The role of freshwater availability and terrestrial land cover change in the distribution of a declining terrestrial, insectivorous bird.

Abstract

Insectivorous, Afro-Palearctic migrant birds provide cross-border ecosystem services, but many are declining rapidly. The complex life cycle of migrant birds makes it difficult to target conservation actions, but understanding where they spend time during the breeding season can help indicate where those actions will be most effective. We used the spotted flycatcher (*Muscicapa striata*), a declining Afro-Palearctic migratory insectivore and habitat generalist, as a model to understand how changes in occupancy of survey squares during the breeding season are associated with land cover change. We tested how river density and land cover change were associated with loss and colonisation of 2 km x 2 km survey squares between 1990 and 2010. Greater river density was associated with a lower probability of loss (odds ratio (OR) 0.8) between survey periods, and a higher probability of colonisation (OR 1.25). Loss was associated with increases in urban land cover (OR 1.17) and, unexpectedly, colonisation was negatively associated with increases in woodland (OR 0.91) and standing freshwater (OR 0.94). Our study suggests that habitat creation is unlikely to provide sufficient benefits for some insectivorous birds in the timeframe needed for population recovery, and so efforts should be focussed on the protection and improvement of established habitats. Rivers were strongly associated with the persistence of the spotted flycatcher, and these findings highlight that understanding the benefits of freshwater habitat for terrestrial species should be a priority for conservation management.

Introduction

Management actions are urgently needed to counteract long-term declines of Afro-Palearctic migrant birds, most of which rely on insects at some point during the annual cycle (Vickery et al., 2023). Difficulties in understanding the drivers of decline arise from the complex life cycle and wide spatial range occupied by these birds, breeding in one continent and overwintering in another (Newton, 2007). Climate change and land use change are regularly cited as important factors in the species' declines, but there is little consensus on the individual mechanisms involved (Vickery et al., 2023; Suggitt et al., 2023).

The effects of land use change may be more directly managed than those of climate change, and so they present a more achievable short-term conservation focus. Land use change can affect Afro-Palearctic migrants across the entire flyway; in Africa, the suitability of land cover for long-distance migrants has decreased (Howard et al., 2020), and, in Britain, changing management of woodland (Amar et al., 2006; Holt et al., 2011) and farmland (Bowler et al., 2019) have had negative impacts on some species. Much of the research to date has focussed on understanding drivers of population change on the breeding grounds, with limited attention paid to the wintering grounds due to a scarcity of information on their specific locations (Vickery and Adams, 2020; Vickery et al., 2023). Hence, management actions to improve productivity on the breeding grounds present a more achievable and potentially more effective strategy to improve population trends than attempts to improve survival elsewhere (Saether and Bakke, 2000; Morrison et al., 2016), provided that no density-dependent effects are operating outside the breeding range that could undermine the efficacy of such actions, or even result in unintended negative consequences (Taylor and Norris, 2007).

Insectivorous birds consume huge amounts of invertebrates, so the degradation of this system could have serious implications for ecosystem functioning and biological pest control (Nyffeler et al., 2018; Roseo et al., 2024). Afro-Palearctic migrants that feed on insects have undergone more severe declines than other foraging guilds (Sanderson et al., 2006). Declines have also been observed in non-migratory European (Bowler et al., 2019) and North American (Tallamy and Gregory Shriver, 2021) insectivores, suggesting shared pressures across the globe. These losses likely follow worldwide crashes in terrestrial insect abundance, which have been associated with land use change and agricultural intensification (Hallmann et al., 2017; Sánchez-Bayo and Wyckhuys, 2019; Reif and Hanzelka, 2020). For example, the distribution of the common cuckoo (*Cuculus canorus*), a declining Afro-Palearctic migrant reliant predominantly on Lepidoptera larvae during the breeding season, appears to have shifted away from agricultural lowland in response to reduced food availability (Denerley et al., 2019). Conversely, aquatic insects may provide an increasingly important food source as their numbers have increased in Europe since the early 2000s, perhaps due to regulations on water quality and warmer temperatures (van Klink et al., 2020; Qu et al., 2023).

The flux of emergent aquatic insects into terrestrial habitats represents an important ‘aquatic subsidy’ for insectivores that has received little attention (Lafage et al., 2019). The exploitation of these resources by insectivorous birds is evidenced by their greater abundance near to rivers and streams and increased predation of flying insects in these areas (Murakami and Nakano, 2002; Iwata et al., 2003; Bradbury and Kirby, 2006). This behaviour may positively influence population dynamics, particularly in resource-limited populations (Richardson et al., 2010). As well as providing additional food, freshwater may subsidise terrestrial habitats by offering food of higher nutritional quality (Moyo et al., 2017). Aquatic insects are richer in essential omega-3 fatty acids (Moyo et al., 2017; Twining et al., 2019), which have been associated with improved breeding success in some birds (Twining et al., 2018). Moreover, the timing of aquatic insect emergence is asynchronous with the peak of terrestrial insect emergences, increasing the temporal coverage of food (Nakano and Murakami, 2001). This could be a key driver of more favourable population trends among Afro-Palearctic migrants occupying freshwater habitats, perhaps buffering against phenological mismatch (Both et al., 2010). Thus, an examination of the use of freshwater habitats would provide greater understanding of the population dynamics of migratory insectivorous birds.

Several studies have investigated local breeding habitat associations of Afro-Palearctic migrants (Stevens et al., 2007; Mallord et al., 2016), but few have assessed the landscape-scale relationship between habitat and occupancy or decline (but see Denerley et al. 2019), limiting the scalability of results. Similarly, research on the importance of freshwater habitats for insectivorous species has been limited to local populations (Berzins et al., 2022) or small geographical ranges (Iwata et al., 2003). Here, we test whether terrestrial and freshwater land cover predict national-scale changes in distribution in a model migratory insectivore.

The spotted flycatcher (*Muscicapa striata*) is a widespread obligate insectivore and habitat generalist (Cramp and Perrins, 1993), and the most rapidly declining Afro-Palearctic migrant passerine in the UK (Burns et al., 2020). This species has three main fine-scale structural habitat requirements during the breeding season: a perch to hunt from, open space to catch flying insects, and ledges or shallow cavities for nesting (Cramp and Perrins, 1993). These requirements are met in a range of habitats across the UK, including woodland, farmland and rural settlements, making it the ideal model system in which to test whether national distribution and population change vary with land cover, and between terrestrial and freshwater habitats. While previous studies have suggested that habitat-specific predation pressure may explain the rate of decline in breeding success at the local scale (Stoate and Szczur, 2006; Stevens et al., 2007), there has been no research on variation in population status at a larger spatial scale. Such work is not only vital in the UK, where spotted flycatchers declined by 92% between 1967 and 2020 (Woodward et al., 2020), but it will also inform conservation management across the European population, which has decreased by 56% since 1980

(PECBMS, 2025), and have important implications for other declining insectivores in the Afro-Palearctic region.

Using comprehensive national atlas surveys of breeding birds in Britain, we quantified how freshwater availability and changes in land cover between two time periods were related to colonisation and extinction during the same period. We assessed these relationships for all suitable land cover types, including agricultural land, woodland, grassland, freshwater and urban land. Although climate change is likely to have had an important effect on the distribution of spotted flycatchers, the aim of this study was to identify specific land use types positively associated with colonisation, or negatively associated with local extinction, thereby indicating priority land use types for protection or creation. Specifically, we aimed to (1) examine how changes in land cover are related to changes in occupancy between 1990 and 2010, and (2) assess the importance of freshwater habitats for this insectivorous bird species, all at a national scale.

Methods

Occupancy change data sources

The occupancy of spotted flycatchers in 2 km x 2 km tetrads in Britain during two survey periods was extracted from the 1988–91 and 2008–11 British Trust for Ornithology (BTO) Bird Atlases (Gibbons, 1993; Balmer et al., 2013), hereafter BA1990 and BA2010. During the spring breeding seasons of 1988–91 and 2008–11, volunteers recorded the presence of all bird species along transects within tetrads on two separate visits, achieving near-total coverage for Britain (Gillings et al., 2019). Each visit lasted one hour during BA1990, but for BA2010 there was an option for volunteers to visit for an additional hour. To ensure standardisation, we only included records from the first hour in BA2010.

The recorded presence of spotted flycatchers in tetrads surveyed during BA1990 and BA2010 was extracted as a measure of occupancy or apparent absence for each period. The difference in occupancy between BA1990 and BA2010 was used to explore associations with occupancy change. Presence and absence data from each atlas period were used to assign categories of colonisation (absent 1990, present 2010), loss (present 1990, absent 2010), persistence (present 1990 and 2010), or absence (never present) to each tetrad. To maximise the proportion of breeding birds and minimise the inclusion of transient birds (i.e. birds migrating through a square), presence was only included for tetrads that had probable or confirmed breeding evidence for the encompassing 10 km x 10 km square (Balmer et al., 2013). The chance of recording the same bird in adjacent squares was minimal, as the majority of foraging occurs within 50m of the nest during the breeding season, with occasional foraging trips of up to 200m (Davies, 1977). Two datasets were created from the categorised squares: one to test the probability of colonisation, which included all squares from which birds were absent during BA1990, and one to test the probability of loss, including only those squares in which birds were present during BA1990.

Environmental data sources

To identify factors associated with spotted flycatcher distribution and change, we derived a set of covariates describing the environmental conditions in each surveyed tetrad. Mean elevation for each tetrad was calculated using the ASTER Global Digital Elevation Model V003 (NASA/METI/AIST/Japan Space systems and U.S./Japan ASTER Science Team, 2019). Latitude and longitude of the central point of each tetrad were also extracted. Land cover change was calculated using the UKCEH Land Cover Change 1990–2015 dataset (Rowland et al., 2020a) as the proportion of each land cover type in 2015 subtracted from the proportion in 1990 (Table S1, Fig. S1). These data were provided as a 25 m raster and report land use cover in six simplified, but comparable, land cover types across the UK: woodland, urban, arable, grassland, freshwater and other.

As spotted flycatchers are typically associated with broadleaf woodland, rather than coniferous woodland, the change in proportion of coniferous and broadleaf woodland were extracted from detailed maps of LCM1990 and LCM2007 (Morton et al., 2014; Rowland et al., 2020b), as changes in the methods used to classify these habitats was likely minimal. River density in each tetrad was calculated as the length of river (km) per km^2 of the tetrad using the vector lines shapefile from the UKCEH Digital River Network Of Britain (1:50,000) (UKCEH, 2000). There should be minimal overlap between the freshwater and river variables, as the former only included standing and running water bodies > 0.5 ha or > 50 m wide, representing mainly still open water, whereas the river density was derived from the 1:50000 Ordinance Survey map.

Data analysis - Model construction

Statistical analyses were carried out using R (V4.3.1; R Core Team, 2020) and the '*lme4'* package (Bates et al., 2015). GLMMs with a binomial error structure were used to test the association between environmental variables and occupancy change. Two models were tested: one testing the correlates of colonisation between BA1990 and BA2010 and one testing correlates of loss during the same period.

To account for maximal spatial associations unrelated to land cover, such as climate or geography, all models included an interaction between latitude and longitude, and a second-order polynomial term for elevation. Additionally, the encompassing 100 km x 100 km square for each tetrad was included as a random effect to further account for geographical trends unrelated to land cover. Explanatory variables were scaled, centred and tested for collinearity prior to model fitting.

The global models for occupancy change included river density and the changes in proportions of woodland, arable, freshwater and urban land. To avoid ambiguity, the land cover change category 'other' was excluded. Grassland cover change was highly correlated with arable cover change (r = 0.79), and so only arable change was included (as the alternative model including grassland failed to converge). Change in proportions are constrained by original proportions and so effects may be reflective of original proportions rather than absolute change. We checked for correlations between original proportions and proportion change values and found no correlation between the original proportion and change in proportion of any land cover types, suggesting the effect of original proportions to be minimal. As we were specifically interested in the effect of change, we chose to include only proportion changes in the models. To examine whether woodland effects were driven by a specific type of woodland, a version of the best model (see *model selection & validation* below) was tested using the individual changes in proportions of coniferous and broadleaf woodland, instead of the combined, simplified woodland variable. Both woodland types responded similarly, and so the simplest model is presented.

Data analysis - Model selection and validation

For each model the 'dredge' function from the MuMin package (Bartoń, 2023) was used to select the combination of variables with the lowest AIC value (i.e., the best-fitting model). The 100 km x 100 km random effect and latitude, longitude and elevation were retained in all models. The predictive accuracy of the best models was then tested using 10-fold cross-validation. First, all tetrads were randomly allocated to one of 10 subsets of data (folds). To ensure a representative sample of Britain in each fold, folds were allocated at the level of each 10 km x 10 km square.

This approach ensured that each subset was representative of the overall geographic distribution within Britain. The model was tested 10 times in total, once for each subset after training on the remaining nine.

For each fold of validation, the area under the receiver operating characteristic (ROC) curve (AUC) was calculated using the *'pROC'* package (Robin et al., 2011). AUC is a measure of predictive accuracy incorporating model sensitivity (true positive rate) and model specificity (true negative rate), ranging between 0.5 and 1. An AUC of 0.5 depicts a model assigning outcomes at random, whereas an AUC of 1 depicts perfect predictability. Average AUC ± standard deviation of the 10 folds is reported.

Results

Colonisation

In total, 20,951 tetrads were included in the colonisation model; 19,465 squares never had spotted flycatchers present and 1,486 were colonised between BA1990 and BA2010 (Fig. 1a). The best model for colonisation retained all land cover change variables and river density (Table 1). Mean AUC for the model was 0.7 (± 0.02). After accounting for the effects of latitude, longitude and elevation, urban land cover change had the strongest negative effect: tetrads with a greater increase in urban land cover were less likely to have been colonised (Table 1, Fig. 1f). Colonisation was also less likely in tetrads that had a larger increase in woodland cover (Table 1, Fig. 1c), which was the same for both coniferous and broadleaf woodland change (data not shown). The same was found for freshwater cover, though the relationship was weaker and uncertainty greater (Table 1, Fig. 1e). River density had the strongest positive effect, with tetrads containing a higher density of rivers more likely to have been colonised by spotted flycatchers (Table 1, Fig. 1b). Arable land cover change was also associated with a higher probability of colonisation, although this effect was weak (p = 0.06; Table 1, Fig. 1d).

Loss

In total, 7,356 tetrads were included in the loss model; spotted flycatchers were lost from 6,390 tetrads between BA1990 and BA2010 and were present in 966 tetrads during both periods. The best model for loss had a mean AUC of 0.67 (± 0.03). Arable and woodland cover change were not retained in the best model (Table 1). After accounting for the effects of latitude, longitude and elevation, the strongest effect on loss was river density, which was associated with a lower probability of loss from a tetrad (Table 1, Fig. 2b). A greater increase in urban land was associated with a higher probability of flycatcher loss (Table 1, Fig. 2d). The same was found for freshwater cover, but with greater levels of uncertainty (Table 1, Fig. 2c).

Discussion

Spotted flycatchers occupy a range of habitats in the UK, but our results show that colonisation and extinction from 2 km x 2 km squares were correlated with land cover change and river density. We found that river density was strongly associated with a higher probability of colonisation and a lower probability of loss, highlighting a relationship that has been largely overlooked for terrestrial species. Our results also demonstrated a strong aversion to urbanisation, which was associated with a lower probability of colonisation, and higher probability of loss of flycatchers from survey squares. Although habitat change was associated with the loss of flycatchers in Britain, the low variation explained by the model indicates that multiple factors are operating, likely across the entire range. Nonetheless, the results highlight habitats where conservation actions are most likely to be influential, with an emphasis on the importance of running freshwater habitats. Despite accounting for spatial factors in the model to disentangle the influence of land cover, land cover is not randomly distributed across Britain and so some residual spatial or climatic influences may still be reflected in the land cover results.

Urbanisation

Urban areas are associated with numerous ecological novelties, including non-native species, impervious surfaces, high density infrastructure and high human disturbance (Evans et al., 2009). These environmental changes result in altered ecosystem functioning, with higher temperatures, greater fragmentation, more pollution and reduced biodiversity (Grimm et al., 2008; Fenoglio et al., 2021). Previous research has demonstrated the avoidance of urban areas by insectivorous birds (Máthé and Batáry, 2015), likely driven by reduced food availability and suitability (Teglhøj, 2017; Narango et al., 2018). Similarly, urban expansion led to lower probabilities of colonisation and higher probabilities of loss from survey squares. Urban areas will continue to expand (Seto et al., 2012; Ministry of Housing, Communities and Local Government, 2024), so urban planning should accommodate greater biodiversity by providing more greenspaces and connectivity through habitat corridors (Beninde et al., 2015). Moreover, identifying the most favourable areas for insectivorous species to protect from urbanisation is essential.

Agricultural land cover

Agricultural land covers at least 40% of Britain and is somewhat protected from urban development due to its economic importance (Marston et al., 2023). However, of the declining insectivorous birds in Europe, those occupying farmland have undergone the largest declines (Bowler et al., 2019), owing to large-scale insect declines related to agricultural intensification, including increased pesticide and fertiliser application (Vickery et al., 2001; Hallmann et al., 2017; Seibold et al., 2019). Conversely, less intensive management can benefit insects and insectivores by allowing greater structural diversity (Britschgi et al., 2006; Hannappel and Fischer, 2020). We found only weak effects of arable land cover change on spotted flycatcher distribution change, which is difficult to interpret due to its collinearity with grassland cover change.

Broadleaf and coniferous woodland

Woodland management also has important implications for declining birds. In Britain, woodland cover has almost tripled since the beginning of the 20th century, from 4.7% in 1905 to 13.4% in 2023 (Forest Research, 2023). Despite an historical association of spotted flycatchers with broadleaved woodland (e.g. DEFRA, 2025), colonisation was less likely in tetrads that had gained more woodland, and this effect was similar for broadleaves and conifers. New woodlands in this study had only 20 years to mature during the two survey periods. Young plantations provide a lower abundance of flying insects and lack the structural features required for spotted flycatcher nesting, whereas mature woodlands are typically more structurally and biologically diverse (Fuller et al., 2014; Seibold et al., 2019; Whytock et al., 2018). Hence, the protection of established woodlands, as well as allowing younger woodlands to mature, is likely to be more beneficial for spotted flycatchers than planting new woodlands, at least in the short term.

Freshwater

For insectivorous birds, healthy freshwater habitats provide a periodic surplus of high quality food in the form of emergent aquatic insects (Manning and Sullivan, 2021; Berzins et al., 2022). In addition, the peaks of terrestrial and aquatic insect abundance are asynchronous, creating a greater temporal availability of food, which may help to buffer a declining population by improving chick growth and fledging success (Nakano and Murakami, 2001; Twining et al., 2016, 2018). Both et al. (2010) demonstrated how insectivorous migrants have more favourable population trends in marshland areas compared to terrestrial, which may be due to the extended availability, increased abundance or higher nutritional quality of food, or a combination of these factors.

In accordance with this, river density had one of the highest effect sizes in both our colonisation and loss models. Insectivorous bird abundance has been shown to be greater adjacent to rivers compared to terrestrial habitats at a local scale (Iwata et al., 2003; Uesugi and Murakami, 2007), and our results demonstrate that this effect expands to the landscape scale. For each 1 km of river per km^2 of landscape the probability of colonisation increased by 31% and the probability of loss decreased by 25%, suggesting strong potential for riverine habitats to attract and conserve insectivorous species. Given that aquatic habitats are threatened by both land management and climate change (Lafage et al., 2019; van Rees et al., 2021), the restoration and protection of these waterbodies, and their surrounding habitats, should be a conservation priority.

Key factors influencing river quality and biodiversity include climate change, anthropogenic wastewater discharge and agricultural pollution, with the latter having a substantial impact (Whelan et al., 2022). Promoting freshwater-friendly farming practices, such as buffer margins around waterbodies, could enhance terrestrial and aquatic habitats for insects, ultimately benefiting insectivorous species (Keenleyside and Costa Domingo, 2023). Our results suggest that improving the availability of freshwater within or adjacent to land already utilised by insectivorous birds, such as agricultural grassland and woodland, may have disproportionate benefits. For example, appropriately managed agricultural ponds, likely excluded from our analysis due to scale, are associated with improved breeding success and survival of some species (Berzins et al., 2022). Additionally, restoring natural hydrology by blocking ditches may improve breeding densities of species with a preference for freshwater habitats (Hoover, 2009). Hence, incorporating freshwater systems into conservation management for declining species offers an opportunity for wide reaching benefits, especially given the importance of freshwater for human health and economies (Lynch et al., 2023).

Interestingly, the relationship between standing freshwater change and distribution change differed from that with river density. Areas where freshwater had increased had a negative impact on colonisation and a positive impact on loss. While the driver of this relationship is unclear, it suggests that, like woodlands, newly created or modified standing freshwater habitats might not be as beneficial as established ones. New or modified freshwater habitats may be associated with other unfavourable conditions, but finer scale research is needed to understand the drivers of this relationship.

Our study highlights an important interaction between the presence and persistence of a declining, insectivorous bird and the availability of river habitats across Britain, which supports similar findings from North America (Berzins et al., 2022) and Asia (Iwata et al., 2003). Due to the scale of this study, we are unable to make assumptions about the mechanisms driving the relationship, which could be due to the biological or physical structure of riverine environments. Hence, future work should aim to study the fine-scale relationships between insectivorous species and rivers, for example by investigating the relationship between breeding success and the quantity and quality of invertebrates available in riverine habitats. Nonetheless, these findings have major implications for the design of conservation interventions, especially given the lack of focus on aquatic habitats for terrestrial species, and we hope that these results serve as encouragement to investigate this relationship further.

Supporting information

Additional supporting information may be found in the online version of the article at the publisher's website.

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Figures & tables

Table 1. Model estimates of generalized linear mixed models testing the associations between environmental and land cover variables and spotted flycatcher colonisation and loss. Bold denotes significant effect.

	Colonisation		**Loss**	
Predictors	**Odds Ratios (confidence interval)**	***p***	**Odds Ratios (confidence interval)**	***p***
(Intercept)	0.09 (0.07 – 0.12)	**<0.001**	6.74 (6.07 – 7.48)	**<0.001**
Longitude	0.96 (0.82 – 1.14)	0.654	1.04 (0.94 – 1.15)	0.427
Latitude	0.83 (0.68 – 1.02)	0.072	0.90 (0.81 – 1.01)	0.075
Longitude * Latitude	1.25 (1.07 – 1.46)	**0.005**	1.10 (1.00 – 1.20)	**0.043**
Mean elevation (m)	1.68 (1.51 – 1.86)	**<0.001**	0.62 (0.56 – 0.70)	**<0.001**
Mean elevation (m)^2	0.65 (0.61 – 0.69)	**<0.001**	1.18 (1.12 – 1.24)	**<0.001**
River density (km/km^2)	1.25 (1.17 – 1.32)	**<0.001**	0.80 (0.74 – 0.87)	**<0.001**
% change freshwater	0.94 (0.88 – 1.00)	**0.043**	1.12 (1.01 – 1.24)	**0.038**
% change urban	0.74 (0.68 – 0.80)	**<0.001**	1.17 (1.06 – 1.29)	**0.002**
% change woodland	0.91 (0.86 – 0.96)	**0.001**		
% change arable	1.06 (1.00 – 1.12)	0.060		
N	52 $_{\text{centad}}$		46 $_{\text{centad}}$	
Observations	20951		7356	
Marginal R^2 / Conditional R^2	0.173 / 0.288		0.097 / 0.100	

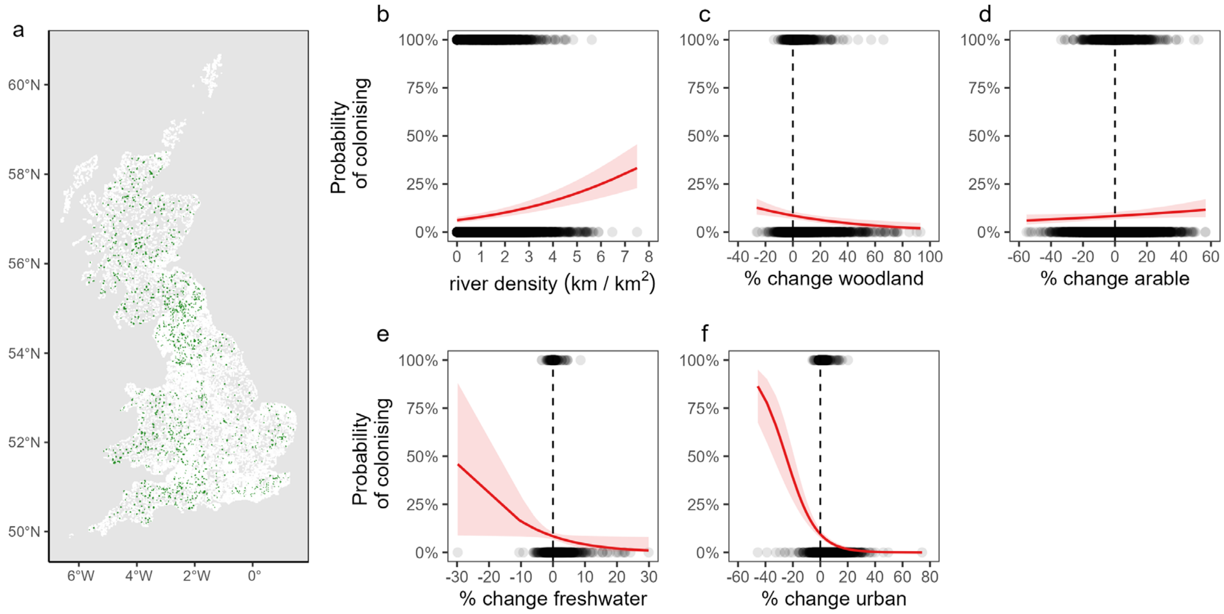

Figure 1. Distribution of squares colonised by spotted flycatchers (a) and predicted probability of colonising squares based on river density (b), change in woodland (c), arable (d), freshwater (e) and urban (f) land cover. On the map (a) colonisation is represented in green, absence in white, and tetrads not included in grey. In b-f, lines and shading represent predicted probability and standard error. Black points signify raw data. Dashed lines indicate the point of no change.

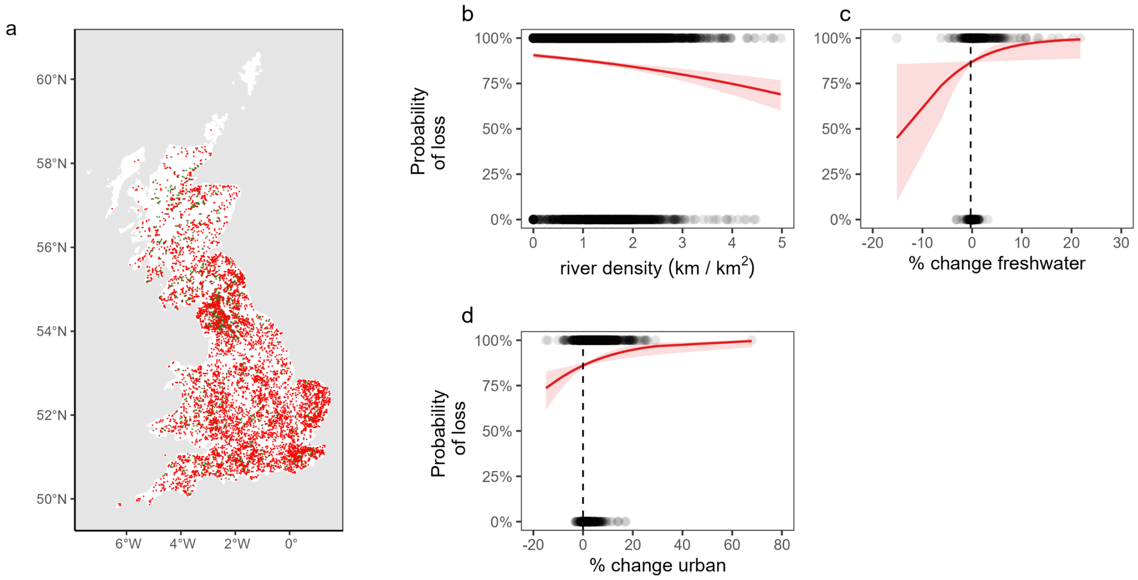

Figure 2. Spatial distribution of spotted flycatcher loss (a) and predicted probability of loss from squares determined by river density (b), change in freshwater (c) and urban (d) cover. On the map (a) loss is represented in red, persistence in green and tetrads not included in white. Lines on b-d represent predicted probability and highlighted areas represent standard error. Black points signify raw data. Dashed lines represent the point of no change.