the 'slope' and 'hillshade' tools in the Spatial Analyst toolbox of ArcGIS 10.1. Distance to forest cover in 1854 and all variables of percentages within 50 m were calculated using the Multiscale MaxEnt ArcGIS toolbox (Bellamy et al., 2013). A biologically relevant scale was chosen, as wood ants will forage extensively within that 50 m circle around the nest (Ellis et al., 2014) and though they are known to forage further, this occurs relatively rarely. Variables were checked for multicollinearity in ENMTools 1.43 (Warren et al., 2010), but as there were no correlations greater than 0.46 (Table S2) this was not deemed to be a problem.

In order for habitat suitability models to be fitted reliably, spatial independence of points is a prerequisite. Clustering of points within homogenous areas leads to over-fitting towards environmental biases and false inflation of model performance values (Boria et al., 2014; Veloz, 2009). To deal with this problem, heterogeneity of spatial covariates was assessed using the 'calculate climate heterogeneity' steps 1 and 2 tools in SDMTtoolbox v1.1 (Brown, 2014). Repeat points within areas of spatial homogeneity were then removed using the 'Spatially Rarefy Occurrence Data' tool in SDMTtoolbox 1.1. The modelled area was separated into five categories of heterogeneity based on natural breaks in the data,

implemented in ArcMap by Jenks' optimisation algorithm, and duplicate points were removed within 10 m radius for the highest heterogeneity category then at 70 m, 130 m, 190 m and 250 m for the categories of reducing heterogeneity. The 10 m radius was chosen as that is the resolution of the spatial covariates so it is not possible to have spatial heterogeneity within that scale. The maximum value of 250 m was chosen after visual inspection of test output values as it led to very small numbers of occurrence points being within the areas of low heterogeneity. The numbers of points removed at the different levels were 1169 at 10 m, 650 at 70 m, 131 at 130 m, 51 at 190 m and 16 at 250 m. After removing points within each level of heterogeneity, 1734 unique occurrence points remained upon which to build the model.

Models were initially tested for feature combinations and values of regularisation multiplier by running 5-fold cross-validated models with raw output and each combination of: linear features only, linear and quadratic features, linear, quadratic and hinge features, hinge features only and all features together and regularisation multiplier set at 1, 5, 10 and 20. The regularisation multiplier affects the smoothness of the modelled relationships between variables, with higher values giving smoother results (Elith et al., 2011). These models were compared in ENMTools 1.43 (Warren and Seifert, 2011) using Akaike Information Criteria (AIC) to select the best performing model. Models containing all feature combinations together consistently performed best in terms of AIC irrespective of regularisation multiplier (Table S3). A regularisation multiplier of one was found to perform best in terms of AIC so that was used for the remaining analyses (Table S3).

Models were run with raw output, 5000 maximum iterations and fivefold cross validation, in which the study site data were randomly partitioned into five approximately equal subsets, four of which were used to train the model and one to test the model. Five repeats of the model were run with averages across models reported. Model selection was done in ENMTools 1.43 (Warren and Seifert, 2011) using AIC. Model pruning consisted of removing each variable and comparing the difference in AIC between each pruned model and the full model, the best performing of which was then used and pruned further if possible. Models were considered equivalent if the difference in AIC was within two of the minimum AIC. The minimum model was then re-run with logistic output which can be interpreted as probability of occupancy relative to a given level of sampling effort (Elith et al., 2011). This scaling of probability of occupancy with sampling effort can lead to problems when comparing between species; however, this is not a problem for our analysis because we are comparing different variations of the model within one species and using the same dataset.

In order to test the predictive power of the model, it was then projected across all of the study landscape for which data were available. There are two other wood ant populations within the study landscape, which were identified in the initial survey work and are of known geographical extent. These populations were not mapped accurately and so their data are not included in the model. If the model predicts that these areas containing other populations have a high probability of occupancy of wood ant nests then that constitutes a test of the predictive power of the model.

3. Results

3.1. Forest cover change

Between 1854 and 2013, forest cover across the whole of the study area increased from 73.1 km² to 240.8 km², an increase of 229.5% (Table 1, Fig. 1), the majority of which occurred between 1952 and 1976–81 (Table 1). In the area within 1 km of existing

wood ant populations the percentage increase was slightly lower at 175% (Table 1, Fig. 2) but shows the same general pattern. The majority of current forests across the study landscape consist of conifers and non-native species (Table 2).

3.2. Mapping populations of the study species and their spread

In total, we discovered 5506 nests of *F. lugubris* distributed across five geographically discrete populations (Fig. 2). There is a minimum distance of 6 km between two areas we define as different populations. Nests were unevenly distributed among populations with nests per population numbering 48, 400, 856, 1264 and 2938 (Fig. 2). Due to the mapping methods (see Methods section) this should represent approximately 80% of the true number of nests per population.

The majority of current nest locations (87.9%) are in areas that have been planted with forest since 1854 (Fig. 3). Almost half the current nests (49.7%) occur in areas that were planted with forest only between 61 and 37 years ago (Fig. 3). Current nest locations were significantly further away from historic forest cover than current nest locations were from more recent forest cover (Kruskal–Wallis, $\chi^2_5 = 9530.6$, $P < 0.001$, Fig. 4). Current nest locations were significantly further from the nearest forest cover in 1854 than from the nearest forest cover at all other time points (Fig. 4, K–W multiple comparisons, $P < 0.001$). Current nest locations were not significantly further away from forest cover in 1894 than 1914 but distances at both these dates were significantly greater than to those at all subsequent time points (Fig. 4, K–W multiple comparisons, $P < 0.001$). Therefore, there was no detectable expansion of populations into forests planted between 1894 and 1914 but expansion into forest planted after 1914 clearly occurred. Current nests were significantly further away from the nearest forest cover in 1952 than in 1976 and 2013 (Fig. 4, K–W multiple comparisons, $P < 0.001$) but there was no significant difference in this distance between the 1976 and 2013 time points (Fig. 4, K–W multiple comparisons, $P = 0.13$). Therefore, during the intervening periods between those time points that differ least in forest cover (1894 and 1914 and 1976–81 and 2013) there were no significant geographic population expansions. In contrast, the time periods during which there were substantial changes in forest cover were accompanied by population expansions of ant nests. Although we did detect evidence of ant population expansions into plantations, the total expansion distance is low given the long time period, with the furthest a current nest is found from the nearest forest cover in 1854 being 773 m (Fig. 4). This equates at most to a mean rate of population expansion of only 5 m yr^{-1} . In comparison, referring to the forest contiguously connected to current ant populations, the maximum distance of current forest from forest cover in 1854 is 4500 m. Therefore, there is a large amount of accessible forest into which wood ants have not yet spread.

3.3. Habitat suitability modelling

The previous section describes how *F. lugubris* expanded in the past; in order to allow us to predict whether this expansion is

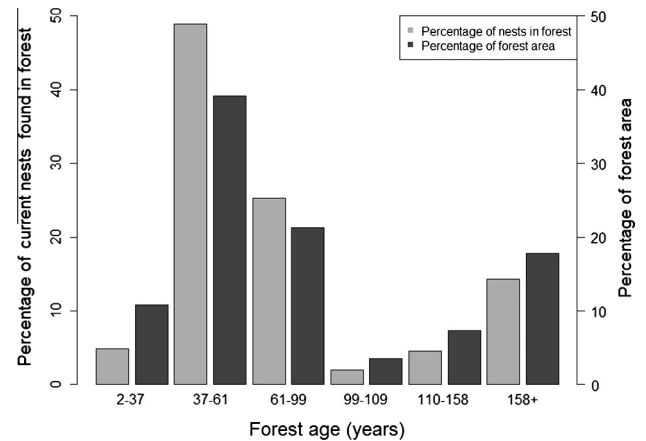


Fig. 3. Percentage of current *F. lugubris* nests found in forest (light bars) and the percentage area of that forest in the study landscape (dark bars) against the age of the forest.

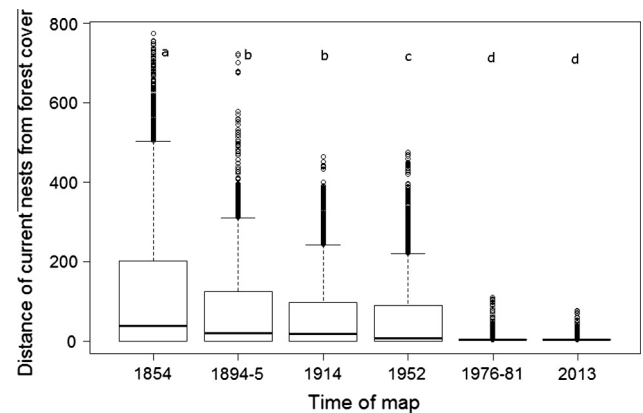


Fig. 4. The distance of current nest locations from where forest cover was at the times of different maps; an estimate of the expansion of the population. Letters denote significant differences (Kruskal–Wallis with multiple comparisons, all $p < 0.001$).

likely to continue and whether a lag in colonisation of suitable habitat is present, we modelled habitat suitability across our study site. We found that the most important variable in determining where wood ant nests are currently found is the distance to the nearest forest cover in 1854 (Table 3). If we remove this effect, large areas of currently unoccupied forest are predicted to have a high probability of occupancy for *F. lugubris*.

If any spatial covariates were removed the performance of the model in terms of AIC (Table S4) was worse, so the full model is also the minimum model. AUC is the area under the receiver operating characteristic (ROC) curve, and is a commonly used measure of model performance in distribution modelling, although with known issues (Lobo et al., 2008). The fit of the model is considered better, the higher above 0.5 the value of AUC is. The mean AUC

Table 2

Current percentages of conifer and broadleaved forest and non-native and native species both with the area in which habitat suitability was modelled and across all Forestry Commission (FC) land across the landscape; other land did not have the data available.

Within area used in habitat suitability model				Within all FC land across landscape			
Forest type	Percentage of forest	Species origin	Percentage of forest	Forest type	Percentage of forest	Species origin	Percentage of forest
Conifer	61.0	Non-native	43.2	Conifer	65.0	Non-native	50.6
Broadleaf	16.1	Native	34.0	Broadleaf	11.3	Native	25.6
Not specified	22.9	Not specified	22.9	Not specified	23.7	Not specified	23.8

Table 3

Relative importance of variables to the model. Percentage contribution is determined by summing the increase in regularised training gain due to that variable per iteration of the model. Permutation importance is a measure of how much worse the model performs if that variable is randomised.

Variable	Percent contribution	Permutation importance
Distance to forest cover in 1854	42.9	31.7
Mean percentage of conifers within 50 m	23.3	9.1
Mean percentage of open ground within 50 m	16.9	26.0
Mean percentage of trees under 20 years old within 50 m	4.7	8.6
Slope	2.8	5.6
Primary tree genus	2.8	3.0
Hillshade	2.1	2.8
Mean percentage of trees 31–80 years old within 50 m	1.3	5.0
Mean percentage of broadleaves within 50 m	1.2	3.6
Mean percentage of trees 20–30 years old within 50 m	1.1	2.1
Mean percentage of trees over 80 years old within 50 m	1.0	2.4

from five replicates of the full model was 0.793 with a standard deviation of 0.01. The most important variable in predicting the probability of occupancy, i.e. the likelihood that an ant nest is found at a particular location, was its distance to forest cover in 1854 (Table 3), with probability of occupancy decreasing the further it was from the historic forest cover (Fig. 5a). The next most important variables were percentage of conifers within 50 m and percentage of open ground within 50 m (Table 3). The probability of occupancy is highest in the mid values of percentage of conifers within 50 m, decreasing slightly as the value approaches 100% and more strongly as the value approaches 0% (Fig. 5b). Probability of occupancy was highest for the minimum values of percentage of open ground within 50 m, and decreased to almost 0 as 100% was approached (Fig. 5c). The age classes of the forest were of fairly low importance (Table 3) but all showed the same trend, with probability of occupancy decreasing slightly as the percentage of that age class within 50 m approached 100% (Fig. 6). The remaining variables contributed very little to the model (Table 3), and so their relationships with probability of occupancy are not presented here, but can be found in the supplementary material (Figs. S3–S5).

When the modelled relationships were predicted to the study landscape, the areas covered by two populations of *F. lugubris* of known geographical extent identified in initial surveys but not included in the model also showed high probabilities of occupancy (Fig. 7a and b). This supports a high predictive power of our model. The initial prediction showed large areas of forest with a low

probability of occupancy of *F. lugubris* (Fig. 7b). When the same projection is made with the effect of distance to forest cover in 1854 removed, virtually all the forest across the landscape had a medium to high probability of occupancy (Fig. 7c).

4. Discussion

4.1. How has recent afforestation impacted the forest cover of our study landscape?

We have documented the change in forest cover across our study site caused by afforestation programs in Britain during the last 160 years, resulting in a substantial increase in forest cover. This level of increase reflects the scale of woodland expansion for Britain as a whole, where forest cover has increased from 5% in 1900 (Mason, 2007) to the current figure of 13% (Forestry Commission, 2013a). Currently across our study landscape, the majority of the forest consists of conifers (Table 2), which again, is consistent with the pattern throughout Britain, although the ratio of conifer to broadleaved is substantially more skewed towards conifers in our study site than in the country as a whole (conifer 42% of forest area, broadleaved 37%, the remainder consists of felled areas, mixed woodland, ground in preparation and assumed woodland of unknown structure, Forestry Commission, 2013). A high proportion of conifers may not be novel conditions for the North York Moors, as archaeological evidence suggests significant numbers of Scots pine, *P. sylvestris*, used to occur across the North York Moors (Atherden, 1976). However, the dominance of non-native species that we currently see (Table 2) and the management of plantation woodland certainly represents a change in habitat for forest specialists.

4.2. Do non-native conifer plantations offer suitable habitat for *F. lugubris*?

The novel and artificial habitat created by afforestation with non-native conifer plantations in the last 100 years has allowed large expansions of the forest specialist *F. lugubris*. This historical expansion indicates that non-native conifer plantations offer suitable habitat for this species, a finding that is reinforced by our habitat suitability model. All wood ant populations are directly bordered by forest that displays high probability of occupancy, therefore we expect that the historical expansion of these ant population will continue into the future.

In the past, the impact of plantation forests of non-native conifers were interpreted as being negative in terms of their effects on biodiversity but recently there have been suggestions that even

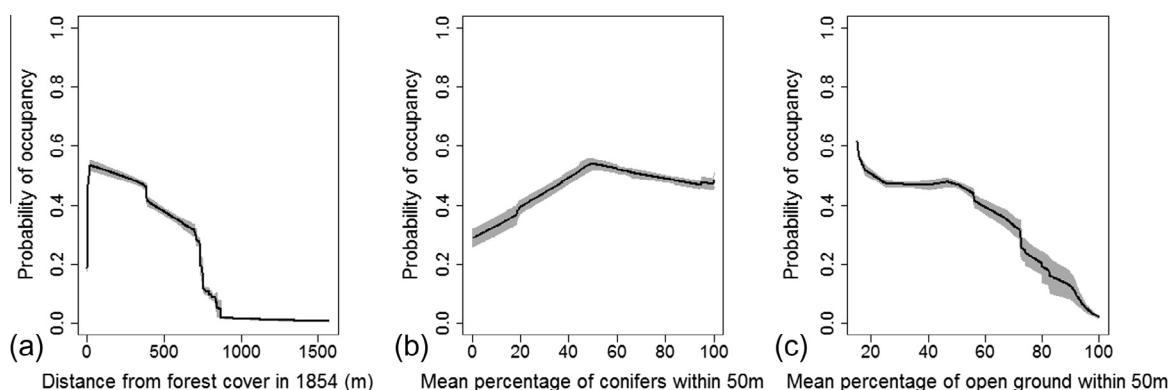


Fig. 5. The relationships between probability of occupancy of *F. lugubris* and (a) distance to forest cover in 1854, (b) mean percentage of conifers within 50 m, (c) mean percentage of open ground within 50 m. Lines are means of 5 models with the grey polygons being standard deviations of those models.

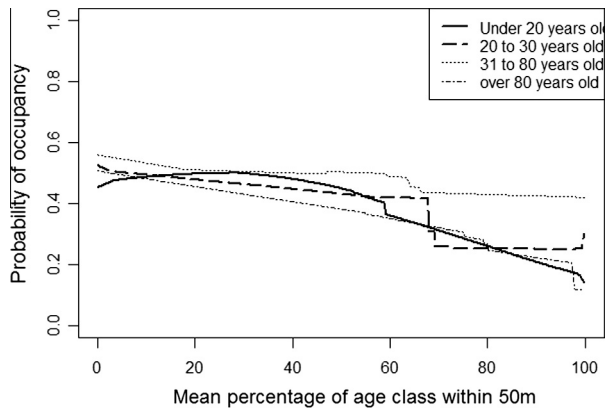


Fig. 6. The relationship between probability of occupancy of *F. lugubris* and the percentage of 4 separate age classes within 50 m. Lines are means of 5 models. See Fig. S6 for each relationship separately with standard deviations.

intensively managed plantations of non-native species can provide an opportunity to enhance the biodiversity of the world's ever diminishing forest resource (Brockerhoff et al., 2008; Humphrey et al., 2003; Quine and Humphrey, 2010). Our study supports the idea that non-native conifer plantations can offer valuable habitat for some native forest specialist species. Afforestation with non-native conifers in Britain has been shown to facilitate connections between previously isolated forest fragments for forest specialists (Hale et al., 2001; Vanhala et al., 2014). While the impact of conifer plantations increasing connectivity of populations is positive, demonstration that non-native conifer plantations provide breeding habitat would make them even more valued habitats for supporting woodland biodiversity. Our results confirm the ability of non-native conifer plantations to support this forest specialist species.

F. lugubris is widely distributed throughout the Palearctic (Goropashnaya et al., 2004) and is known to forage on both broadleaves and conifers (Robinson et al., 2008). *F. lugubris* is therefore able to use a range of forest habitats, and may not be representative of species that specialise on a subset of forest habitats. Although there are a number of broader studies on community structure that do find beneficial contributions of conifer plantations to biodiversity (Humphrey et al., 2003; Moss et al., 1979), there will be species such as those dependent on broadleaved trees that have not done as well (Quine et al., 2007). Our results do suggest that those species that find natural conifer forest to be suitable habitat should be able to expand into recently planted conifer plantations.

Management has a large effect on forest species (Hartley, 2002). Several findings from our model are informative for development of appropriate management of forests for wood ants. The variables for the 4 age classes of plantation forest within 50 m represent the level of variation in structure of the forest within 50 m of a nest: as each variable increases the variability of plantation within 50 m decreases. Our results show that there is a lower probability of occupancy of *F. lugubris* as each of the 4 age classes of forest increases towards 100% (Fig. 6). Therefore, as the variation in the age of trees within 50 m decreases, the probability of a wood ant nest occurring also decreases. Increased heterogeneity of plantation woodland has already been suggested to increase potential biodiversity (Buse and Good, 1993; Moore and Allen, 1999; Nájera and Simonetti, 2010). Our results support this and we also present a scale within which species heterogeneity is relevant for this species: 50 m. The relationship between openness within 50 m and probability of occupancy will show if *F. lugubris* benefits from opening of the canopy. Due to the strong positive relationship

with the edge of plantations that we found for *F. lugubris* (Fig. S2), we expected to find that there would be an optimum level of openness above the minimum value; however, we did not find this trend (Fig. 5c). It appears the standard layout of plantation woodland with wide tracks allowing sunlight at the edges of the plantations is sufficient for *F. lugubris* and we would not predict further opening of the canopy at a 50 m scale to increase the suitability of the habitat for *F. lugubris*.

4.3. What degree of lag is there between establishment of non-native conifer plantations and their colonisation by this forest specialist species?

Although the rate of expansion of *F. lugubris* into new habitat is substantial in terms of nest numbers, the total distance over which *F. lugubris* has expanded is remarkably short (Fig. 4). Between 1854 and 2013, *F. lugubris* exhibited an average expansion rate of just 5 m yr⁻¹. Each population of *F. lugubris* is bordered by at least 3 km² of unoccupied forest that our model predicts to be suitable habitat, therefore expansion of wood ant populations is not limited by habitat availability. It is, instead, the speed at which *F. lugubris* populations expand that is limiting colonisation. *Formica lugubris* is expected to be a poor disperser, with new nests formed a short distance from the parent nest by budding (Hughes and Broome, 2007). A poor disperser is an ideal study organism for this question as lag between formation and colonisation of new forest habitat should be clearly identifiable; however, the rate of expansion we found did not keep abreast with availability of new forest habitat. There are neither major roads through the connected forest, nor major water bodies that could act as barriers. The minor roads throughout the study site in many cases cut straight through populations that have expanded. As a result we have no reason to consider them to be a barrier to further dispersal. Our habitat suitability model reinforces the view that the rate of expansion of *F. lugubris* is the limiting factor in this system; we have shown that large areas of connected suitable habitat are available for *F. lugubris*, with the main limiting factor to colonisation being the distance from where historic ant populations occurred. It is well known that species responses generally lag well behind the speed of ecological change (Ellis and Coppins, 2007; Tilman et al., 1994), and there is no reason that this should be different for creation of novel forest ecosystems. The severity of the lag we have discovered, with wood ant population expansions of under 800 m in 160 years of forest expansion, demonstrate the level of lag that should be expected, at least for the more poorly dispersing forest specialist organisms.

Species may be dependent on a particular phase within the dynamic cycle of plantations; for example, over-mature stands show unique assemblages of fungi (Humphrey et al., 2000), clear felled areas support a distinct range of Carabid beetle species compared to mature plantations (Butterfield et al., 1995) and a range of bird species specialise on either young or old growth (Fuller et al., 2007). Specialisation on a specific part of the forestry cycle reduces the suitability of the habitat to a smaller temporal window within each cycle, which will inevitably slow expansion of woodland specialists throughout plantation forests. However, *F. lugubris* does not show specialisation on a specific stage of the forestry cycle and in plantation forests they are edge specialists (Fig. S2), likely driven by the importance of sunlight on the nest in thermoregulation (Chen and Robinson, 2014; Kadochová and Frouz, 2014). As a result, *F. lugubris* will most likely spread along edges and not through plantation blocks, with populations possibly ceasing to expand for a time when suitable edge habitat is unavailable and then continuing when forest management opens a new area and exposes new forest edge. Researchers studying recently created landscapes must take this colonisation lag into account in the

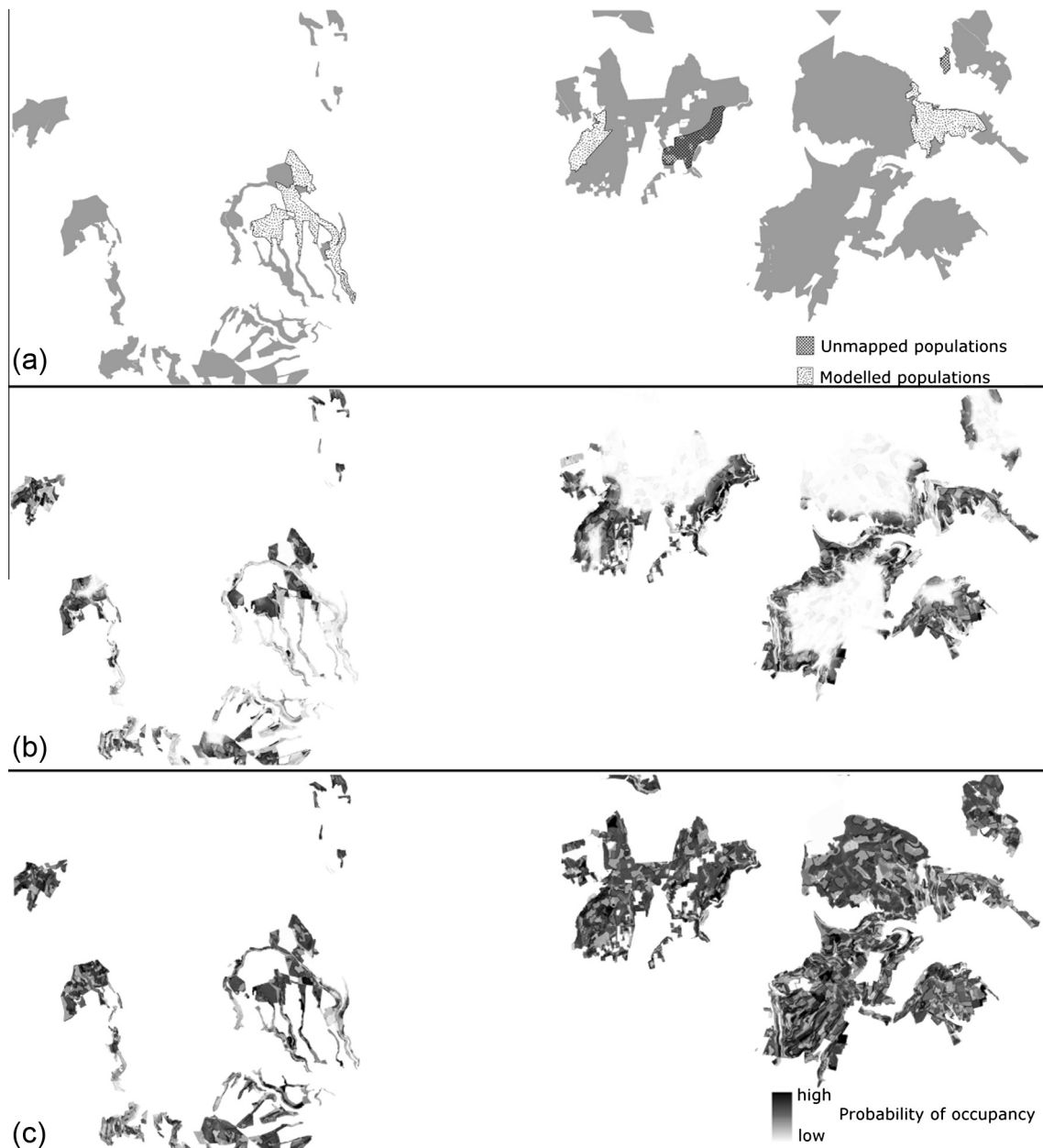


Fig. 7. (a) Grey polygons display the forest area with sufficient data available to allow application of habitat suitability modelling. Dotted areas denote the modelled areas and hashed areas are known populations not included in the model. (b) A projection of the fitted model to the whole landscape. Darker areas denote higher probabilities of occupancy of *F. lugubris*. (c) A projection of the fitted model to the whole landscape with the effect of where forest cover was in 1854 removed, again darker areas denote higher probabilities of occupancy of *F. lugubris*.

study design, data analysis and model creation stages, or risk drawing fallacious conclusions. The colonisation lag that we display means that land managers must not expect short-term colonisation of newly afforested land: it will take time for forest specialists to colonise. The time taken will depend on the distance from a source population and the dispersal capabilities and specificity of habitat required by each organism.

Within the 13% forest cover in Britain as a whole, the forest cover in England currently stands at 10% (Forestry Commission, 2013a), with plans to increase this to 12% by 2060 (Forestry Policy Team, 2013), an ambition that will require planting of large areas of new forest. It is a stated aim of the Forestry Commission to maximise the biodiversity supported by their estate (Forestry Commission, 2013b) and therefore new forests should be planted in such a way as to maximise their contribution to biodiversity.

The colonisation lag we have shown highlights the importance of planting new forest as close as possible to existing forest, especially historic fragments of native woodland, to allow colonisation of forest specialists as quickly as possible. For species that are extremely poor dispersers, such as *F. lugubris*, any form of gap between forest blocks greater than tens of metres wide will hinder colonisation. Our study landscape does not contain any populations that appear to have traversed gaps between fragments, so it would appear this occurs rarely if at all in *F. lugubris*. However as our study was not set up explicitly to examine this problem we cannot be sure that dispersal between separate fragments does not happen. There are a great many more mobile species that will be able to expand longer distances and across intervening habitats, however our findings are an indication of the potential lagging of important parts of the forest ecosystem behind initial colonisation.

5. Conclusion

We have shown a large change in forest cover over our study landscape due to afforestation, primarily with non-native conifer species. Our data lend support to the recent suggestions that non-native plantations can have positive influences on forest dependent species: non-native plantations have facilitated large population expansions of the forest specialist *F. lugubris* from existing fragments of native woodland, and provide large areas of suitable habitat into which expansion can continue. We have also shown that despite availability of appropriate habitat a considerable lag should be expected between the creation of plantation forests and their colonisation by forest specialists. This has implications for further work in recently created ecosystems, which must take into account the ability of organisms to colonise the habitat, and for land managers, who should not expect short-term responses of organisms to the availability of new habitat. We suggest future planting of forest in Britain should be as close as possible to existent forest fragments to encourage the colonisation of the new habitat by forest specialists.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2015.07.034>.

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