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Occupancy dynamics of the Wood Warbler assessed with habitat and remote sensing data

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Abstract

The study of population dynamics and species habitat interactions is important for many ecological and conservation issues. We analysed the occupancy dynamics of the Wood Warbler *Phylloscopus sibilatrix*, a forest-interior passerine that has suffered long-term declines in many European countries. Considering a broad range of habitat descriptors, including LiDAR-based variables characterizing forest structure, we identified environmental factors influencing the probabilities of occupancy, colonization, extinction and detection, and mapped these probabilities at a landscape scale. We used presence-absence data collected between 1999 and 2013 in a robust-design protocol with replicated surveys within each primary sampling

season (i.e. breeding season). To analyse occupancy dynamics, we fitted dynamic occupancy models with covariates describing topography, forest extent and structure, soil, seed masting (as a proxy for rodent abundance) and weather conditions during settlement. Initial occupancy was positively related to slope, forest cover and the proportion of broadleaf forest, and negatively related to forest edge length, canopy height variation and soil nutrients. Colonization probability was positively associated with slope and negatively with canopy height variation and soil nutrients. Extinction probability was negatively related to slope, positively related to forest edge length and was the lowest at intermediate vegetation heights. Detection probability decreased during the season and was positively related to forest cover. This study provides insights into the settlement dynamics of a declining forest species by identifying potential drivers of the processes underlying occupancy dynamics, instead of simply modelling species abundance or occurrence. Forest-related covariates were of overwhelming importance for the settlement dynamics of the Wood Warbler. Conservation measures should focus on providing and maintaining the species' preferred forest structure, specifically in extended forests. In Switzerland, forests located on slopes and on nutrient-poor soils should be prioritized for conservation. Finally, comparing findings derived from the relatively coarse scale of this study with those from the small scale of individual territories suggests that conservation recommendations deduced from large-scale monitoring schemes alone may be incomplete, and *vice versa*.

Keywords: LiDAR, *Pyhloscopus sibilatrix*, Switzerland, Sylviidae, Wood Warbler

Based on the concept of the ecological niche (Hutchinson 1957), species distribution models are constructed by correlating species presence/absence data with environmental variables and applying the estimated relationships to areas where the species' occurrence is unknown (e.g. Dettmers & Bart 1999, Gibson *et al.* 2004, Elith & Leathwick 2009, Goetz *et al.* 2010). Most traditional species distribution models typically refer to static species distributions and disregard the issue of imperfect detection, i.e. that a species can be overlooked where present. Imperfect detection is ubiquitous in ecological field data and leads, unless corrected for, to biased inferences concerning habitat relationships and estimated probabilities of occupancy, colonization and extinction (Moilanen 2002, Tyre *et al.* 2003, Gu and Swihart 2004, MacKenzie 2005, 2006, Kéry 2011, Kéry *et al.* 2011, 2013). Traditional species distribution models assume that species presence/absence is measured without error or, that errors are constant across the sample. Both assumptions are likely to be violated for almost every presence/absence dataset collected in the wild and may bias all estimators of species distributions and their dynamics. To overcome the limitations of traditional species distribution models, dynamic occupancy models have been proposed by MacKenzie *et al.* (2003, 2006). These models allow the joint modelling of time-specific probabilities of occupancy, colonization, local extinction, and detection as functions of covariates, while correcting for measurement errors arising due to false-negative observations.

Remote sensing information has become increasingly important in biological studies (Turner *et al.* 2003). For species living in forest ecosystems, horizontal and vertical forest structure often determine habitat suitability (e.g. Dunlavy 1935, Noss 1990, Barnes *et al.* 1998, Franklin *et al.* 2002, Shaw *et al.* 2002). With the help of light detection and ranging (LiDAR), an active remote sensing technique, the three-dimensional structure of forests can be quantified over large areas at a high level of detail. This makes LiDAR a promising tool for ecosystem studies (e.g. Nelson *et al.* 2005, Bellamy *et al.* 2009, Müller & Brandl 2009, Coops *et al.* 2010, Vierling *et al.* 2011, Jung *et al.* 2012, Palminteri *et al.* 2012, Farrell *et al.* 2013, Müller *et al.*

2014, Zellweger *et al.* 2013, 2014), particularly when used at broad spatial scales and in combination with other environmental variables. Vierling *et al.* (2013) applied a single-season occupancy model to study the joint influence of satellite and airborne LiDAR data on Red-naped Sapsucker *Sphyrapicus nuchalis* occupancy. However, to our knowledge, LiDAR-derived habitat variables combined with a broad set of variables from other data sources have so far not been included in multiple-season occupancy modelling studies.

The Wood Warbler *Phylloscopus sibilatrix* is a ground-nesting, long-distance migratory passerine that occurs predominantly in the interior of mixed-deciduous forests at low to medium altitudes within a mostly European range that extends into parts of Russia, Kazakhstan, Georgia and Azerbaijan (BirdLife International 2016). Low natal and breeding philopatry and the avoidance of areas with high rodent density are considered to be responsible for strong annual fluctuations of local occurrence or abundance (Glutz von Blotzheim & Bauer 1991, Wesolowski *et al.* 2009, Szymkowiak & Kuczynski 2015, Grendelmeier 2016). Furthermore, conspecific attraction via social cues, especially singing males, results in a clustering of territories and nests (Grendelmeier *et al.* 2016, Szymkowiak *et al.* 2016). Wood Warblers have been found to be positively associated with structurally homogeneous forests of intermediate age, closed canopy, low canopy height diversity and absence of shrubs. In addition, the species' occurrence has been shown to be positively related to ground vegetation cover such as grass and sedge tussocks, sloping areas and potential direct solar radiation before tree leaf emergence in March (Quelle & Tiedemann 1972, Bibby 1989, Glutz von Blotzheim & Bauer 1991, Hölzinger 1999, Pavlovic 2009, Mallord *et al.* 2012, Huber *et al.* 2016). Well-defined habitat requirements and low philopatry make the Wood Warbler a particularly suitable model species with which to study the processes underlying occupancy because patterns of local extinction and re-colonization of previously occupied sites are expected to be fairly dynamic.

This study aims to analyse the dynamics of the presence or absence of Wood Warblers in northern Switzerland across a broad range of habitat characteristics, including LiDAR-derived variables of forest structure. Our objectives were (1) to identify environmental factors influencing the probabilities of occupancy, colonization, extinction and detection, respectively, and (2) to visualize these probabilities at a landscape scale, specifically for the Swiss Jura Mountains and the Swiss Plateau, by using predictive maps. We also compare results obtained at the scale of the pre-breeding and breeding territory (Huber *et al.* 2016, Pasinelli *et al.* 2016) with the findings from the analyses presented here.

METHODS

Species data

We used data collected yearly between 1999 and 2013 in the Swiss common breeding bird survey ('Monitoring Häufige Brutvögel, or MHB; Swiss Ornithological Institute 2015). The MHB sample surveys 267 squares of 1 km² laid out as a systematic grid across the whole of Switzerland. Each square is surveyed by an experienced observer three times during the breeding season (only twice for squares situated largely above the treeline). Surveys are conducted along a square-specific route which is fixed across years. Routes do not follow an altitudinal gradient by design, but naturally cover a large altitudinal range, owing to the requirement to cover as much of the square as possible. Routes in the 80 squares considered for this study (see below) averaged 5.4 km in length (interquartile range 4.6-6.1 km; Schmid *et al.* 2004, Kéry & Schmid, 2006).

The Wood Warbler's territorial song is loud and distinctive, making the species fairly easy to detect. For this study, the survey-specific counts of observed territories per square were reduced to detection/non-detection observations. Furthermore, we restricted our analysis to the

two biogeographical regions of northern Switzerland: the Jura Mountains (4307 km²) and the Plateau (11168 km²; Gonseth *et al.* 2001). Squares devoid of any forest were dropped from the analyses because Wood Warblers occur only in forest. Altogether, we analysed yearly data from 80 squares (Fig. 1). Results of surveys conducted before 1 May were set to missing because Wood Warblers may still be migrating before that date. For most squares, data from two surveys per year were thus available for the analysis. On average ($\pm$ sd), 2.11 ± 0.18 surveys were analysed per square and year (see Appendix S1 for more details).

Environmental covariates

We used three types of covariates: (1) covariates varying by site (= square) only (site covariates), (2) covariates varying by site and year (yearly site covariates), and (3) covariates varying by site, year and survey (observational covariates). Based on the literature, we defined expectations about the relationship between Wood Warbler occupancy and these covariates (Table 1), but not on dynamic parameters and environmental covariates due to lack of information.

Site covariates

Topography-related covariates were elevation (referred to as *elev*), potential direct solar radiation in March (*r_march*), slope (*slope*) and biogeographical region (*biogreg*). *Elev* was considered as a covariate because the squares ranged from 350 to 1300 m asl and many environmental variables covary with elevation. *R_march* and *slope* were included because the Wood Warbler has been reported to prefer sloping areas and areas with a high solar radiation (Huber *et al.* 2016). *Elev* and *slope* were extracted from the swissALTI3D grid (Swisstopo 2013) and averaged across each square. *R_march* values, calculated by Zimmermann and Kienast (1999), were resampled to a resolution of 5 m and averaged across each square.

Biogreg (Gonseth *et al.* 2001) was included in the analyses to account for systematic

environmental differences between the Jura Mountains and the Plateau that are not captured by the other variables in the analyses, for example in relation to topography or geology. Moreover, we evaluated interactions between *biogreg* and covariates because relationships between the probability parameters (occupancy, colonization and extinction) and covariates may depend on *biogreg*.

Forest-related covariates were the percentage of forest cover (*forest*), the length of forest edge per forest area (*f_edge*), the length of forest trails (maximal width = 2m) per forest area (*f_trail*), the percentage of broadleaf forest (*broadleaf*), mean vegetation height (*meanVH*) and the standard deviation of canopy height (*sdCH*). *Forest* and *f_edge* were considered because the Wood Warbler is known to be forest-dwelling species. *F_trail* was considered because a high density of forest trails may increase disturbance to which open-cup nesters breeding on the ground may be sensitive (Kangas *et al.* 2010). Furthermore, a well-established trail network facilitates timber harvesting, which may reduce habitat quality locally, for example when relatively closed forests are opened up (Huber *et al.* 2016). The three covariates *forest*, *f_edge* and *f_trail* were extracted from swissTLM3D1.1, the large-scale topographical landscape model of Switzerland including both natural and artificial landscape features (Swisstopo 2014). To account for the species' preference for deciduous or deciduous-mixed forests, *broadleaf* was derived from the vegetation classification provided by the Swiss Federal Statistical Office (2004a), categorizing forest cells (resolution, 25x25 m) into broadleaf, broadleaf-mixed, coniferous-mixed and coniferous forests. *Broadleaf* was then calculated as the sum of cells consisting of broadleaf and broadleaf-mixed forest, respectively, divided by all forest cells per 1-km square.

The species' requirements in terms of forest structure were accounted for by the two LiDAR covariates *meanVH* and *sdCH*, describing vegetation height and vertical forest structure, respectively. Among a broad set of LiDAR-derived variables, these two covariates were found to distinguish well between occupied Wood Warbler areas and unoccupied areas

(Huber *et al.* 2016). We derived the two LiDAR covariates from a nationally available first and last return LiDAR dataset, namely the digital terrain model (DTM, corresponding to the swissALTI3D) and the digital surface model (DSM; Swisstopo 2012) (for further detail see Supporting Information Appendix S2). The data of the squares analysed were acquired between November and May in the years 2000-02. The standard deviation of height accuracy and mean point density were 1.5 m and 0.5 m⁻², respectively (Swisstopo 2012) (for further details see Appendix S2). Forest stands with a well-developed overstorey have high *meanVH* values, whereas young or scattered stands feature low *meanVH* values. Forest stands with a homogeneous tree height are expected to exhibit small *sdCH* values, whereas stands with heterogeneous tree heights exhibit large values for *sdCH* (Müller *et al.* 2009).

Soil-related covariates were soil depth (*s_depth*) and soil nutrients (*s_nutrients*), which influence forest vegetation physiology and structure, and the formation and distribution of ground vegetation (Schulze *et al.* 2005). As Wood Warblers avoid stands with a well-developed and tall shrub layer, but prefer a relatively dense low-growing grass layer, occupancy was expected to decrease with soil deepness and nutrient availability. The national soil suitability map (Swiss Federal Statistical Office 2004b), a vector data layer, classifies soil depth and soil nutrients, respectively, into six categories. To calculate *s_depth* and *s_nutrients* per square, the ordinal vector data were resampled to a resolution of 5 m. An average value was then derived for each square.

Yearly site covariates

The yearly site covariates included mast and weather covariates, and the categorical covariate year (*year*). The latter was used as a covariate for colonization, local extinction and detection to account for annual variation in these parameters.

Wood Warbler population size varies inversely with local rodent numbers (Wesolowski *et al.* 2009, Szymkowiak & Kuczynski 2015, Grendelmeier 2016), and Wood Warblers prefer to settle in areas with low rodent numbers (Pasinelli *et al.* 2016). Rodent populations typically peak

in springs following years of high mast crop (e.g. Ostfeld *et al.* 1996, McShea 2000, Clotfelter *et al.* 2007). As no data on rodent population sizes were available for our sample squares across years, we used two mast covariates: the intensity of Common Beech *Fagus sylvatica* mast in the preceding year (*mast_b*) and the intensity of Common Oak *Quercus robur* mast in the preceding year (*mast_o*). Annual records of mast crop size were available for both species as a factor with four categories assessed at one representative site in lowland Switzerland: full, partial, poor, and no mast (Burkart 2015). Although these data were not collected area-wide throughout the Jura Mountains and the Plateau, we considered them applicable for our study, since masting tends to be synchronized over large geographical areas (e.g. Drobyshev *et al.* 2010).

Settlement behaviour of the Wood Warbler in April and May may be affected by weather conditions (Møller 1994, Newton 2007). Thus, we included the following weather covariates in our analysis: monthly precipitation sum in April (*pp4*) and May (*pp5*), the mean of *pp4* and *pp5* (*ppa*), average daily temperature in April (*te4*) and May (*te5*), and the mean of *te4* and *te5* (*tea*). To calculate these covariates, first, the daily values of the MeteoSwiss weather stations were first interpolated across Switzerland with a resolution of 100x100 m using the daymet software of Thornton *et al.* (1997). Means per 1-km square were then derived for summed daily precipitation and mean daily temperature, respectively.

Observational covariates

Survey date (*date*) was used as an observational covariate to account for differences in detection probability because of seasonal changes in male singing activity (Glutz von Blotzheim & Bauer 1991, Trees 1996). All covariates, except for *date*, *mast_b* and *mast_o*, were processed in the Geographic Information System ESRI ArcInfo 10.2.1 and the software R 3.0.2. LAStools was used for the operational processing of LiDAR data (Isenburg 2012).

Data analysis

Occupancy modelling

We used the likelihood-based multiple-season occupancy modelling approach of MacKenzie *et al.* (2003), as implemented in the R package `unmarked` (Fiske *et al.* 2014). This approach explicitly describes the mechanisms underlying occupancy dynamics and the detection process by modelling site occupancy dynamics as a two-state first-order Markov chain. Thus, the initial presence/absence (z , with $z = 1$ for presence, and $z = 0$ for absence) at a site was expressed as a function of initial occupancy probability (ψ_1). For all later time steps, the presence or absence at a site at $t + 1$ (z_{t+1}) is described as a function of the presence/absence at the previous time step (z_t) and the probabilities that a previously occupied site became unoccupied (local extinction probability ϵ) and that a previously unoccupied site became occupied (colonization probability γ). Hence, $\text{Prob}(z_{t+1} = 1 \mid z_t) = z_t * (1 - \epsilon) + (1 - z_t) * \gamma$. Furthermore, the model accounted for imperfect detection probability (ρ) by explicitly describing the observation process. Not detecting the species could mean that the species was truly absent (occurring with probability $1 - \psi_t$), or that it was present but not detected (occurring with probability $\psi_t * (1 - \rho)$; resulting in a ‘false absence’). See Kéry *et al.* (2013) for a more detailed description of the model.

Main assumptions of multiple-season occupancy models include: (1) no unmodelled heterogeneity in any of the probability parameters (ψ_1 , γ , ϵ , ρ), (2) occupancy state at each site does not change over surveys within a season (closure assumption), (3) detection of species and detection histories at each location are independent and (4) the species is not falsely detected (MacKenzie *et al.* 2006). By not including surveys conducted before May, we deemed the closure assumption to be met. Moreover, if singing males were observed within a season, more than one singing male was detected in $60 \pm 12\%$ of the occupied squares. For one site in

one year, we had evidence that a migrating bird was observed. The other assumptions were considered to be adequately met.

Analysis of Wood Warbler data in northern Switzerland

To model patterns of Wood Warbler distributional dynamics between 1999 and 2013, we followed a sequential approach (following Kéry *et al.* 2013), by consecutively modelling ρ , ψ_1 , γ and ε in four steps (Fig. 2). First, ρ was modelled to account for imperfect detection within a season. All main-effects combinations of the covariates *year*, *date*, the quadratic effect of *date* (composed of a linear and a quadratic component) and *forest* were considered. The other parameters (ψ_1 , γ and ε) were kept constant and thus were not affected by covariates. For all candidate models, Akaike information criterion differences (ΔAIC) were calculated (Akaike 1974, Burnham & Anderson 2002). For step 2, the covariates of the best-supported model were kept for ρ . In step 2, the initial presence at a site (ψ_1) was modelled using all site covariates. While doing so, γ and ε probabilities were kept constant. Then, γ and ε were modelled considering all site and yearly site covariates. To avoid a subjective choice of the priority of one over the other, we modelled γ once before ε (steps 3a, 4a; Fig. 2) and once after ε (steps 3b, 4b; Fig. 2).

For ψ_1 , γ and ε , first, the following model types were evaluated: (1) one covariate, (2) one covariate and *biogreg*, and (3) the interaction term between the covariate and *biogreg*. We did not evaluate other interactions because we had no specific reasons for doing so and wanted to avoid overfitting the models. All possible combinations of the covariates appearing in models having $\Delta\text{AIC} \leq 7$ (considered to have some support; Burnham & Anderson 2002) were modelled. Interactions of covariates with *biogreg* or the main effects (i.e. ‘the covariate and *biogreg*’) were included only if the respective models received more support according to AIC than did the model with only the covariate. In addition to the linear effects, quadratic effects

were included to allow a more precise description of the relationship if a non-linear relationship was expected (Table 1; *elev*, *meanVH* and *f_trail*).

For all steps, no more than four covariates per probability parameter were analysed jointly in the same model. Covariates correlated by more than $r = |0.5|$ were not included together in the same model (Supporting Information Appendix S3). All covariates were standardized (mean = 0, standard deviation = 1) prior to analyses. We computed model-averaged maximum-likelihood estimates (MLEs) and model-averaged asymptotic standard errors (ASEs) of the supported covariates (appearing in the best model and in all models with $\Delta AIC \leq 7$ compared with the best one) for every step. Model-averaging was carried out across all models within a given step by weighting the parameter estimates based on AIC model weights.

Visualizations

We used the best-supported model for the visualization of predictions and uncertainty in geographical space. To produce maps, we used the `predict` function in the R package `unmarked` as well as the R packages `raster 2.2-31` (Hijmans *et al.* 2014) and `rgdal 0.8-16` (Bivand *et al.* 2014). We expressed the uncertainty in the estimates as the ratio of the ASEs and the MLEs as a coefficient of variation (CV).

RESULTS

Probability parameters

Detection probability p (step 1)

The best supported model included forest and date ($\Delta AIC = 37.77$ compared with the null model $\psi_1(.)\gamma(.)\epsilon(.)\rho(.)$, where dots denote constant parameters). Only one other model received

support and included forest and the quadratic effect of date ($\Delta AIC = 0.83$ compared with the best model). All other models had $\Delta AIC > 7$ to the best model. There was a positive relation of ρ to *forest* and a negative relation to the linear effect of *date*, respectively (Table 2). The quadratic effect of *date* indicated that ρ declined non-linearly on the logit scale over the season. Summed AIC weights indicated that the linear effect of *date* (0.59) received more support than did its quadratic effect (0.39). The following model was retained for further modelling of ψ_1 :

$$\psi_1(.)\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date}).$$

Initial occupancy probability ψ_1 (step 2)

There was a positive relation of ψ_1 to *slope*, *forest* and *broadleaf*, and a negative relation to *f_edge*, *sdCH* and *s_nutrients* (Table 2, Appendix S5a). The interaction term *forest*biogreg* indicated that a unit increase in forest area resulted in a stronger increase of ψ_1 in the Jura Mountains than on the Plateau. Moreover, the interaction term *f_edge*biogreg* indicated that an increase in forest edge length resulted in a stronger decrease of ψ_1 on the Plateau than in the Jura Mountains. After comparing all combinations of the best supported covariates (Supporting Information Appendix S5b), the following model structure for ψ_1 and p was retained to model γ and ϵ : $\psi_1(\text{slope}+\text{forest*biogreg}+\text{broadleaf})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$ where an asterisk denotes the presence of both main effects and their interaction.

Colonization probability γ

Colonization was positively related to *slope* when modelled before ϵ (step 3a; Table 2 and Appendix S6a). When γ was modelled after ϵ , γ was negatively related to *sdCH* and *s_nutrients* (step 4b; Appendix S6c&d).

Local extinction probability ϵ

When ε was modelled before γ , ε was negatively related to *slope* (step 3b; Appendix S7a).

When ε was modelled after γ , models including *slope*, *broadleaf*, *f_edge* or the interaction between the quadratic effect of *meanVH* with *biogreg* received support (step 4a; Appendix S7c&d). Thus, ε was positively related to *f_edge* and the quadratic effect of *meanVH*, and negatively related to *slope* (Table 2).

Comparing all models (details of the sequential modelling procedure are available in Appendix S4-S7), the overall-best supported model (i.e. the one with the lowest AIC value) used for the visualizations was the following:

$$\psi_1(\text{slope} + \text{forest} * \text{biogreg} + \text{broadleaf}) \gamma(\text{sdCH} + \text{s_nutrients}) \varepsilon(\text{slope}) \rho(\text{forest} + \text{date}).$$

According to this model, ψ_1 was positively related to *slope*, *forest* and *broadleaf*. γ was negatively related to both *sdCH* and *s_nutrients*, and ε was negatively related to *slope*. There was a positive relation of ρ to *forest* and a negative relation to *date* (Table 3, Fig. 3). A number of covariates never appeared in any of the best-supported models or in a model with $\Delta\text{AIC} \leq 7$: *elev*, *r_march*, *f_trail*, *s_depth*, *year* and the mast- and weather-related covariates.

Visualizations

Predictive maps (Fig. 4) revealed strong differences in ψ_1 and ε between the Jura Mountains and Plateau (for the location of the biogeographical regions see Fig. 1). Generally, ψ_1 was predicted to be higher in the Jura Mountains than on the Plateau, whereas the average ε was predicted to be higher on the Plateau than in the Jura Mountains. The average γ was predicted at a very low value in both biogeographical regions. Prediction uncertainty expressed as CV (Appendix S8) was lowest for ρ (mean = 0.17) and highest for ψ_1 (mean = 0.86), with that for γ (mean=0.31) and ε (mean=0.25) being in between. Predicted occupancy probability declined

from 0.27 to 0.22 within the time period investigated (Fig. 5), while observed occupancy of the squares analysed varied between 0.05 and 0.24.

DISCUSSION

Forest-related covariates describing amount, composition and structure of the forest were important for the settlement dynamics of the Wood Warbler in Switzerland. In addition, slope, soil nutrients and survey date were important, whereas elevation, solar radiation in March, mast in the previous year and weather conditions during settlement were not associated with any probability parameter examined. That we were able to capture specific potential drivers of the dynamic occupancy process instead of just modelling species presence/absence or abundance overall provides new insights into the settlement dynamics of this declining forest-dwelling bird species. In addition, by explicitly modelling detection probability ρ and therefore accounting for false-negative measurement error, the hallmark of most ecological data, our inferences were arguably much less biased than those of traditional species distribution models that do not accommodate presence/absence measurement error (Kéry & Royle 2016).

Habitat factors related to occupancy dynamics

Some covariates were related to more than one probability parameter. Hence, a site with suitable Wood Warbler habitat in Switzerland was characterized by a high share of broadleaved forest interior, low canopy height variation and intermediate vegetation height, and was located in fairly steep areas on nutrient-poor soils. Slope was related not only to initial occupancy ψ_1 but also to both γ and ε . One explanation for this finding could be that disturbance intensity due to recreational activity or forest management decreases with increasing slope. Alternatively, forests along steep slopes may more often offer the favourable

combination of relatively closed canopy and intermediate ground vegetation cover as a consequence of nutrient-poor soil conditions compared with forests in the flat lowlands on nutrient-rich soils. Furthermore, nest territories are preferentially established along slopes (Bauer & Hölzinger 1999, Mallord *et al.* 2012, Huber *et al.* 2016, Pasinelli *et al.* 2016), although the generality of this finding is unclear (Wesolowski 1985). Nests built on slopes may allow breeding adults to escape from predators (Piotrowska & Wesolowski 1989), as nest predation accounts for the majority of nest losses in this species (Wesolowski & Maziarz 2009, Mallord *et al.* 2012, Grendelmeier *et al.* 2015). Slope may also act as a surrogate for some important characteristics of habitat quality of the Wood Warbler that were not addressed by other covariates in the model.

Forest and forest edge were highly correlated ($r_s = -0.9$, Appendix S3) and were related to the probabilities of ψ_1 , ε and ρ . Because forest, and particularly broadleaf forest (this study, Glutz von Blotzheim & Bauer 1991), represents the main habitat of the species, the probability that suitable habitat is present in a square increases with increasing forest cover. In our study, a 50% occupancy probability was associated with 56% and 90% forest cover per km² for the Jura Mountains and the Plateau, respectively. Similarly, previous studies showed that Wood Warblers do not commonly settle in small forest patches (< 10 ha) surrounded by an open landscape, even though forest structure might be suitable, but prefer to settle in the forest interior (Glutz von Blotzheim & Bauer 1991).

Mean vegetation height was only related to ε . Accordingly, extinction is higher in either low or high stands (i.e. young and old stands) than in stands of intermediate height. A preference for intermediate vegetation heights has been observed previously (Quelle & Tiedemann 1972, Glutz von Blotzheim & Bauer 1991, Reinhardt & Bauer 2009, Huber *et al.* 2016, Pasinelli *et al.* 2016).

The vertical diversity of canopy height was related to the probabilities of ψ_1 and γ . Squares with homogeneous canopy height were initially occupied and colonized with higher

probability than squares with heterogeneous canopy height. Such stands featured a low tree height diversity of the canopy trees and few gaps, allowing for an open stem space and inhibiting the development of dense regeneration, herbs and shrubs. Thus, vertical forest structure is an important potential driver of the Wood Warbler's occupancy dynamics. In line with Huber *et al.* (2016), the results of this study indicate that the Wood Warbler prefers homogeneously structured forests as opposed to many other avian species (Winter *et al.* 2005; Goetz *et al.* 2007; Müller *et al.* 2009).

The probabilities of ψ_1 and γ were negatively related to soil nutrients. In general, deep, nutrient-rich and/or moist soils promote the development of a dense and tall herbaceous layer including tall forbs, whereas shallow, nutrient-poor and/or dry soils favour the occurrence of grasses and sedges (Ellenberg & Klötzli 1972). As the Wood Warbler as a ground-nesting species generally avoids stands with a well-developed and tall herbaceous layer (e.g. Glutz von Blotzheim & Bauer 1991), but prefers a relatively dense grass layer (Pasinelli *et al.* 2016) promoting nest survival (Grendelmeier *et al.* 2015), the finding concerning soil nutrients may indirectly explain the strong preference of the grassy ground vegetation.

We found no relationships between any parameter describing Wood Warbler occupancy and its dynamics and the occurrence of masting in the preceding autumn. This is surprising, because masting affects rodent population densities (e.g. Ostfeld *et al.* 1996, McShea 2000, Clotfelter *et al.* 2007), which have been suggested to play a role in the striking annual population fluctuations (Wesolowski *et al.* 2009, Szymkowiak & Kuczynski 2015, Grendelmeier 2016) and in the selection of territories (Pasinelli *et al.* 2016). Perhaps the presence/absence data used here were not sufficiently fine-grained to capture the effects of rodents following mast years on Wood Warbler numbers. That is, numbers of territories might well have fluctuated in response to rodents, but this variation may not have resulted in local extinctions or colonizations, which would have been necessary in our presence/absence framework for finding an effect of masting on Wood Warblers.

Comparing findings from small- and large-scale studies

Results of this study conducted at the scale of 1-km squares partly match-up with findings presented in Huber *et al.* (2016) and Pasinelli *et al.* (2016) who studied habitat selection at the territory scale. At both spatial scales, Wood Warbler occurrence was positively related to slope. Slope may allow development of forest structures, particularly on nutrient-poor soils, favourable to the Wood Warbler and may thus represent an indirect driver of the species' occurrence. That the LiDAR variables explaining occurrence at the territory scale were also affecting occupancy dynamics at the 1-km scale suggests that these variables capture important properties of Wood Warbler habitats from small to large spatial scales. These properties are structurally homogeneous forests of intermediate height with low height diversity of canopy trees and an open stem space. Solar radiation was important at the territory scale (Huber *et al.* 2016), but not at the 1-km scale addressed here, suggesting that Wood Warblers specifically select small patches, but not necessarily large areas, of increased solar radiation. The importance of small-scale ground vegetation cover was revealed at the territory scale (Pasinelli *et al.* 2016), but could not be directly assessed at the 1-km scale. In turn, analyses at the 1-km scale showed the relevance of rather extensive broad-leaved forests with relatively low amounts of forest edge for the occupancy dynamics of the Wood Warbler. These aspects could not be addressed in the small-scale study at the territory scale. Conservation recommendations deduced from either small-scale (e.g. breeding territories) or large-scale studies (e.g. monitoring schemes) alone may thus be incomplete, emphasizing the need for studies addressing habitat selection from small to large spatial scales (Bunnell & Huggard 1999).

Advantages of dynamic occupancy models for elucidating settlement dynamics

From a methodological point of view, we emphasize the ability in a dynamic species distribution modelling study to show not only the predicted occurrence probability (Fig. 4a), but also produce maps of the probabilities that govern distribution change, namely colonization and local extinction (Fig. 4b & 4c). Resulting maps provide an attractive summary of species distribution modelling, but they are hypotheses conditional on the model applied. For instance, a high ψ_1 does not mean that the Wood Warbler was actually present, only that there is a high likelihood of Wood Warbler presence, given the site characteristics of the modelled covariates at the site. Further, a high p means that *if* the species occurs, then, based on the covariates at the site, it would be expected to be detected with higher probability.

One key feature of our study is the explicit modelling of binary presence/absence measurement error, i.e. of p . Accounting for p should result in more robust and less biased estimates of the biological parameters underlying colonization-extinction dynamics (Kéry *et al.* 2013). For instance, the strong spatial patterning of annual p (Fig. 4d) suggests substantial spatial bias in any modelling that does not accommodate the non-detection error in this species and probably in most other species as well.

Conservation implications

The Wood Warbler appears to be an area-sensitive species, showing high occupancy probability and low extinction probability in squares featuring large tracts of (broadleaved) forests with relatively low forest edge length, that is, a high share of forest interior. Area-sensitivity has been reported in other bird species, particularly often in forest-inhabiting species (Bayard & Elphick 2010). The mechanisms underlying area sensitivity can be manifold (Dolman 2012). In the Wood Warbler, a clustering of territories has been reported (Herremans 1991) and conspecific attraction experimentally demonstrated (Grendelmeier *et al.* 2016, Szymkowiak *et al.* 2016). Larger areas of suitable habitat give more chances for clustering to

occur than smaller areas, making social constraints a likely explanation for area sensitivity. Forest edge length might additionally underlie area sensitivity, as Wood Warblers nowadays appear to be nesting at larger distances from forest edges than previously (Pasinelli *et al.* 2016).

With regard to the conservation of the study species in Switzerland, large (broadleaved) forest stands in fairly steep areas on nutrient-poor soils should be managed with the needs of the Wood Warbler in mind, because these areas appear to more likely to offer habitats of high suitability. Moreover, managing the forest structure in terms of low vertical diversity, high canopy closure and sparse ground vegetation cover appears to be key for maintaining and improving habitat suitability because of their major importance for occupancy dynamics (this study) and breeding territory selection of the Wood Warbler (Huber *et al.* 2016, Pasinelli *et al.* 2016).

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662 **Supplementary Information**

663 **Appendix S1.** Summary of territory numbers per occupied square

664 **Appendix S2.** Description of the calculations of LiDAR covariates

665 **Appendix S3.** Coefficients of correlations among covariates

666 **Appendix S4.** Summary of model selection procedure for detection probability p

667 **Appendix S5.** Summary of model selection procedure for initial occupancy probability Ψ_1

668 **Appendix S6.** Summary of model selection procedure for colonization probability γ

669 **Appendix S7.** Summary of model selection procedure for extinction probability ε

670 **Appendix S8.** Uncertainty of predicted probabilities

671 **Table 1.** Covariates analysed and expected relationships with occupancy.

Covariate	Unit	Definition	Expected relationships between occupancy and the covariate
Site covariates (topography)			
elev	[m]	elevation	negative/optimum ¹
r_march	[10 MJ/m ²]	potential direct solar radiation in March	positive
slope	[°]	slope	positive
biogreg	[-]	biogeographic region	Jura Mountains > Plateau
Site covariates (forest)			
forest	[%]	percentage of forest	positive
f_edge	[m ⁻¹]	length of forest edge per forest area	negative
f_trail	[m ⁻¹]	length of forest trails per forest area	negative/optimum
broadleaf	[%]	percentage of broadleaf forest	positive
meanVH	[m]	mean vegetation height	optimum
sdCH	[m]	standard deviation of canopy height > 3 m	negative
Soil-related covariates			
s_depth	[-]	soil depth	negative
s_nutrients	[-]	soil nutrients	negative
Yearly site covariates			
year	[-]	year	
mast_b	[-]	beech mast of the preceding year	negative
mast_o	[-]	oak mast of the preceding year	negative
pp4	[cm]	summed daily precipitation April	negative
pp5	[cm]	summed daily precipitation May	negative
ppa	[cm]	summed daily precipitation April-May	negative
te4	[°C]	average daily temperature in April	positive

¹An optimum refers to a hump-shaped curve, with maximum occupancy at intermediate covariate values and would be represented by a negative quadratic relationship between occupancy and the covariate.

te5	[°C]	average daily temperature in May	positive
tea	[°C]	average daily temperature for April-May	positive

Observational covariates

date	[-]	survey date	negative
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672

Table 2. Parameter estimates of the covariates appearing in the best-supported model and in the models with $\Delta AIC \leq 7$ compared with the best-supported one. Model-averaging was carried out across all models within a given step (number of models listed in parantheses) based on AIC model weights. ASE: model-averaged asymptotic standard error; MLE: model-averaged maximum-likelihood estimate.

Parameter	MLE	ASE
Detection probability ρ (12 models)		
forest	1.08	0.17
date (linear term of linear effect)	-0.37	0.13
date (linear term of quadratic effect)	-0.36	0.13
date ² (quadratic term of quadratic effect)	0.12	0.11
Initial occupancy probability Ψ_1 (83 models)		
slope	1.30	0.89
forest*biogreg _{Jura}	2.18	2.07
forest*biogreg _{Plateau}	1.93	0.90
f_edge*biogreg _{Jura}	-1.53	1.68
f_edge*biogreg _{Plateau}	-2.15	1.15
broadleaf	1.70	0.95
sdCH	-0.97	0.73
s_nutrients	-0.95	0.87
Colonization probability γ		
γ modelled before ε (70 models)		
slope	1.25	0.24
γ modelled after ε (71 models)		
sdCH	-0.80	0.25
s_nutrients	-0.39	0.21
Extinction probability ε		
ε modelled before γ (70 models)		
slope	-1.81	0.43
ε modelled after γ (81 models)		
slope	-0.83	0.43
f_edge	1.34	0.54
broadleaf	-0.25	0.54
meanVH*biogreg _{Jura} (linear term of quadratic effect)	0.70	0.69
meanVH*biogreg _{Plateau} (linear term of quadratic effect)	2.74	1.96
meanVH ² *biogreg _{Jura} (quadratic term of quadratic effect)	0.55	0.97
meanVH ² *biogreg _{Plateau} (quadratic term of quadratic effect)	3.88	3.36

679 **Table 3.** Parameter estimates of the best supported dynamic occupancy model. ASE:
680 asymptotic standard error; MLE: model-averaged maximum-likelihood estimate. * Interactions
681 among covariates (x+y+x*y).

Parameter of the best supported model	MLE	ASE
Initial occupancy probability Ψ_1		
Intercept	-1.53	0.60
slope	1.10	0.59
forest*biogreg _{Jura}	1.58	1.69
forest*biogreg _{Plateau}	0.68	0.58
broadleaf	1.24	0.63
Colonization probability γ		
Intercept	-2.15	0.23
sdCH	-0.64	0.23
s_nutrients	-0.38	0.21
Extinction probability ε		
Intercept	0.47	0.43
slope	-1.66	0.39
Detection probability ρ		
Intercept	-0.68	0.23
forest	0.88	0.17
date	-0.45	0.13

682

Figure legends

Figure 1. Location of sample squares within the two biogeographical regions (© BFS GEOSTAT / BUWAL) Swiss Jura Mountains and Swiss Plateau and observed occupancy of the Wood Warbler between 1999 and 2013. $n = 80$.

Figure 2. Sequential modelling procedure. The models highlighted in grey represent the respective null model of the following modelling step. Dots (.) denote probability parameters that were kept constant. (c) The set of covariates selected by the preceding modelling step(s). If (c) is printed in bold and red, it represents the newest set of covariates introduced in the model. The quadratic effect of a covariate (composed of a linear and a quadratic component), is denoted as ². A description of the covariates is given in Table 1.

Figure 3. Relationships between probability parameters (ψ_1 : initial occupancy, γ : colonization, ε : extinction and ρ : detection probability) and covariates of the best-supported model for the Wood Warbler in Switzerland from 1999 to 2013. Black lines are fitted values, values of the other covariates in the model are set to their means. Grey lines represent 95% confidence intervals. Variable descriptions are available in Table 1. $n = 80$ squares.

Figure 4. Predictive maps of Wood Warbler occupancy dynamics in north and west Switzerland 1999-2013. Occupancy probability in 1999 (a), annual colonization probability (b), annual extinction probability (c), and detection probability (at mean survey date) (d). Crosses indicate the locations of the sampled 80 squares.

707 **Figure 5.** Observed occupancy proportion and predicted estimates of occupancy probability
708 (maximum-likelihood estimates with bootstrapped asymptotic SE) between 1999 and 2013.

709

710 Fig. 1

711
712 Fig. 2

Fig. 3

Fig. 4

717
718 Fig. 5

Appendices

Appendix S1. Summary of territory numbers per occupied square.

Year	1-km squares with at least one territory	Territories	Mean territories $\pm$ sd per occupied square	Maximal number of territories per square
1999	16	53	3.3 $\pm$ 3.0	12
2000	13	33	2.5 $\pm$ 1.9	6
2001	19	49	2.6 $\pm$ 2.1	8
2002	17	40	2.4 $\pm$ 1.9	8
2003	19	42	2.2 $\pm$ 1.6	6
2004	10	27	2.7 $\pm$ 1.6	6
2005	9	22	2.4 $\pm$ 1.6	5
2006	13	30	2.3 $\pm$ 1.9	8
2007	9	24	2.7 $\pm$ 1.7	6
2008	16	34	2.1 $\pm$ 2.1	10
2009	10	27	2.7 $\pm$ 1.7	6
2010	4	12	3.0 $\pm$ 2.3	7
2011	6	27	4.5 $\pm$ 2.4	9
2012	9	18	2.0 $\pm$ 1.1	4
2013	13	23	1.8 $\pm$ 0.9	4
1999-2013	43	461	2.5 $\pm$ 2.0	12

Appendix S2. Description of the calculations of LiDAR covariates.

The LiDAR data of the squares analysed were acquired between November and May in the years 2000-02. The standard deviation of height accuracy and mean point density were 1.5 m and 0.5 m^{-2} , respectively (Swisstopo 2012). We derived the normalized digital surface model (nDSM), representing the height above ground of every LiDAR signal of the DSM, by subtracting the DSM from the swissALTI3D. *MeanVH* was derived by calculating the mean of the nDSM within 80x80 m forest cells and then averaging the values across all forest cells per sample square, where the 80x80 m forest cells approximate to Wood Warbler territory size (Glutz von Blotzheim & Bauer 1991).

To calculate *sdCH*, referring specifically to the canopy layer, we first derived a canopy model by selecting the LiDAR signal with the maximum height above ground for each cell in a 2x2 m grid within the 80x80 m forest cells. Second, values below 3 m were excluded so that the covariate refers specifically to the tree layer, and gaps within the forest or non-forested surroundings were not considered. Finally, the standard deviation of this canopy height model was calculated for the 80x80 m forest cells and then averaged across all forest cells per sample square.

Appendix S3. Spearman's rank correlation coefficients (r_s) among the covariates: Correlations $\geq |0.50|$ are printed in bold. $n = 80$

	tea (1999)	te5 (1999)	te4 (1999)	ppa (1999)	pp5 (1999)	pp4 (1999)	s_nutrients	s_depth	sdCH	meanVH	broadleaf	f_trail	f_edge	forest	slope	r_march
elev	-1.0	-0.9	-1.0	0.3	-0.1	0.8	-0.5	-0.4	-0.1	0.1	-0.0	-0.3	0.1	0.1	0.5	0.9
r_march	-0.9	-0.8	-0.9	0.2	-0.2	0.7	-0.4	-0.4	-0.2	-0.1	0.1	-0.3	0.2	-0.0	0.3	1.0
slope	-0.5	-0.6	-0.5	0.3	0.2	0.4	-0.5	-0.4	-0.1	0.2	0.2	0.0	-0.2	0.4	1.0	
forest	-0.2	-0.2	-0.1	-0.0	-0.1	0.2	-0.3	-0.1	-0.2	0.4	-0.1	0.2	-0.9	1.0		
f_edge	-0.0	-0.0	-0.1	0.2	0.1	-0.0	0.2	-0.0	0.2	-0.4	0.1	-0.4	1.0			
f_trail	0.3	0.3	0.3	-0.0	0.1	-0.2	0.1	0.2	0.0	0.1	-0.2	1.0				
broadleaf	0.0	0.0	0.0	-0.3	-0.2	-0.2	-0.2	-0.2	-0.4	-0.1	1.0					
meanVH	-0.1	-0.1	-0.1	-0.1	-0.1	0.1	-0.0	0.3	0.1	1.0						
sdCH	0.0	-0.0	0.1	0.3	0.5	-0.1	0.3	0.4	1.0							
f_trail	0.3	0.3	0.3	-0.0	0.1	-0.2	0.1	0.2								
s_depth	0.4	0.5	0.4	-0.3	-0.1	-0.4	0.6	1.0								
s_nutrients	0.5	0.5	0.5	-0.2	0.0	-0.3	1.0									
pp4 (1999)	-0.8	-0.8	-0.8	0.4	-0.1	1.0										
pp5 (1999)	0.0	-0.1	0.1	0.9	1.0											

ppa (1999)	-0.3	-0.4	-0.3	1.0
te4 (1999)	1.0	0.9	1.0	
te5 (1999)	1.0	1.0		
tea (1999)	1.0			

Appendix S4. Summary of model selection procedure for detection probability p (step 1). Shown are models with $\Delta AIC \leq 7$ compared to the best-supported model and the null model with constant parameters. The quadratic effect of a variable, composed of a linear and a quadratic component ($x+x^2$), is denoted as x^2 . The model marked in bold and italic passed to the next steps of the sequential modelling

Models on detection probability p	ΔAIC
<i>$\Psi_1(.)\gamma(.)\varepsilon(.)p(\text{forest}+\text{date})$</i>	0
$\Psi_1(.)\gamma(.)\varepsilon(.)p(\text{forest}+\text{date}^2)$	0.83
...	
$\Psi_1(.)\gamma(.)\varepsilon(.)p(.)$	37.77

Appendix S5. Summary of model selection procedure on initial occupancy probability Ψ_1 (step 2). Shown are models with $\Delta AIC \leq 7$ compared to the best-supported model and the (null) model with Ψ_1 kept constant (.). Covariates in bold were selected for modelling combinations. Asterisks (*) denote interactions among covariates ($x+y+x*y$). The model marked in bold under b) and italic passed to the next steps of the sequential modelling (steps 3a and 3b in the Tables S5 and S6, respectively)

Models on initial occupancy probability Ψ_1	ΔAIC
a) Covariates modelled individually	
$\Psi_1(\text{slope})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	0
$\Psi_1(\text{slope}+\text{biogreg})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	1.48
$\Psi_1(\text{slope}*\text{biogreg})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	1.59
$\Psi_1(\text{s_nutrients})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	1.86
$\Psi_1(\text{f_edge}*\text{biogreg})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	1.90
$\Psi_1(\text{broadleaf})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	2.04
$\Psi_1(\text{s_nutrients}+\text{biogreg})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	2.33
$\Psi_1(\text{forest}*\text{biogreg})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	2.65
$\Psi_1(\text{sdCH})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	2.69
$\Psi_1(\text{broadleaf}*\text{biogreg})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	2.82
$\Psi_1(\text{forest})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	3.18
$\Psi_1(\text{broadleaf}+\text{biogreg})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	3.50
$\Psi_1(\text{s_nutrients}*\text{biogreg})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	3.81
$\Psi_1(\text{sdCH}+\text{biogreg})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	4.11
$\Psi_1(\text{sdCH}*\text{biogreg})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	4.19
$\Psi_1(\text{f_edge})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	4.33
$\Psi_1(\text{forest}+\text{biogreg})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	5.10
$\Psi_1(\text{f_edge}+\text{biogreg})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	5.77
...	
$\Psi_1(.)\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	10.78
b) Combinations of covariates	
<i>$\Psi_1(\text{slope}+\text{forest}*\text{biogreg}+\text{broadleaf})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$</i>	0
$\Psi_1(\text{f_edge}*\text{biogreg}+\text{broadleaf}+\text{s_nutrients})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	0.21
$\Psi_1(\text{slope}+\text{f_edge}*\text{biogreg}+\text{broadleaf})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	0.44
$\Psi_1(\text{slope}+\text{f_edge}*\text{biogreg}+\text{broadleaf}+\text{sdCH})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	0.62
$\Psi_1(\text{f_edge}*\text{biogreg}+\text{broadleaf}+\text{s_nutrients})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	0.65
$\Psi_1(\text{slope}+\text{f_edge}*\text{biogreg}+\text{broadleaf}+\text{s_nutrients})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	0.70
$\Psi_1(\text{slope}+\text{forest}*\text{biogreg}+\text{broadleaf}+\text{sdCH})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	0.98
$\Psi_1(\text{slope}+\text{f_edge}*\text{biogreg}+\text{sdCH})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	1.07
$\Psi_1(\text{slope}+\text{f_edge}*\text{biogreg}+\text{broadleaf}+\text{sdCH}+\text{s_nutrients})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	1.25
$\Psi_1(\text{forest}*\text{biogreg}+\text{broadleaf})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	1.27

$\Psi_1(\text{slope}+\text{forest}*\text{biogreg}+\text{broadleaf}+\text{s_nutrients})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	1.45
$\Psi_1(\text{f_edge}*\text{biogreg}+\text{broadleaf}+\text{sdCH}+\text{s_nutrients})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	1.50
$\Psi_1(\text{slope}+\text{forest}*\text{biogreg}+\text{sdCH})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	1.54
$\Psi_1(\text{f_edge}*\text{biogreg}+\text{broadleaf})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	1.63
$\Psi_1(\text{forest}*\text{biogreg}+\text{broadleaf}+\text{sdCH}+\text{s_nutrients})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	2.35
$\Psi_1(\text{slope}+\text{forest}*\text{biogreg}+\text{broadleaf}+\text{sdCH}+\text{s_nutrients})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	2.69
$\Psi_1(\text{slope}+\text{f_edge}*\text{biogreg}+\text{sdCH}+\text{s_nutrients})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	2.83
$\Psi_1(\text{forest}*\text{biogreg}+\text{broadleaf}+\text{sdCH})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	2.95
$\Psi_1(\text{slope}+\text{sdCH})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	3.20
$\Psi_1(\text{f_edge}*\text{biogreg}+\text{broadleaf}+\text{sdCH})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	3.30
$\Psi_1(\text{slope}+\text{forest}*\text{biogreg}+\text{sdCH}+\text{s_nutrients})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	3.36
$\Psi_1(\text{f_edge}*\text{biogreg}+\text{sdCH}+\text{s_nutrients})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	4.27
$\Psi_1(\text{slope}+\text{broadleaf}+\text{sdCH})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	4.80
$\Psi_1(\text{broadleaf}+\text{s_nutrients})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	4.86
$\Psi_1(\text{slope}+\text{f_edge}*\text{biogreg})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	5.09
$\Psi_1(\text{slope}+\text{sdCH}+\text{s_nutrients})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	5.19
$\Psi_1(\text{slope}+\text{broadleaf})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	5.58
$\Psi_1(\text{broadleaf}+\text{sdCH}+\text{s_nutrients})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	5.71
$\Psi_1(\text{slope}+\text{broadleaf}+\text{s_nutrients})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	5.76
$\Psi_1(\text{slope}+\text{broadleaf}+\text{sdCH}+\text{s_nutrients})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	6.01
$\Psi_1(\text{slope}+\text{forest}*\text{biogreg})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	6.45
$\Psi_1(\text{sdCH}+\text{s_nutrients})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	6.68
$\Psi_1(\text{slope}+\text{f_edge}*\text{biogreg}+\text{s_nutrients})\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	6.96
...	
$\Psi_1(.)\gamma(.)\epsilon(.)\rho(\text{forest}+\text{date})$	18.22

Appendix S6. Summary of model selection procedure on colonization probability γ (steps 3a and 4b). Shown are models with $\Delta AIC \leq 7$ compared to the best-supported model and the (null) model of the previous step with γ kept constant (.). Covariates in bold were selected for modelling combinations. Asterisks (*) denote interactions among covariates ($x+y+x*y$). The model marked in bold and italic passed to the next step of the sequential modelling (from step 3a to step 4a in Table S6c)

Models on colonization probability γ	ΔAIC
γ modelled before ε (step 3a)	
a) Covariates modelled individually	
<i>$\Psi_1(\text{slope}+\text{forest}*\text{biogreg}+\text{broadleaf})\gamma(\text{slope})\varepsilon(.)\rho(\text{forest}+\text{date})$</i>	0
$\Psi_1(\text{slope}+\text{forest}*\text{biogreg}+\text{broadleaf})\gamma(\text{slope}+\text{biogreg})\varepsilon(.)\rho(\text{forest}+\text{date})$	1.27
$\Psi_1(\text{slope}+\text{forest}*\text{biogreg}+\text{broadleaf})\gamma(\text{slope}*\text{biogreg})\varepsilon(.)\rho(\text{forest}+\text{date})$	1.95
...	
$\Psi_1(\text{slope}+\text{forest}*\text{biogreg}+\text{broadleaf})\gamma(.)\varepsilon(.)\rho(\text{forest}+\text{date})$	20.18
b) Combinations of covariates	
-	
γ modelled after ε (step 4b)	
c) Covariates modelled individually	
$\Psi_1(\text{slope}+\text{forest}*\text{biogreg}+\text{broadleaf})\gamma(\text{sdCH})\varepsilon(\text{slope})\rho(\text{forest}+\text{date})$	0
$\Psi_1(\text{slope}+\text{forest}*\text{biogreg}+\text{broadleaf})\gamma(\text{sdCH}+\text{biogreg})\varepsilon(\text{slope})\rho(\text{forest}+\text{date})$	1.04
$\Psi_1(\text{slope}+\text{forest}*\text{biogreg}+\text{broadleaf})\gamma(\text{sdCH}*\text{biogreg})\varepsilon(\text{slope})\rho(\text{forest}+\text{date})$	1.99
$\Psi_1(\text{slope}+\text{forest}*\text{biogreg}+\text{broadleaf})\gamma(\text{s_nutrients})\varepsilon(\text{slope})\rho(\text{forest}+\text{date})$	6.77
...	
$\Psi_1(\text{slope}+\text{forest}*\text{biogreg}+\text{broadleaf})\gamma(.)\varepsilon(\text{slope})\rho(\text{forest}+\text{date})$	14.29
d) Combinations of covariates	
$\Psi_1(\text{slope}+\text{forest}*\text{biogreg}+\text{broadleaf})\gamma(\text{sdCH}+\text{s_nutrients})\varepsilon(\text{slope})\rho(\text{forest}+\text{date})$	0
$\Psi_1(\text{slope}+\text{forest}*\text{biogreg}+\text{broadleaf})\gamma(\text{sdCH})\varepsilon(\text{slope})\rho(\text{forest}+\text{date})$	0.99
$\Psi_1(\text{slope}+\text{forest}*\text{biogreg}+\text{broadleaf})\gamma(\text{sdCH}+\text{biogreg})\varepsilon(\text{slope})\rho(\text{forest}+\text{date})$	2.02
$\Psi_1(\text{slope}+\text{forest}*\text{biogreg}+\text{broadleaf})\gamma(\text{sdCH}*\text{biogreg})\varepsilon(\text{slope})\rho(\text{forest}+\text{date})$	2.97
...	
$\Psi_1(\text{slope}+\text{forest}*\text{biogreg}+\text{broadleaf})\gamma(.)\varepsilon(\text{slope})\rho(\text{forest}+\text{date})$	15.27

Appendix S7. Summary of model selection procedure on extinction probability ε (steps 3b and 4a). Shown are models with $\Delta AIC \leq 7$ compared to the best-supported model and the (null) model of the previous step with ε kept constant (.). Covariates in bold were selected for modelling combinations. Asterisks (*) denote interactions among covariates ($x+y+x*y$). The quadratic effect of a covariate, composed of a linear and a quadratic component ($x+x^2$), is denoted as x^2 . The model marked in bold and italic passed to the next step of the sequential modelling (from step 3b to step 4b in Table S5c)

Models on extinction probability ε	ΔAIC
ε modelled before γ (step 3b)	
a) Covariates modelled individually	
<i>$\Psi_1(\text{slope}+\text{forest}*\text{biogreg}+\text{broadleaf})\gamma(.)\varepsilon(\text{slope})\rho(\text{forest}+\text{date})$</i>	0
$\Psi_1(\text{slope}+\text{forest}*\text{biogreg}+\text{broadleaf})\gamma(.)\varepsilon(\text{slope}+\text{biogreg})\rho(\text{forest}+\text{date})$	1.03
$\Psi_1(\text{slope}+\text{forest}*\text{biogreg}+\text{broadleaf})\gamma(.)\varepsilon(\text{slope}*\text{biogreg})\rho(\text{forest}+\text{date})$	1.85
...	
$\Psi_1(\text{slope}+\text{forest}*\text{biogreg}+\text{broadleaf})\gamma(.)\varepsilon(.)\rho(\text{forest}+\text{date})$	31.12
b) Combinations of covariates	
-	
ε modelled after γ (step 4a)	
c) Covariates modelled individually	
$\Psi_1(\text{slope}+\text{forest}*\text{biogreg}+\text{broadleaf})\gamma(\text{slope})\varepsilon(\text{meanVH}^2*\text{biogreg})\rho(\text{forest}+\text{date})$	0
$\Psi_1(\text{slope}+\text{forest}*\text{biogreg}+\text{broadleaf})\gamma(\text{slope})\varepsilon(\text{slope})\rho(\text{forest}+\text{date})$	3.23
$\Psi_1(\text{slope}+\text{forest}*\text{biogreg}+\text{broadleaf})\gamma(\text{slope})\varepsilon(\text{meanVH}^2+\text{biogreg})\rho(\text{forest}+\text{date})$	3.36
$\Psi_1(\text{slope}+\text{forest}*\text{biogreg}+\text{broadleaf})\gamma(\text{slope})\varepsilon(\text{slope}*\text{biogreg})\rho(\text{forest}+\text{date})$	4.58
$\Psi_1(\text{slope}+\text{forest}*\text{biogreg}+\text{broadleaf})\gamma(\text{slope})\varepsilon(\text{slope}+\text{biogreg})\rho(\text{forest}+\text{date})$	4.61
$\Psi_1(\text{slope}+\text{forest}*\text{biogreg}+\text{broadleaf})\gamma(\text{slope})\varepsilon(\text{broadleaf}+\text{biogreg})\rho(\text{forest}+\text{date})$	6.02
$\Psi_1(\text{slope}+\text{forest}*\text{biogreg}+\text{broadleaf})\gamma(\text{slope})\varepsilon(\text{meanVH}^2)\rho(\text{forest}+\text{date})$	6.32
$\Psi_1(\text{slope}+\text{forest}*\text{biogreg}+\text{broadleaf})\gamma(\text{slope})\varepsilon(\text{f_edge}+\text{biogreg})\rho(\text{forest}+\text{date})$	7.00
...	
$\Psi_1(\text{slope}+\text{forest}*\text{biogreg}+\text{broadleaf})\gamma(\text{slope})\varepsilon(.)\rho(\text{forest}+\text{date})$	14.87
d) Combinations of covariates	
$\Psi_1(\text{slope}+\text{forest}*\text{biogreg}+\text{broadleaf})\gamma(\text{slope})\varepsilon(\text{slope}+\text{f_edge}+\text{biogreg}+\text{meanVH}^2*\text{biogreg})\rho(\text{forest}+\text{date})$	0
$\Psi_1(\text{slope}+\text{forest}*\text{biogreg}+\text{broadleaf})\gamma(\text{slope})\varepsilon(\text{slope}+\text{f_edge}+\text{broadleaf}+\text{biogreg}+\text{meanVH}^2*\text{biogreg})\rho(\text{forest}+\text{date})$	1.98
$\Psi_1(\text{slope}+\text{forest}*\text{biogreg}+\text{broadleaf})\gamma(\text{slope})\varepsilon(\text{slope}+\text{meanVH}^2*\text{biogreg})\rho(\text{forest}+\text{date})$	3.05
$\Psi_1(\text{slope}+\text{forest}*\text{biogreg}+\text{broadleaf})\gamma(\text{slope})\varepsilon(\text{f_edge}+\text{biogreg}+\text{meanVH}^2*\text{biogreg})\rho(\text{forest}+\text{date})$	3.21
$\Psi_1(\text{slope}+\text{forest}*\text{biogreg}+\text{broadleaf})\gamma(\text{slope})\varepsilon(\text{slope}+\text{f_edge}+\text{broadleaf}+\text{biogreg})\rho(\text{forest}+\text{date})$	3.86
$\Psi_1(\text{slope}+\text{forest}*\text{biogreg}+\text{broadleaf})\gamma(\text{slope})\varepsilon(\text{f_edge}+\text{broadleaf}+\text{biogreg}+\text{meanVH}^2*\text{biogreg})\rho(\text{forest}+\text{date})$	5.01

$\Psi_1(\text{slope}+\text{forest}*\text{biogreg}+\text{broadleaf})\gamma(\text{slope})\varepsilon(\text{slope}+\text{broadleaf}+\text{biogreg}+\text{meanVH}^2*\text{biogreg})\rho(\text{forest}+\text{date})$	6.38
$\Psi_1(\text{slope}+\text{forest}*\text{biogreg}+\text{broadleaf})\gamma(\text{slope})\varepsilon(\text{slope}+\text{f_edge}+\text{biogreg})\rho(\text{forest}+\text{date})$	6.74
...	
$\Psi_1(\text{slope}+\text{forest}*\text{biogreg}+\text{broadleaf})\gamma(\text{slope})\varepsilon(.)\rho(\text{forest}+\text{date})$	22.43

Figure S8. Uncertainty of predicted probabilities (as the coefficient of the standard error and the predicted probability) of the Wood Warbler in the Jura Mountains and the Swiss Plateau. Uncertainty of the occupancy probability in 1999 (a), uncertainty of the interannual colonization probability 1999-2013 (b), uncertainty of the interannual extinction probability 1999-2013 (c), and uncertainty of the detection probability 1999-2013 (for a single survey at mean survey date; d). Crosses indicate the locations of the sampled 80 squares.