

Context-dependent colonisation of terrestrial habitat ‘islands’ by a long-distance migrant bird

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Type of article: Research article

Abstract word count: 204

Main text word count: 5038

Number of references: 55

Number of tables: 2

Number of figures: 3

Running head: Context-dependent colonisation

Keywords: forest; fragmentation; landscape; *Phylloscopus trochilus*

Supplementary material: Whytock_et_al_supp_mat.docx

Abstract

Landscape context can affect how individuals perceive patch quality during colonisation. However, although context-dependent colonisation has been observed in aquatic environments it has rarely been studied in terrestrial environments or at large spatial scales. Here, we assessed how landscape context influenced colonisation rates in a large-scale ($c.7000 \text{ km}^2$) terrestrial system where colonisers (Willow Warbler *Phylloscopus trochilus*) are capable of rapid, long-distance movements. Bioacoustic recorders were used to detect first song dates (an indicator of colonisation or re-colonisation) and settlement in 23 naturally replicated habitat patches. We compared support for three competing hypotheses describing colonisation patterns that depend on landscape context ('redirection', 'landscape-selection' and 'relative patch size') with two patch-level hypotheses (patch 'quality' and 'heterospecific attraction'). First song was earlier when habitat availability in the landscape was low, supporting the 'redirection' hypothesis. Settlement probability was best predicted by patch 'quality' and was lower in woodlands with a dense understorey. Results suggest that colonisation of habitat patches by male *P. trochilus* after spring migration is spatially hierarchical. First, initial colonisation depends on landscape context, and settlement is then determined by fine-scale vegetation characteristics. More broadly, we suggest that patterns observed in fragmented aquatic environments (e.g. 'redirection') can, in some circumstances, be extended to large-scale terrestrial environments.

Introduction

Understanding how landscape-scale habitat patterns influence colonisation dynamics in fragmented landscapes is an important theme in ecology and conservation [1,2]. Theories of landscape connectivity broadly predict that during dispersal and colonisation the importance of habitat composition and configuration is related to a species' mobility and degree of habitat specialism [3,4]. Colonisation can also be context-dependent, where colonisers select patches based on the relative availability or quality of alternative habitat in the landscape [2,5,6]. For many taxa, our understanding of how landscape context influences colonisation dynamics is limited to relatively coarse temporal scales, for example annual colonisation and extinction patterns [7,8] and this can mask fine-scale behavioural processes that are important during initial colonisation [4]. This knowledge gap is especially true for highly mobile, terrestrial species that are capable of rapid, kilometre-scale movements.

Evidence from aquatic islands provides some of the strongest support for context-dependent colonisation. In experimental coral landscapes, the number of colonisers is higher when focal patches have no adjacent patches, supporting the 'propagule redirection' hypothesis [6,9]. This hypothesis predicts that colonisation rates are lower when isolated patches have more habitat in the surrounding landscape because colonists are redirected away from the focal patch. In the opposite direction, the 'field of dreams' hypothesis predicts 'if you build it, they will come' and colonisation rates are expected to be proportional to habitat amount, which leads to higher colonisation rates in landscapes with more habitat [6,10]. Perceived patch quality can also be context-dependent. For example, predator presence in one patch can reduce the perceived quality of neighbouring patches in the local landscape [2,11,12].

In terrestrial environments, the effects of landscape composition and configuration on species turnover and community assembly are well-studied, but less is known about the influence of landscape context on colonisation behaviour [4]. The reasons for this knowledge gap are two-fold: (i) it is often difficult to precisely detect colonisation events and their timing (e.g. first arrival), despite technological advances such as global positioning system (GPS) tracking, and (ii) it is difficult to conduct studies over large spatial scales to ensure habitat patches are sufficiently replicated and spatially independent (i.e. colonisers should not move between focal patches).

Birds are among the most well-studied taxa in landscape ecology but although landscape configuration plays an important role in shaping bird communities the link between pattern and process is poorly understood [4]. Homing experiments show that displaced Ovenbirds *Seiurus aurocapilla* return faster to established territories when forest cover in the landscape is high [13,14]. This could suggest that the amount of habitat in the landscape is likely to be important during colonisation because birds might view the landscape as more favourable [7], or because individuals can move more easily between potential territories. Gap-crossing experiments have also been used to quantify how individuals cross non-habitat and indicate that forest species prefer to move through forest and forest edge rather than cross non-forest areas [14-16]. Although this work has provided valuable insights into the movement behaviour of birds, such experiments have been criticised for being unrealistic [17] and any link between experimental movement behaviour (e.g. during translocations) and natural colonisation behaviour remains speculative. Furthermore, there is usually a significant trade-off between spatial and temporal resolutions, where studies at large spatial scales tend to have low temporal resolution (e.g. monthly or yearly assessments of patch occupancy), and studies with high temporal resolution (daily counts of birds or translocation experiments) are usually limited to relatively small spatial

scales. To meaningfully assess how landscape-scale habitat patterns influence colonisation behaviour in highly mobile taxa such as birds there is a need to achieve both high spatial and temporal resolutions [4].

Entire populations of migratory birds move biannually between their breeding and wintering grounds. In spring in the northern hemisphere, individuals arrive on the breeding grounds and compete to secure the ‘best’ territories [18]. Changes in timing of arrival at the breeding grounds can have significant reproductive consequences due to phenological match or mismatch with resource availability [19,20]. Many migrant birds also show strong natal and breeding philopatry [18,21]. Thus, the amount of available breeding habitat (i.e. territory availability) in a landscape should correlate with the number of individuals that return annually to breed in a given area. Migration and subsequent selection of breeding territories occurs over a varied range of landscapes, presenting an ideal natural experiment to test the effects of local and landscape context on colonisation behaviour. However, most previous work has focused on the effects of landscape context on habitat-use during migratory stopovers and it is unclear how landscape context influences initial selection of breeding territories. Bennet et al. [7] found that migrant bird communities responded to regional gradients of land-use, but were unable to disentangle which factors were most important because of high multicollinearity between measures of land-cover. Despite a lack of empirical evidence, it is predicted that migrant birds will select landscapes with high habitat availability during initial colonisation [7] but subsequent settlement of territories is likely to depend on local, patch-level characteristics such as resource availability or vegetation structure. Recent global declines of migratory birds are also poorly understood, and land-use change along migratory routes has been implicated in the population declines of some species [22]. Understanding how large-scale habitat patterns influence colonisation behaviour is therefore a conservation priority.

Here, we used a natural experiment and novel approach to test whether colonisation of terrestrial habitat ‘islands’ is context-dependent when individuals are capable of rapid, large scale movements that are independent of habitat availability (i.e. direct, nocturnal migratory flights). We used bioacoustic recorders to monitor migrant bird (Willow Warbler *Phylloscopus trochilus* L.) colonisation or re-colonisation (date of first male song) and settlement in discrete habitat patches (post-agricultural woodlands) across large spatial scales and with high temporal resolution. Habitat patches were of similar size but varied in the amount and configuration of habitat in the landscape (i.e. context). We explicitly tested three competing, *a priori* hypotheses that described how landscape context might affect colonisation rates and settlement probability (‘redirection’, ‘landscape-selection’ and ‘relative patch size’), and compared support for these with two patch-level hypotheses (patch ‘quality’ and ‘heterospecific attraction’ [23]).

Methods

Model species

To test whether colonisation rates of habitat islands depend on landscape context, the study system must satisfy five key criteria: (i) the focal species must use habitats that can easily be characterised at coarse spatial scales (e.g. any wooded habitat in the landscape); (ii) territory densities must be proportional to habitat amount (this assumption is tested in electronic supplementary material; Table S1; Fig. S1); (iii) individuals must initially be absent from a patch; (iv) focal patches must provide suitable habitat for potential colonisers; (v) the timing of colonisation events must be detected with high precision and accuracy. To meet these criteria, we selected *P. trochilus*, a generalist woodland passerine that breeds in northern Eurasia (above approximately 41° N) and overwinters in sub-Saharan Africa [24] as a model species.

In Great Britain, *P. trochilus* breeds in coniferous and broadleaf woodland and scrub, with an estimated 2.2 million territories across the island [25]. Birds prefer woodland patches larger than 0.5 ha with intermediate canopy cover and vegetation ranging in height from roughly 3 to 6 m [26,27]. Historical reporting rates show that *P. trochilus* begins to arrive in Great Britain in the last week of March and the population is fully installed by the end of April [28]. Migration occurs mainly at night and birds travel at average speeds ranging from 40 to 85 km per day, but speeds of up to 218 km per day have been recorded [29,30]. Males arrive before females and are highly vocal when establishing territories, producing a loud, easily detected song that can be repeated up to six times or more per minute [31]. Males of breeding age are highly philopatric, but adult interannual survival is relatively low at around 40% and thus individual turnover is high [21,32]. Once on the breeding grounds, males compete for the best territories, with higher quality territories occupied earlier in the season. Territory sizes range from approximately 0.2 - 0.3 ha [33,34].

Habitat islands

To obtain a set of habitat islands for the study, a subset of post-agricultural broadleaf woodlands was selected from 101 patches used by the Woodland Creation and Ecological Networks (WrEN) research project (Fig. S2). The WrEN project (<http://www.wren-project.com>) comprises a large-scale natural experiment that aims to evaluate how landscape structure and patch characteristics influence biodiversity responses to habitat creation [35]. Patch size is often a stronger predictor of bird species occurrence than other factors such as landscape context [36,37]. Since our primary interest was the influence of landscape context on the timing of colonisation, we controlled for patch area by selecting small woodlands of similar size (0.5 - 2.6 ha), but which varied in the amount and configuration of suitable habitat in the surrounding landscape (see Fig. 7a in [38]). Using these criteria and

information from previous bird surveys in the 101 WrEN study sites [37], we selected a sample of 23 woodlands previously occupied by *P. trochilus* for inclusion in the study. Territory mapping (i.e. mapping of singing males) over three visits in April, May and June 2015 [37] indicated that each woodland held on average one territory. A further 12 previously unoccupied woods that satisfied the size criteria and which appeared to offer suitable habitat (based on a visual assessment) were also selected in an attempt to increase the sample size, but none of these was subsequently occupied by *P. trochilus* and they were excluded from further analysis (Fig. S2).

Patches were typically ≥ 3 km apart and were considered spatially independent because male *P. trochilus* dispersal distances (i.e. distance between breeding and natal site) are typically < 1 km [33]. Patch age (years since woodland establishment) ranged from 10 to 160 years (median 90 years), and age was correlated significantly with mean tree diameter at breast height (DBH) ($r = 0.78$, $P < 0.001$, $n = 23$ patches).

Detecting colonisation

We used Solo audio recorders [39] to record male *P. trochilus* song in each patch. Pilot tests were used to calibrate microphones so that songs could be detected at distances of approximately 50 m (Fig. S3), which is equivalent to a sampling area of 0.3 ha (i.e. one *P. trochilus* territory).

A single recorder was deployed in the centre of each woodland patch during the last week of March 2016 in advance of birds arriving, and set to record audio continuously (24 hr, 7 days) until 1st May 2016. On the day of deployment, we used song playback to ensure that no territorial males were present in the study sites. *P. trochilus* song was broadcast using an .mp3 player and handheld speaker in 10 second bursts at 1 minute intervals for 3 minutes. No

birds responded to song playback, indicating that patches were vacant when data collection commenced.

To identify initial colonisation (or re-colonisation of patches occupied in the previous year) and subsequent settlement we used a sub-sampling approach. Three continuous 10-minute blocks of audio were randomly sampled from the three-hour period after sunrise per day of audio recording (i.e. 30 minutes of audio per day). We then manually examined audio spectrograms for *P. trochilus* song and, after the first detection, we counted the number of calls in the sub-sampled audio for 14 consecutive days to determine if the patch had been settled. Patches with no songs on two consecutive days of the 14 were considered not settled. We also evaluated how song rates in a patch changed over time after the first song date, expecting the pattern to be consistent with Fig. 4 in [19] if there was minimal turnover (i.e. an initial steep rise in song rates followed by a gradual decline). We also compared first arrival dates with countrywide data from the British Trust for Ornithology [28] to ensure that results were representative of those across Great Britain in 2016.

Hypotheses

The ‘propagule redirection’ hypothesis [6,9] predicts that when habitat availability in the landscape is low, focal patches will receive more individuals over time. This is based on the expectation that individuals randomly sample from the available habitat in a landscape. In the system used here, this would be indicated by earlier first song dates in more isolated patches because the probability of receiving an individual is higher per unit time (Fig. 1a). In this case the individual birds are not ‘propagules’ *per se* but an adult male of breeding age, and we refer to this hypothesis as ‘redirection’.

Alternatively, if the ‘initial cue to settlement’ [7] is based on landscape units (i.e. not individual patches) that appear more favourable in general, then focal patches might be

colonised earlier when the amount of woodland in the landscape is higher. We call this the ‘landscape-selection’ hypothesis, which would be consistent with the predictions made by Bennet et al. [7]. The expectation is that individuals select landscapes with high habitat availability, with subsequent sorting into territories based on local, territory-level factors (e.g. food availability, vegetation characteristics, etc.). Thus, when habitat availability in the landscape is high, focal patches will be colonised earlier (Fig. 1b). The direction of this predicted relationship could also be caused by the effects of philopatry. Landscapes with more habitat (and therefore a higher number of potential territories) will receive more individuals returning to their previous breeding territories or close to their natal sites, which should lead to earlier colonisation of patches with more habitat in the surrounding landscape. The two mechanisms (i.e. ‘landscape selection’ vs philopatry effects) are not mutually exclusive, however. It is therefore important to acknowledge that our study design cannot disentangle these if first song date is earlier in focal patches with more habitat in the landscape.

Larger patches have higher woodland bird abundance and occupancy [36,37]. Individuals might therefore select patches based on their *relative* size compared to other patches in the surrounding landscape, with relatively large patches occupied earlier than relatively small patches. The same pattern might also occur due to random sampling (e.g. a target area effect [40,41]), where relatively large patches are more likely to ‘capture’ individuals than relatively small patches in the same landscape due to probability alone. Focal patches might therefore be colonised earlier if they are large *relative* to nearby patches in the landscape, which we call the ‘relative patch size’ hypothesis (Fig. 1c).

Measures of patch ‘quality’ or vegetation characteristics such as canopy cover, understorey cover, tree DBH and tree diversity can be used to describe habitat suitability for breeding *P. trochilus* [26,27]. Since the 23 patches used here were occupied by *P. trochilus* in

the previous year and were generally similar in structure (i.e. broadleaf post-agricultural woodlands), and because we assumed that initial colonisation occurred rapidly at dawn after nocturnal flights, we predicted that patch-level factors would have no effect on the timing of initial colonisation (Fig. 1d).

Manipulative experiments have demonstrated that migrant birds are attracted to the vocalisations of other woodland birds (heterospecific attraction) when establishing territories [23], perhaps because social information from heterospecifics is indicative of patch quality, such as predation risk [42]. To test for the existence of heterospecific attraction we calculated an index of acoustic complexity in the patch on the day of first *P. trochilus* song, expecting that patches would be colonised earlier as soundscape complexity (i.e. bird song richness) increased (Fig. 1e).

We attempted to control for patch size during site selection as far as possible (i.e. patches were all of similar size), but since there was some small variation between patches we tested for an effect, expecting no relationship between patch size and colonisation rates (not illustrated). Finally, our null model for initial colonisation predicted that woodlands further north and east would be colonised later (not illustrated) based on knowledge of large-scale *P. trochilus* migration patterns in the UK [29].

Although the primary focus of the study was on the timing of initial colonisation, we also repeated the analyses for settlement probability, since not all sites were considered settled (see Results). Settlement was expected to depend on patch-level factors at the territory scale, and we therefore predicted that settlement probability would not depend on landscape context (Figs 1f and 1g). However, individuals might decide to move to neighbouring patches if their initial patch appears poor relative to others in the landscape, and we predicted that settlement probability would therefore be lower when patches were small relative to their neighbours (Fig 1h). Settlement probability was expected to be higher in better ‘quality’

patches (e.g. with an open understorey) (Fig. 1i) and in patches with higher bird song complexity (Fig. 1j).

Predictor variables

Two variables were used to test our three primary hypotheses of interest. The amount of habitat (any woodland) in the landscape was used to test the ‘redirection’ and ‘landscape-selection’ hypotheses, and the ratio between the focal patch size and the median patch size of any woodland in the landscape was used to test the ‘relative patch size’ hypothesis. Habitat amount, patch size and relative patch size were calculated from Forestry Commission spatial data [43] at seven scales (nested Geographic Information System buffers surrounding the focal patch with radiuses of 250 m, 500 m, 1000 m, 1500 m, 2000 m, 2500 m and 3000 m). To test the effects of vegetation structure we used four variables, which were percent canopy cover, tree mean DBH, tree species richness and percent understorey cover (obtained during field surveys: Tables S2 & S3). Acoustic complexity was used to test the ‘heterospecific attraction’ hypothesis and was calculated as the mean acoustic complexity index [44] (Table S2) for the 3 x 10-minute sub-sampled audio files from the date of first *P. trochilus* song in a patch. To validate the index we regressed the averaged acoustic complexity value against raw bird species richness per site ($n = 23$) in 2015, confirming that there was a positive (although noisy) relationship (Fig. S4).

Modelling approach

We used generalised linear models (GLMs) to quantify the relative effects of each predictor on first *P. trochilus* song date and settlement probability. Geographical position (i.e. northing and easting) was expected to have the strongest effect on first song date, and our null model included northing and easting only as continuous predictors. GLMs were fitted by maximum

likelihood, and residual diagnostics suggested a Poisson error structure was more appropriate than a Gaussian error structure for first arrival dates. For settlement probability, we used GLMs with a binomial error structure, and an intercept only model was used as the null. To avoid overfitting the data (i.e. modeling the residual variation because the ratio between n and the number of parameters is too low) and because we were primarily interested in the relative magnitude of effects, separate models were constructed for each predictor of interest (but note that northing and easting were included as covariates in all models of first song date). We selected a single ‘scale of effect’ [38] for each landscape variable using univariate generalised linear models and corrected Akaike Information Criterion (AIC_c), selecting the most appropriate scale by evaluating those models (after validation [45]) with the lowest AIC_c and largest effect size for the predictor of interest. Predictors were mean centered and scaled by one standard deviation to compare relative effect sizes (β). AIC_c was used to compare goodness of fit between each model and the null, and 95% confidence intervals for effect sizes were bootstrapped from 500 resamples of the data. Likelihood-ratio based pseudo-R-squared values were calculated using the `r.squaredLR` function in the `MuMIn` R package [46]. Multicollinearity between predictors in models of first song date (i.e. northing, easting and the predictor of interest) was assessed using variance inflation factors (threshold < 5) and model validation followed [45]. A correlation matrix for all predictors is in Table S4 and results for the null models are given in Tables S5 and S6. R statistical software was used for all analyses [47].

Results

The median arrival date was the 16th of April (range 5th - 22nd April; Table S3; Fig S5).

Arrival dates were consistent with British Trust for Ornithology countrywide data in the same year (Fig. S5), indicating that results were representative. Although *P. trochilus* was detected

in 23 woodlands, birds did not settle in five of them. In settled patches, song rates increased over time after the first detection before gradually declining, and the shape of the relationship was generally consistent with those observed in [19] (Fig. S6). Data were often noisy, however, and in some instances males may have been replaced during the study period (e.g. Fig. S6f and Fig. S6g).

After accounting for geographic location, first song dates were significantly earlier in patches with low amounts of woodland in the surrounding landscape within 2 km (Table 1; Figs. 2a and 3). The effect size was relatively large (although with high uncertainty, Table 1) and first song was delayed by approximately 5 days as woodland cover in a 2 km radius increased from 5% to 30%. The positive direction of this effect was consistent with the ‘redirection’ hypothesis (Fig. 1a), and the variance explained (36%) was 11 – 12% higher than alternative models (Table 1). Based on AIC_c alone, however, the ‘redirection’ hypothesis had only marginally more support than the null, but it was more strongly supported than alternative hypotheses (Table 1).

Contradicting expectations, there was no evidence to suggest that the relative size of the focal patch in the landscape or bird song complexity in a patch affected first song dates. Patch ‘quality’ had no detectable effects on first song date, as expected.

Probability of settlement depended on patch-level vegetation characteristics and declined as understorey vegetation cover increased (Fig 1b; Table 2). Probability of settlement was also lower when there was more woodland in the surrounding landscape, but the model was only weakly supported based on AIC_c . Alternative hypotheses for settlement probability had minimal support and effect sizes were small (Table 2).

Discussion

The importance of landscape context for community assembly and dispersal behaviour is well known, but the relationship between landscape context and colonisation behaviour is less clear, particularly in terrestrial systems and for organisms that undertake very large-scale, rapid movements. In agreement with experimental work in aquatic environments [6], our results support the ‘redirection’ hypothesis (i.e. colonists are redirected away from the focal patch if habitat amount in the landscape is high) and we found little support for the ‘landscape selection’ [7] or ‘relative patch size’ hypotheses. Previous work in our study area also supports the ‘redirection’ hypothesis: we found that, after controlling for patch size and other factors, the relative abundance of woodland birds was lower in focal patches ($n = 101$) when the amount of broadleaf woodland within 1 km was higher (Fig. 3b in [37]). As predicted, settlement probability depended on vegetation characteristics (understorey cover) at the local, patch-scale. This is consistent with *P. trochilus* preference for woodlands and woodland edges with a relatively open, grassy understorey, which facilitates ground nesting. This result provides some of the first empirical support for the hypothesis that landscape context acts as an initial cue for colonisation, and that more local, patch-level factors then dictate whether the territory is eventually settled or abandoned.

Whether earlier first song dates in sparse landscapes are caused by a random sampling process (i.e. higher probability of ‘capturing’ a colonist in a focal patch when there is less habitat in the landscape), or whether individuals are actively selecting patches with low amounts of habitat in the surrounding landscape cannot be determined using these results. Philopatry also plays an important mechanistic role in dictating where birds return to breed each year. Adult males will typically return to their previous territory if they bred successfully in the previous year, and first year male *P. trochilus* will return to within 1 km (on average) of their natal territory. Despite strong philopatry in *P. trochilus*, however, it

cannot explain the observed relationship between first song date and the amount of woodland in the landscape based on our *a priori* expectations. Therefore, given the remarkable navigational skills of migrant birds and because many species are known to actively select vacant territories based on their relative quality (e.g. prospecting behaviour in Collared Flycatchers *Ficedula albicollis* [47,48]) we suggest that the relationship between first song date and amount of habitat in the landscape is unlikely to be due to a random sampling process, and propose that isolated patches become disproportionately attractive to early male *P. trochilus* in landscapes with less alternative habitat.

The relatively isolated agricultural woodlands studied here probably represent poor quality habitat patches for *P. trochilus*. Yet, when they are situated in landscapes with little alternative habitat they appear to become relatively more attractive, resulting in males arriving earlier. Paradoxically, this is despite *P. trochilus*' ability to travel more than 100 km per night during migration, which implies that individuals could avoid sparsely wooded landscapes with relative ease. This relationship would have been overlooked by studies of patch occupancy or abundance [8,37,50] because most patches were eventually occupied and thus would appear equally 'attractive' if surveys were made at coarse temporal resolutions or later in the season.

During migration and stopover, body mass gain in *P. trochilus* is higher when landscapes have more forest cover [51]. Assuming that the same is true on breeding territories, it therefore appears counter-intuitive that first song date is earlier in the most isolated woodlands, since these individuals are likely to experience fitness costs. Perhaps isolated woodland patches are acting as ecological traps [52,53], leading individuals to trade off current vs future fitness potential by avoiding further, potentially risky long-distance migratory flights when the landscape appears to have limited habitat availability. Other migratory birds are also attracted to 'ecological traps' that arise from novel habitat patterns in

the landscape, such as selectively harvested forest [53]. Considering recorded declines of *P. trochilus* across much of its range [22] there is a need to understand whether the patterns observed here are causing relatively high-quality individuals (as measured by earlier arrival date) to select sub-optimal breeding territories.

Translocation experiments have shown that forest birds (including long-distance migrants such as Ovenbird) return faster to established territories when landscapes are more favourable and have more habitat [13,14]. This suggests that the same could be true during initial selection of breeding territories, and it might be expected that patches located in landscapes with more habitat would be occupied earlier than patches in sparse landscapes. However, our results are consistent with initial colonisation occurring after nocturnal flights that are not constrained by habitat availability in the landscape, and colonisation was earlier when habitat availability was low. In the case of translocation experiments, individuals probably take advantage of favourable habitat to travel by day and return rapidly to their existing territory. We should therefore be cautious when extrapolating findings from experimental work on movement ecology to natural behaviour.

Contradicting expectations, we detected no relationship between acoustic complexity in a patch and first song date or settlement of *P. trochilus*, providing no support for ‘heterospecific attraction’. Heterospecific attraction is well supported by evidence from other studies that have tested for its existence experimentally [23,54]. These have shown that migrant bird abundance tracks the abundance of other woodland bird species. However, we did not quantify *P. trochilus* abundance in this study (indeed most patches could support only one territory), and this could explain why we detected no effect, since we did not quantify post-colonisation dynamics beyond settlement probability.

The lack of support for the relative patch size hypothesis during initial colonisation was surprising given the apparent importance of patch size for *P. trochilus* and other

woodland birds [7,36,37]. There is ongoing debate surrounding the importance of habitat amount *vs* habitat configuration (i.e. relative patch size in this study) for community assembly in fragmented landscapes [38,55]. This result suggests that habitat amount is more important than habitat configuration for *P. trochilus* during selection of territories after spring migration.

It is important to acknowledge that these results are from a single year and differences in weather conditions or population densities between years, for example, might also interact with landscape context to influence first song dates and settlement probabilities. Other factors not measured here could also affect first song dates and settlement, such as fine-scale measures of prey availability or the age of individual birds. Nonetheless, our arrival times were consistent with the historical average in Great Britain and those recorded in 2016, and results supported well-defined, *a priori* hypotheses.

Conclusions

We suggest that landscape context plays an important role during initial colonisation (or re-colonisation) of discrete habitat patches by a long-distance migrant bird after spring migration, which is surprising given that movement through the landscape is not constrained by landscape context (because the species travels long distances at night). These results represent an important step forward in understanding how landscape context influences the spatial and temporal dynamics of colonisation by extending results from smaller aquatic systems to considerably larger scales and to a terrestrial environment under natural conditions. The non-invasive method used to detect first song dates also offers considerable promise for studying how landscape context influences the colonisation behaviour of other highly mobile, acoustically active taxa that might be too small to track in time and space using existing tracking technology.

Authors' contributions

RW co-designed the study, analysed the data, wrote the first draft of the manuscript and collected the data with LW. KP, EFM, KW and NM co-designed the study and co-wrote the manuscript. All authors contributed substantially to manuscript revisions.

Acknowledgements

We are grateful to landowners for permitting access to the study sites. The authors thank Mark Whittingham, Luc Bussiere, Craig Osenberg, Tom Matthews and an anonymous reviewer for their valuable comments on an earlier version of the manuscript. We also thank James Christie for technical advice.

Data accessibility: Data are available from the Dryad Digital

Repository: <https://doi.org/10.5061/dryad.8qf122m>

Ethics statement

The study was approved by The University of Stirling Biological and Environmental Sciences ethics committee.

Funding

RW was funded by the IAPETUS Doctoral Training Partnership via the Natural Environment Research Council (grant number NE/L002590/1), the National Forest Company and Forest Research. The WrEN project (EFM, KW, NAM, KJP) has been funded by the University of Stirling, Natural England, Forestry Commission, Scottish Natural Heritage, the Department for the Environment, Food and Rural Affairs, the National Forest Company, Forest Research, the Woodland Trust and Tarmac Ltd.

Conflicts of interest

The authors declare no conflicts of interest.

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Tables

Table 1. Results from the generalised linear models for first song date (initial colonisation) showing the standardised coefficient estimates (β) for each predictor of interest. Northing and easting were included as covariates in each model but their estimates are not shown. The null model (H_0) included northing and easting only and results are in Table S5. ‘Hypothesis’ indicates which hypothesis in Fig. 1 applies to the model.

Hypothesis (see Fig. 1)	Focal predictor	β	-95%	+95%	<i>P</i>	ΔAIC_c from H_0	R^2
a & b	Proportion any woodland (2 km radius)	0.12	0.01	0.23	0.04	-1.35	0.36
c	Relative patch size (2 km radius)	0.01	-0.12	0.13	0.92	2.95	0.23
d	Canopy cover percent	0.04	-0.09	0.16	0.58	2.65	0.24
d	Tree species richness	0.02	-0.09	0.13	0.68	2.79	0.24
d	Understorey cover percent	0.00	-0.12	0.10	0.93	2.95	0.23
d	Tree DBH mean	-0.01	-0.12	0.10	0.91	2.95	0.23
e	Acoustic complexity index	-0.01	-0.12	0.10	0.91	2.94	0.23
-	Patch size ha (ln transformed)	0.04	-0.10	0.17	0.59	2.67	0.24

Table 2. Results from the generalised linear models for settlement probability showing the standardised coefficient estimates (β) for each predictor of interest. An intercept only model was used as the null (H_0) and results are given in Table S6. ‘Hypothesis’ indicates which hypothesis in Fig.1 applies to the model.

Hypothesis (see Fig. 1)	Focal predictor	β	-95%	+95%	<i>P</i>	ΔAIC_c from H_0	R^2
f & g	Proportion any woodland (2.5 km radius)	-1.14	-2.8	-0.03	0.09	-1.68	0.25
h	Relative patch size (250 m radius)	-0.37	-1.36	0.63	0.63	1.74	0.04
i	Canopy cover percent	-0.87	-2.62	0.3	0.22	0.44	0.13
i	Tree species richness	-0.27	-1.27	0.77	0.59	2.12	0.02
i	Understorey cover percent	-1.32	-2.83	-0.25	0.04	-3.66	0.36
i	Tree DBH mean	-0.59	-1.71	0.41	0.25	1.05	0.09
j	Acoustic complexity index	-0.34	-1.48	0.68	0.52	1.98	0.03
-	Patch size ha (ln transformed)	0.40	-0.63	1.72	0.49	1.89	0.04

Figures

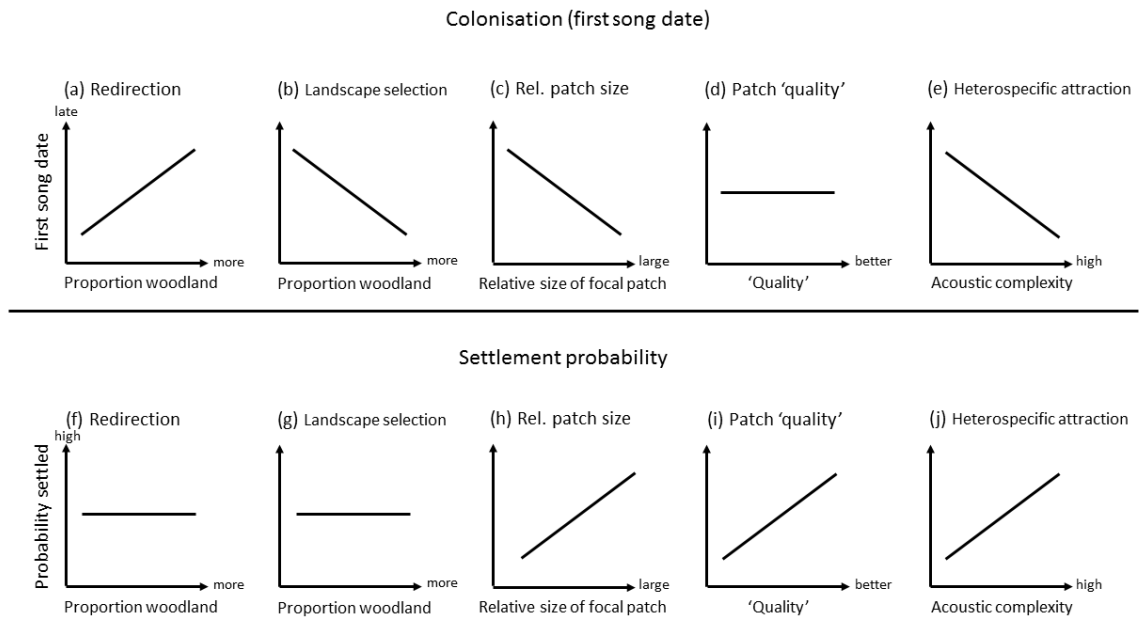


Figure 1. Hypothesised relationships (see Methods) between landscape context, patch characteristics and first song date (a – e), and settlement probability (f – j).

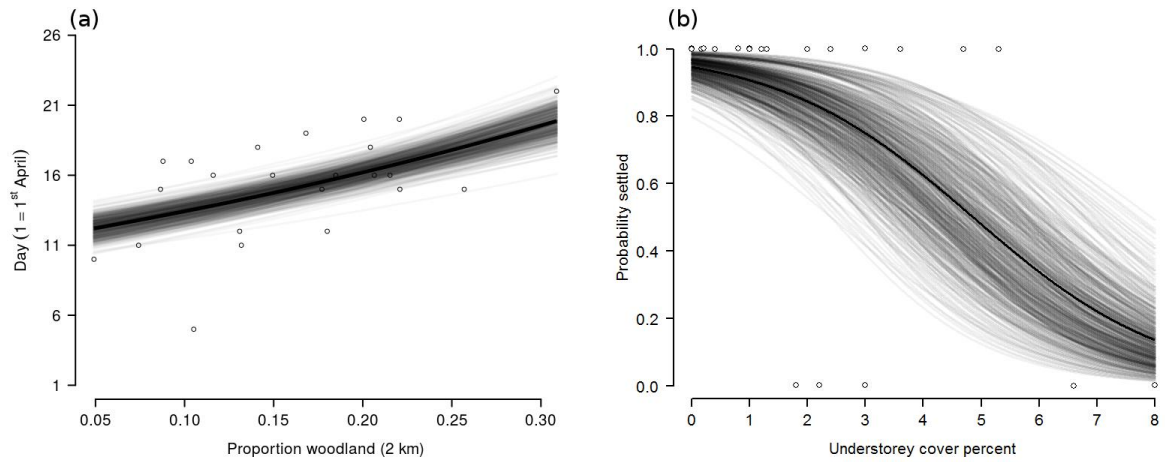


Figure 2. (a) Relationship between *P. trochilus* first song date and habitat amount within a 2 km radius of a woodland patch (holding northing and easting at their mean values), and (b) relationship between settlement probability and understorey cover percent (Domin scale: Table S2). Circles are observed values and semi-transparent lines are bootstrapped 95% confidence intervals from the GLMs.

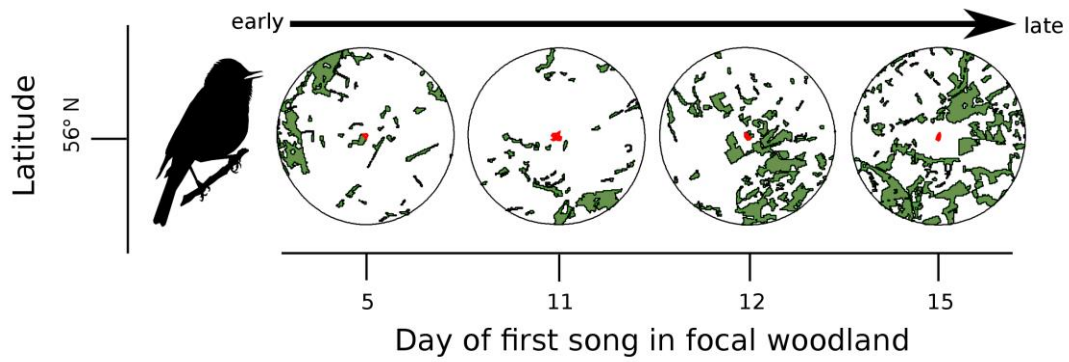


Figure 3. Illustration showing the relationship between the amount of woodland in the landscape (green; within 2 km radius) and first *P. trochilus* song date (day in April 2016) in four example focal woodlands (coloured red) at similar latitudes (near 56° N). *P. trochilus* artwork by Andreas Trepte, www.photo-natur.net (modified under CC BY-SA 2.5).