

This is a self-archived version of an original article. This version may differ from the original in pagination and typographic details.

Author(s): Fabritius, Henna; Knecht, Henrik de; Ovaskainen, Otso

Title: Effects of a mobile disturbance pattern on dynamic patch networks and metapopulation persistence

Year: 2021

Version: Published version

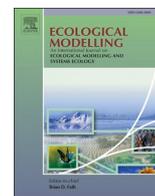
Copyright: © 2022 the Authors

Rights: CC BY 4.0

Rights url: <https://creativecommons.org/licenses/by/4.0/>

Please cite the original version:

Fabritius, H., Knecht, H. D., & Ovaskainen, O. (2021). Effects of a mobile disturbance pattern on dynamic patch networks and metapopulation persistence. *Ecological Modelling*, 460, Article 109738. <https://doi.org/10.1016/j.ecolmodel.2021.109738>



Effects of a mobile disturbance pattern on dynamic patch networks and metapopulation persistence

Henna Fabritius^{a,b,*}, Henrik de Knegt^{a,c}, Otso Ovaskainen^{a,d,e}

^a Organismal and Evolutionary Biology Research Programme, University of Helsinki, P.O. Box 65 (Viikinkaari 1), FI-00014 Helsinki, Finland

^b Smart City Centre of Excellence, Tallinn University of Technology, Ehitajate tee 5, 19086 Tallinn, Estonia

^c Wildlife Ecology and Conservation Group, Wageningen University, 6708 PB Wageningen, Netherlands

^d Centre for Biodiversity Dynamics, Department of Biology, Norwegian University of Science and Technology, N-7491 Trondheim, Norway

^e Department of Biological and Environmental Science, University of Jyväskylä, P.O. Box 35 (Survantie 9C), FI-40014 Jyväskylä, Finland

ARTICLE INFO

Keywords:

Habitat dynamics
Metapopulation dynamics
Habitat suitability models
Metapopulation models
The false heath fritillary
Melitaea diamina

ABSTRACT

Motivation: Certain early-succession habitats may emerge only at restricted locations following disturbance. Therefore, whether disturbances tend to occur at certain sites or not can significantly affect habitat availability and metapopulation persistence of early-successional habitat specialists. Available models that combine metapopulation and landscape processes do not address how to model mobile, spatially shifting disturbance intensities independent of factors of site suitability. We present a model that allows the study on how a mobile disturbance pattern, of either natural or anthropogenic origin, affects patch network and metapopulation dynamics in realistic, heterogeneous landscapes.

Methods: We simulate metapopulation dynamics using a realistic landscape and varying patch destruction (and turnover) rates. We model the local patch emergence rate as the function of site suitability to patch emergence – a permanent factor – and local disturbance intensity, which we first estimate from empirical data and then simulate using annually updating spatial random fields. Using this model, we test whether and how a mobile disturbance pattern affects metapopulation persistence of the false heath fritillary butterfly (*Melitaea diamina*).

Results: In our case study, a mobile disturbance pattern caused new patches to emerge further away from occupied patches over time. This decreased the probability of new patches becoming colonized and thus impaired metapopulation persistence even when the median distance between patches appeared unchanging. However, if disturbances moved to areas that were highly suitable to patch emergence, increased habitat availability could compensate the otherwise detrimental effects of a mobile disturbance pattern. Disturbances that had a moderate degree of mobility had the most uncertain effects to metapopulation persistence.

Conclusions: Our modelling approach distinguishes between two processes behind the spatio-temporal pattern and rates of patch emergence–disturbance dynamics and varying site suitability. It enables the use of social and environmental data for forecasting habitat availability for early-succession habitat specialists under alternative future scenarios. It can be applied and developed further to suit multiple study systems. Our case study suggests that for species conservation, it is either beneficial to organize recurring management activities to take place at constant locations, or to gradually shift them towards areas that are highly suitable to patch emergence.

Abbreviations

AR = autoregressive;
INLA = Integrated Nested Laplace Approximation;
SPOM = Stochastic Patch Occupancy Model;
TWI = Topographic Wetness Index

1. Introduction

Early-succession habitats are open environments that emerge at recently disturbed sites and provide living environments for many pioneering species. Early-succession habitats are typically short-lived: they are quickly taken over by bushes and young trees in the absence of continued disturbances or management (Wahlberg et al., 2002, Harper,

* Corresponding author.

E-mail address: henna.fabritius@helsinki.fi (H. Fabritius).

2007, Greenberg et al., 2011). Certain types of early-succession habitats, for instance certain communities of herbaceous flora (Cousins and Eriksson, 2008), also emerge only at geographically restricted (Chytrý et al., 2003; Schuster and Diekmann 2003) sites that possess specific conditions, such as specific soil moisture, pH and nutrient levels. Therefore, the existence of certain types of early-succession habitats requires that disturbances occur at sites that are suitable for their emergence.

Disturbances that generate early-succession habitats may follow spatio-temporal patterns. Natural disturbances, such as wildfires, floods and windfalls, are driven by climatic, geographic and meteorological factors (Ballinger et al., 2007; Zwolak 2009; Panayotov et al., 2011). Disturbances of anthropogenic origin, such as forestry or agricultural practices (Hodgson et al., 2009), occur at specific locations due to complex socio-economic factors, such as patterns of land ownership, population density, land use regulations and economic demand (Aviron et al., 2005; Renwick et al., 2013). Climatic and cultural changes, including agricultural policies (Storkey et al., 2012, Batáry et al., 2015) or generational shifts in land ownership (Ingram et al., 2013; Duesberg et al., 2017), may break long-term patterns of land use and shift land use activities to new locations. It is therefore vital to understand changes in disturbances with respect to landscape suitability to the emergence of specific types of early-succession habitats, to be able to forecast early-succession habitat availability in changing landscapes.

Changes in habitat availability may be particularly critical to dispersal-limited species, which persist in fragmented habitat patch networks via colonization-extinction dynamics (Hanski 1998). The short lifetimes of early-succession habitats generate turnover, where patches disappear from the patch network and are replaced by new patches elsewhere (e.g. Johst et al., 2011). Thus, metapopulations experience higher local extinction rates (Boughton and Malvadkar 2002; Johst et al., 2011) and need higher colonization rates to persist (Johst et al., 2002; Hastings 2003; Verheyen et al., 2004) in dynamic than in static patch networks. Short patch lifetimes may also cause fluctuations in patch availability, which impair metapopulation persistence (van Teeffelen et al. 2012; De Roissart et al. 2015). In summary, metapopulation persistence in dynamic landscapes depends both on species traits, e.g. species ability to colonize patches, and on the landscape-level pattern of disturbances and patch emergences.

Past models of metapopulation dynamics have accounted for landscape heterogeneity in its suitability to patch emergence in various geographic scales (Larson et al., 2004; Hodgson et al., 2009; Naujokaitis-Lewis et al. 2013). Metapopulation models have also accounted for the disturbance pattern e.g. by modelling metapopulation dynamics under alternative landscape management scenarios (Drechsler et al., 2007, Hodgson 2009, Drechsler and Johst 2010). Landscape heterogeneity in site suitability to patch emergence and disturbance dynamics have also been modelled together (e.g. Midgley et al., 2010, Latif et al., 2013, Miller et al., 2015) in a non-metapopulation context. However, existing models do not provide ways for linking all of the three aspects—the disturbance pattern, metapopulation dynamics and landscape heterogeneity—in wider geographic scales, despite this having been a long-term aim in ecological research (Franklin 2013).

We present a model for the study on how the spatio-temporal disturbance pattern affects patch network and metapopulation persistence in heterogeneous landscapes. We simulate metapopulation dynamics using a realistic landscape and varying patch destruction (and turnover) rates. We model the local patch emergence rate as the product of site suitability to patch emergence—here, a permanent or longer-term characteristic of the site due to e.g. biogeographical factors—and local contemporary disturbance intensity. First, we estimate disturbance intensity from empirical data, assuming it is the cause of unexplained spatial variation in patch locations apart from biogeographical and longer-term land use factors. In our study system, this assumption is based on the well-known characteristics of false heath fritillary habitats, yet the absence of these sites at many sub-regions with suitable climates

and soils. After the initial estimation from empirical data, we subsequently model the disturbance pattern using spatial random fields that change form annually with varying degrees of mobility. Utilizing the fitted spatial pattern allows us to model location changes in disturbances, while maintaining the spatial scale of the disturbance pattern, which is often typical to the type of disturbance modelled (e.g. Johst et al., 2001; Siriwardena 2010).

We test our model using data on the false heath fritillary butterfly *Melitaea diamina* (Lang, 1789) in Finland, where the species is dependent on highly dynamic (Fabritius and McBride, 2017) *Valeriana sambucifolia* meadows on moist and calcareous soils (Wahlberg 1997). Our study aimed at answering the following questions: (Q1) Do false heath fritillary habitat patches occur at sites with distinguishable characteristics, e.g. certain soil and land use types? (Q2) How does increasing mobility of the disturbance pattern affect metapopulation persistence, especially in relation to increasing patch turnover rate? Our results demonstrate that a mobile disturbance pattern may affect the persistence of an early-succession habitat specialist in multiple ways.

2. Material & methods

2.1. Study area and survey data

The false heath fritillary habitat patch network in the West Coast of Finland (62.25°N 21.5°E, 3200 km², Fig. 1 top left) consists of 459 identified habitat patches, with mean patch area of 1.55 ha (range 0.03–9.46 ha). In 2000–2007, the regional environmental authorities recorded 70 patches (location, area and false heath fritillary sightings), and the rest were recorded in 2009–2011 during a false heath fritillary distribution survey conducted for the purpose of this study. Each year of the survey, some of the previously identified patches were revisited to

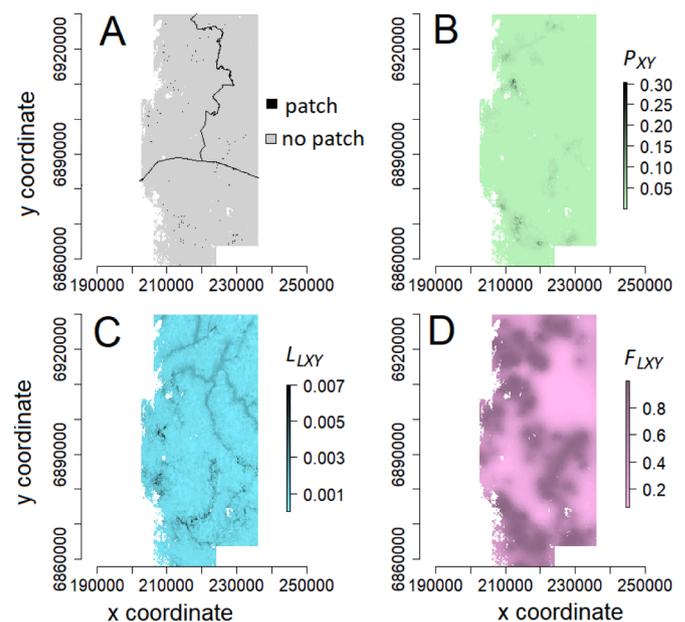


Fig. 1. Empirical data and a predictive model of false heath fritillary habitat patch locations. Locations of false heath fritillary habitat patches in empirical data (panel A) and as predicted by the selected patch location model (P_{XY} , panel B; see section “Patch location and area models”). The prediction of the patch location model for a location (x, y) consists of a linear prediction component (L_{LXY} , panel C), which indicates site suitability to habitat patch emergence due to permanent or longer-term characteristics, and a spatial random field (F_{LXY} , panel D), which indicates local disturbance intensity. The spatial random field, presented here as estimated from empirical data, was simulated in this study to change its form with varying degrees of annual mobility, to simulate changing local patch emergence rates. Territorial borders of administrative regions shown with black lines (top left).

reassess their occupancy (> 0 sightings at occupied patches). The data thus consist of presences or absences for the surveyed populations, but includes missing observations each year. For details of the surveys, see supplement (Appendix 1).

2.2. A stochastic patch occupancy model in a dynamic patch network

We created a continuous-time stochastic patch occupancy model (Ovaskainen and Hanski 2001; for discrete-time SPOMs, see Moilanen 1999, 2004 and references therein) that incorporates the extinction-colonisation dynamics of a false heath fritillary meta-population (events 1–2, Fig. 2) and the emergence-destruction (patch turnover) dynamics of its patch network events 3–4, Fig. 2). At any given time, the simulated patch network consists of a gridded study landscape and a discrete set of patches i characterized by their centroid coordinates (x_i and y_i), patch area (A_i) and occupancy status ($O_i = 1$ for occupied and $O_i = 0$ for empty patches). The dynamics of the model consist of four kinds of events: (1) colonization of unoccupied patches by the butterfly, (2) extinction of occupied patches, (3) destruction of existing patches (implying extinction of the butterfly population if occupied at the time of the destruction) and (4) emergence of new patches (initially not occupied by the butterfly; Fig. 2).

We model the colonization rate of patch i by the butterfly meta-population as a sum of contributions from the occupied patches j ,

$$c_i = C \sum_{j \neq i}^n \left(e^{-\alpha d_{ij}} A_i^{\zeta_{im}} A_j^{\zeta_{em}} \right) O_j, \tag{1}$$

where C is an overall colonization rate parameter, d_{ij} is the distance between patches i and j , the parameter α measures the spatial scale of connectivity (as in Harrison et al., 2011), and the parameters ζ_{im} and ζ_{em} model how patch area influences the processes of immigration and

emigration, respectively (Ovaskainen and Hanski 2001, 2003). We model the extinction rate of a patch i occupied by the butterfly by

$$e_i = E/A_i^{\zeta_{ex}}, \tag{2}$$

where E is an overall extinction rate parameter and ζ_{ex} models how extinction risk depends on patch area (Ovaskainen and Hanski 2001 and references therein). Existing patches were assumed to be destroyed at rate

$$\delta_i = \varepsilon \tag{3}$$

that was assumed to be the same for all patches. We modelled the emergence rate of a patch centroid at a grid cell location (x,y) that does not already contain a patch centroid by

$$\beta_{xy} = \frac{\varepsilon P_{xy}/z}{1 - P_{xy}/z}, \tag{4}$$

where P_{xy} is the probability, predicted by a patch location model, that the grid cell (x,y) is overlaid by a patch, and z is the ratio of the expected size of a patch to the grid cell (see section ‘‘Patch location and area models’’ and Appendix 2 for details). Since in this model β_{xy} increases with increasing ε , parameter ε in practice modelled not only the patch destruction rate, but also the patch turnover rate (the percentage of patches in the system that are replaced by new ones within a given time). Area of a new patch was randomized from a patch area model (see section ‘‘Patch location and area models’’ below for details), including random residual variance. In case the new created patch would overlap with another patch (based on their radii $r = \sqrt{A/\pi}$, assuming patches to be circular), patch location and size were randomized again until the patch did not overlap with others. All patches that emerged during the

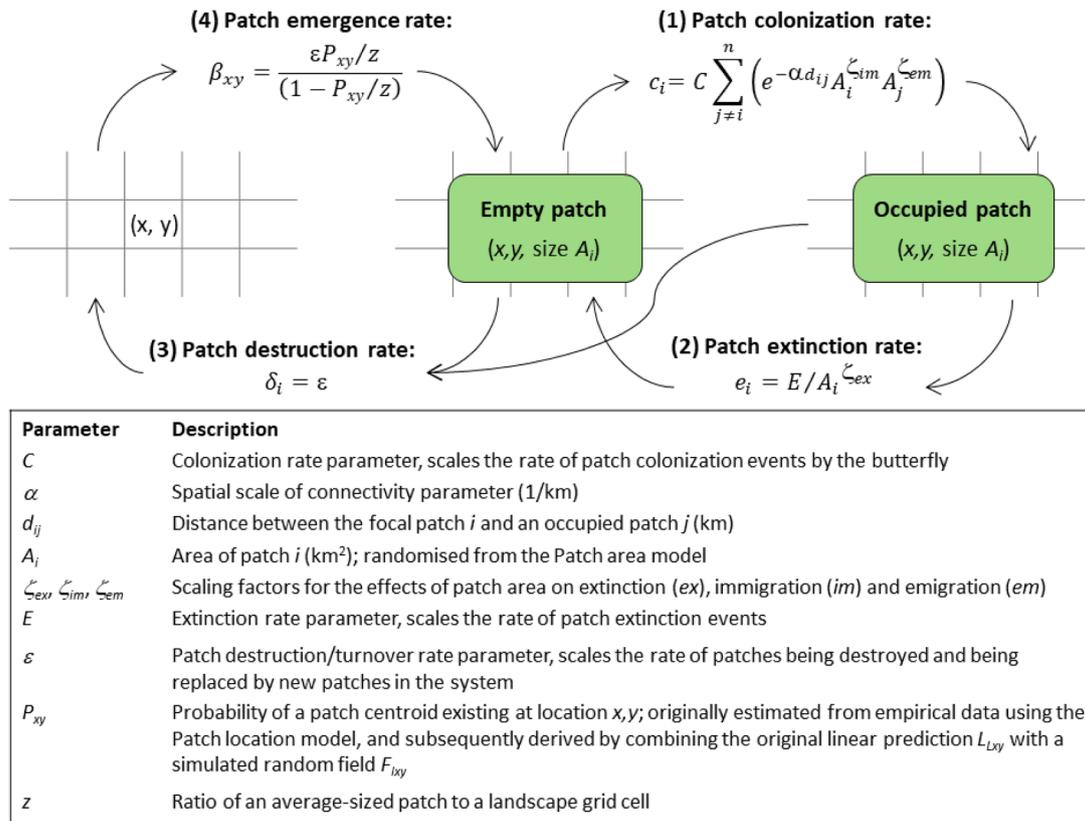


Fig. 2. States, events and event rates of the Stochastic Patch Occupancy Model in a dynamic patch network. The three basic states of the model developed in this study; the empty landscape grid cell (x,y) without a patch centroid (grey grid) and the landscape grid cell with empty and occupied patches (green boxes). Events that cause state transitions (black arrows and corresponding events) are shown together with event rate equations.

simulation were originally unoccupied.

We simulated the continuous-time Markov process with the Gillespie (1977) algorithm, sampling the time until the next event from the exponential distribution with parameter set to the total rate $\sum_{i=1}^n c_i + \sum_{i=1}^n e_i + \sum_{i=1}^n \delta_i + \sum_{xy=1}^m \beta_{xy}$, and then randomizing which event takes place based on the relative rates of the possible individual events.

2.3. Patch location and area models

We modelled the locations and areas of false heath fritillary habitat patches (*patches*) in the study region as a function of soil and land use type suitability to patch emergence (*soil*, suitability categories 1–3 presented in Table 1), distance to fields (*dfield*, in metres), distance to rivers (*driver*, in metres) and Topographic Wetness Index (TWI; Wilson and Gallant 2000, Wilson 2012, *twi*). TWI is a measure of drainage in a landscape and can be used to identify dips and hollows that retain water for longer periods, exclusive of permanent water bodies like lakes and swamps (Wilson 2012; Wilson and Gallant 2000). For technical details on the preparation of the covariate layers, see supplement [Appendix 3]. We transformed variables as needed to account for skewed distributions, then normalized the continuous variables to zero mean and unit variance.

We modelled the locations of patches (Patch location model) by fitting a logistic regression model that had patch existence at a grid cell (*patches*, $n \approx 26\ 000\ 000$) as the response variable and *soil*, *dfield*, *driver*

Table 1
Suitability classifications of the land use types in the CORINE Land use Classification 2000 data set to false heath fritillary habitat patch emergence. 37 land use types of the CORINE Land Cover 2000 25 m x 25 m raster data (Finnish Environment Institute) prevalent in the study region classified into three classes with regard to their suitability for the occurrence or emergence of false heath fritillary habitat patches. Sites were classified based on previous knowledge on the characteristics of false heath fritillary habitat patches (e.g. Wahlberg 1997).

Suitability class	1 (unsuitable: acidic, late-succession, underwater, lacking soil)	2 (areas under intensive land use)	3 (potential areas)
Soil and land use types	Deciduous forests on peat soil Coniferous forests on peat soil Coniferous forests on rocky soil Mixed forests on peat soil Mixed forests on rocky soil Sparse forests, cc 10–30%, on peat soil Sparse forests, cc 10–30%, on rocky soil Shoreline sands and dunes Rocks Inland wetlands underwater Mires Peat extraction areas Marine wetlands underwater Lakes Sea	Densely built residential areas Industry and service regions Traffic regions Harbours Deciduous forests on mineral soils Coniferous forests on mineral soils Mixed forests on mineral soils	Sparsely built residential areas Soil extraction areas Landfills Summer cottages Sports and recreational areas Fields Disused agricultural lands Orchards Pastures Sparse forests, cc < 10% Sparse forests, cc < 10%, on mineral soils Sparse forests on disused agricultural lands Inland wetlands above water Marine wetlands above water Rivers

and *twi* at the respective grid cell as covariates. Since our patch network data were based on a landscape-level survey of aerial photographs before conducting visits to potential sites, we treated the patch network pattern as presence-absence data for modelling patch locations. We modelled the sizes of patches (Patch area model) by fitting a linear model that had log-transformed patch area as the response variable and the average values of *soil*, *dfield*, *driver* and *twi* of the grid cells overlaid by the patch as covariates. We considered the average of *soil* values of grid cells overlaid by a patch as a reasonable proxy for patch quality, even though this measure may contain slight bias due the soil suitability classes not being commensurate. We randomized one grid cell out of each patch and so many grid cells outside of patches that the proportion of meadow versus non-meadow cells in the sample equalled to the corresponding proportion in the *patches* grid layer. We fitted both non-spatial and spatial model versions for both models. The spatial models included a Gaussian Markov random field based on a Matérn covariance function (Matérn 1960; Lindgren et al., 2011) to account for a possible spatial autocorrelation in the model residuals (Dormann et al., 2007). For details on model selection and evaluation, see supplement [Appendix 3].

We interpolated and rasterized the linear predictions L_{Lxy} and L_{Axy} and the Gaussian Markov random fields F_{Lxy} and F_{Axy} of the selected patch location and area models (Fig. 1). Subscripts L_{xy} and A_{xy} refer to the values of the patch location (L) and area (A) models for the location (x, y), respectively. We scaled the random fields F_{Lxy} to zero mean by including the empirical mean $\overline{F_{Lxy}}$ to the linear predictor, and predicted the probabilities of patch occurrence as $P_{xy} = \text{logit}^{-1}(\text{logit}(L_{Lxy}) + \text{logit}(F_{Lxy}))$. Similarly, we defined the predicted size of an emerging patch as $A_{xy} = e^{\text{log}(L_{Axy} + F_{Axy}) + u}$. u stands for the residual variation for each emerging patch and follows the distribution $u \sim N(0, \sigma^2)$, where σ^2 stands for the estimated nugget variance of the patch area model. For details on the interpolation and rasterization of predictions, see supplement [Appendix 3]. For computational reasons, we aggregated the prediction rasters of these models to 200 m x 200 m resolution when applying them as part of the patch occupancy models.

2.4. Parameterisation of the stochastic patch occupancy model

We estimated the overall colonization (C) and extinction (E) rate parameters of the false heath fritillary from the 2009–2012 survey data (Appendix 1) by using an Approximate Bayesian Computation (ABC; Beaumont 2010, Csilléry et al., 2010) approach and a simple rejection algorithm modified from Rubin (1984). As summary statistics in the ABC we used the fraction of occupied patches from the pooled data for all of the years 2009–2012, the fraction of cases in which a patch observed occupied was still observed occupied after 1, 2 or 3 years, and the fraction of cases in which a patch observed empty was still observed empty after 1 or 2 years. We assumed uniform priors for both E and C in the range (0,1) based on initial exploration. We sampled 10 000 candidate values from the prior, simulated metapopulation dynamics using the candidate values and approximated the posterior by the top 1% of the values in terms of their match to the real data with respect to the summaries. In the scenario simulations, we set the parameters E and C to their posterior mean values. For details of the ABC approach, see supplement [Appendix 3]. We set the spatial scale of connectivity $\alpha = 0.7$ (km^{-1}) based on previous studies on the false heath fritillary (Moilanen 1999; Moilanen and Cabeza 2002; Ovaskainen 2008), and the effects of patch area to the extinction $\zeta_{ex} = 0.17$, immigration $\zeta_{im} = 0.30$ and emigration $\zeta_{em} = 0.07$ based on analyses on a closely related species *Glanville fritillary* butterfly (Ovaskainen and Hanski 2004).

2.5. Model analysis

We used the parameterized metapopulation model to examine how an increasing degree of mobility of the disturbance pattern (disturbance

mobility), φ , influences the dynamics of the butterfly metapopulations under increasing patch turnover rates, ε .

We modelled a mobile disturbance pattern letting the random fields F_{Lxy} and F_{Axy} change annually, leading to spatially autocorrelated random annual changes in β_{xy} and $E(A_{xy})$ at each location. This was done by generating Matérn random fields using the *inla.qsample* function in INLA (Rue et al., 2009, 2013; Blangiardo et al., 2013) that had the statistical properties of the random fields of the path location and area models, but that differed each year from the random fields of the previous year. We used the AR(1) process $\omega_t = \varphi\omega_{t-1} + \eta$, where φ depicts the proportion of stability of spatial random fields between two consecutive years, ω_t represents the random field in year t and η represents another random field that was chosen so that the stationary state of the process was the Matérn covariance function with the estimated variance and spatial scale parameters. Thus, decreasing the value of the parameter φ would result in a higher degree of mobility of the disturbance pattern when simulating the system. We varied the parameter of mobility of the disturbance pattern as $\in [1, 0.98, 0.94, 0.61]$, so that the disturbance pattern was either stationary ($\varphi = 1$) or the characteristic decay time of the disturbance pattern $1/\log(\varphi)$ (the time after which the impact of the spatial pattern to future patterns has decreased to $1/e$) equalled 50, 16 or 2 years, respectively. The parameter $\theta_{1\eta}$, the log-transformed local variance parameter of the simulated Matérn random fields η in the INLA implementation, was set to

$$\theta_{1\eta} = \theta_{1\omega} - \log(1 - \varphi^2)/2 \tag{9}$$

based on the respective local variance parameter of the random fields of the original Matérn random fields, $\theta_{1\omega}$. We did not modify the spatial scale parameter θ_2 of the generated random fields. We scaled all resulting fields ω_t to the same variance as the original field ω .

We simulated (Fabritius, 2021) all models with the patch destruction parameter varied as $\varepsilon \in [0.015, 0.03, \dots, 0.15]$, which range includes the estimated annual habitat destruction rate of false heath fritillary habitat patches estimated from field data (0.076 (95% CI 0.058–0.10); Fabritius & McBride 2017). For details of the metapopulation simulations, see supplement [Appendix 3].

3. Results

3.1. Locations and sizes of false heath fritillary habitats with respect to site characteristics

The locations and sizes of false heath fritillary habitat patches depended on site-related covariates. Wet, calcareous soils near rivers, away from cultivated fields, had the highest probabilities for patch occurrence (Table 2). As there was spatial autocorrelation in the patch

Table 2
The effect of environmental covariates on the probability of occurrence of a false heath fritillary habitat patch. The table depicts the environmental covariates, their coefficient estimates, standard error and 0.025, 0.5 and 0.975 quantiles of the best-fitting logistic regression model that had a bivariate raster layer of habitat patch locations as a response variable. θ_1 and θ_2 refer to the parameters of variance and spatial scale of the random fields in the INLA notation, respectively.

	Estimate	Std. error	0.025 quant.	0.5 quant.	0.975 quant.
(Intercept)	-10.0407	0.5298	-11.1492	-10.0165	-9.0655
soil class 2	1.8081	0.373	1.1273	1.7889	2.5939
soil class 3	3.3966	0.368	2.727	3.377	4.1739
sqrt(dfield)	0.3693	0.1381	0.0979	0.3692	0.6406
sqrt (driver)	-0.5302	0.1081	-0.7436	-0.5298	-0.3189
log(twi)	0.4621	0.0496	0.3645	0.4622	0.5592
θ_1	-7.8991	0.148	-8.1915	-7.8983	-7.6104
θ_2	5.979	0.1829	5.6204	5.9785	6.3395

network configuration, a model with a spatial term (marginal likelihood -2176.10) predicted patch occurrences better than a non-spatial model (marginal likelihood -2451.21). The predictions given by the resulting model of patch occurrences correlated well with realized occurrences, while slightly underestimating patch proportions at high predicted probabilities of occurrence (Appendix 4, Figure S1). Largest patches occurred at intermediate moisture and where soil and land use type suitability was high (Table 3).

Extinction and colonization rate estimates for the false heath fritillary had wide credible ranges, but the majority of accepted values were more concentrated around the posterior means, and the posterior means of both parameters fit well within the centre of the joint parameter distribution ($E = 0.154$, 95% Cr.I.: 0.0519–0.271 and $C = 0.749$, 95% Cr.I.: 0.225–0.979; Appendix 4, Figure S2).

3.2. Effects of a mobile disturbance pattern on metapopulation persistence

A mobile disturbance pattern impaired metapopulation persistence in our study system. Patch occupancies decreased, and metapopulations were more likely to go extinct with slower patch turnover rates, when the mobility of the disturbance pattern increased (Fig. 3). Metapopulation persistence was impaired despite the fact that the characteristics of the patch network – median number of patches and the median distance to the nearest neighbour patch (Appendix 4, Figure S3–S4)–decreased only marginally or remained essentially the same in all simulations.

A mobile disturbance pattern ($\varphi < 1$) impaired metapopulation persistence via mechanisms that were different from those of an increased habitat turnover rate. Fast habitat turnover rates increased the proportion of deterministic patch extinctions (Appendix 4, Figure S5) and thus decreased the average lifetimes of local populations (Appendix 4, Figure S6). As a result, more and more patch emergences were required to increase patch colonization rates (Appendix 4, Figure S7). A mobile disturbance pattern caused new emerging patches to appear further away from (i.e. within poorer connectivity to) occupied patches (Appendix 4, Figure S8). This decreased the probability of the new patches becoming colonized (Appendix 4, Figure S9). As a result, metapopulation persistence became more and more dependant on old, large patches, which could maintain local populations from the beginning of the simulation (Appendix 4, Figure S10).

3.3. The degree of mobility of the disturbance pattern and metapopulation persistence

Disturbances that had a moderate degree of mobility, i.e. that changed place at a moderate speed, had the most uncertain effects to habitat availability and metapopulation persistence. The number (Appendix 4, Figure S3), median distance (Appendix, Figure S4) and con-

Table 3
The effect of environmental covariates on false heath fritillary habitat patch size. The table depicts the environmental covariates, their coefficient estimates, standard error and 0.025, 0.5 and 0.975 quantiles of the best-fitting linear regression model that has the log-transformed size of a patch as a response variable. Precision refers to the estimated variance of random effects in the response variable. θ_1 and θ_2 refer to the parameters of variance and spatial scale of the random fields in the INLA notation, respectively. The estimated nugget variance of the patch area model $\sigma^2 = 0.61821$.

	Estimate	Std. error	0.025 quant.	0.5 quant.	0.975 quant.
(Intercept)	9.3931	0.0828	9.2321	9.3923	9.5587
soil	0.1375	0.0479	0.0433	0.1375	0.2315
log(twi)	0.0688	0.0523	-0.0341	0.0689	0.1712
log(twi) ²	-0.1332	0.0319	-0.1959	-0.1332	-0.0706
Precision	1.403	1.176	1.400	1.651	1.395
θ_1	-7.828	-9.067	-7.835	-6.559	-7.856
θ_2	7.087	6.198	7.092	7.955	7.105

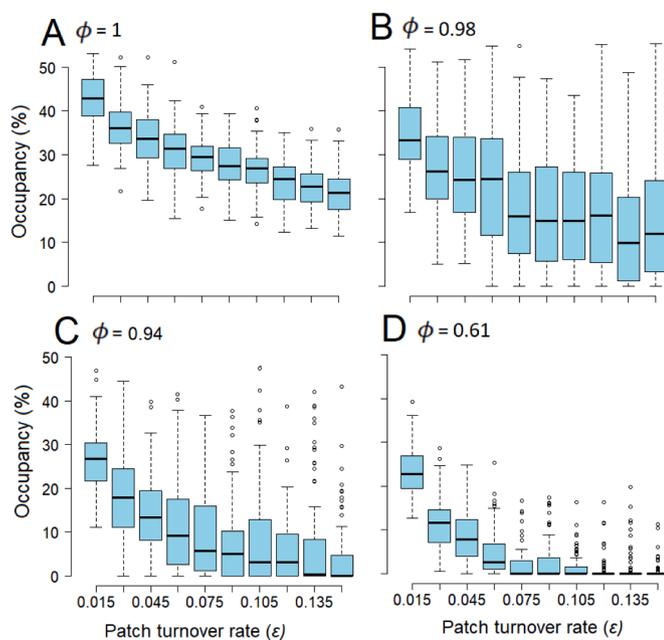


Fig. 3. The effect of habitat turnover rate and mobility of the disturbance pattern on false heath fritillary patch occupancy. Patch occupancy at the end of the 50-year simulation is shown as a function of habitat turnover rate (ϵ ; x-axes) and mobility of the disturbance pattern (ϕ ; panels A-D).

nectivity (Appendix 4, Figure S8) of patches at the end of the simulations varied the most when the mobility of the disturbance pattern equalled characteristic decay times of 16 and 50 years ($\phi = 0.94$ and $\phi = 0.98$, respectively). Patch occupancy varied the most with the characteristic decay time of 50 years ($\phi = 0.98$; Fig. 3), as metapopulations started going extinct if the decay time was shorter than this.

The uncertain effects of the moderately mobile disturbance pattern were caused by the fact that slowly moving disturbances had the largest effect to the patch network in the time scale of the simulations. If disturbances moved to take place at areas of high site suitability to patch emergence (in terms of site-specific covariates), high numbers of new patches emerged especially with high patch turnover rates (Appendix 4, Figure S11), and high numbers of patch emergences increased patch colonizations (Appendix 4, Figure S7). However, the more mobility of the disturbance pattern increased (corresponding to lower values of ϕ), the more likely it became that the overall changes to mean probability to patch emergence started to even out after multiple changes (Appendix 4, Figure S12). Also, since high disturbance mobility reduced the probability of new patches becoming colonized, less colonizations resulted from disturbances occurring at high local site suitability to patch emergence (Appendix 4, Figure S13). Therefore, whether disturbances moved to sites of poor or high suitability patch emergence could greatly affect patch occupancy, but only if disturbance mobility was slow.

4. Discussion

Our case study confirms past findings that metapopulation persistence in dynamic landscapes is maintained best if—apart from increasing the area, quality or lifetime of existing patches (Nicol and Possingham 2010; Marcot et al., 2012; Resetarits and Binckley 2013)—new, emerging patches appear close to occupied patches where they have a high likelihood of becoming colonized (Templeton et al., 2011; Southwell 2016; Southwell et al., 2016). Our modelling approach shows that the prerequisite of such a pattern is a stationary disturbance pattern, or a disturbance pattern with high temporal autocorrelation: if disturbances occur repeatedly at specific regions, local patch networks are likely to remain well-connected even after multiple consecutive patch

destructions and emergences. Along these lines, our simulated false heath fritillary population was able to persist through the simulations with a patch turnover rate that matched the patch destruction rate estimated from empirical data ($\epsilon = 0.075$; (Fabritius and McBride, 2017)) when the disturbance pattern was stationary, but not when it was very mobile ($\phi = 0.61$).

Our case study also suggested that in certain circumstances, it might also be a viable option to gradually direct disturbances (of anthropogenic origin) to take place at areas that would be even more suitable to patch emergence. This was supported by the fact that in our simulations, there was a strong connection between high landscape-level mean probabilities of patch emergence and high patch emergence and colonization rates when the degree of mobility in the disturbance pattern was moderate. With regard to conservation of early-succession habitat specialists, such a management alternative might be attractive e.g. if potential nearby locations were more easily manageable via agri-environment schemes, or if maintenance activities at the nearby location were likely to result in higher-quality habitat. Such an approach, however, may also have drawbacks, as e.g. past studies on climate change-induced range shifts on metapopulations suggest that populations may be either too slow to track the changing habitat networks, or lose genetic diversity while doing so (Cobben et al., 2011; Schippers et al., 2011; Mestre et al., 2017). Often, the optimal solution is heavily dependant on the population dynamics of the species being studied.

Third, our case study also contributes to the discussion on what features of a dynamic patch network may predict, and may thus help to monitor, metapopulation persistence. In our simulations, the number of and median distance between patches did not predict the patch network's capacity to sustain a metapopulation, as sites of high suitability to patch emergence were determined by hydrological patterns and narrow stripes of calcareous soils across the study landscape. Consequently, new patches aggregated in stripe-like areas and maintained nearly unchanging median distance between patches, while occupied patch sub-networks were driven away from each other and metapopulation persistence was impaired. Therefore, with regard to dynamic patch systems, conservation managers might benefit more from monitoring the connectivity of emerging patches to occupied ones than from assessing the structure of the patch network from snapshot data. Moreover, our study shows that conservation managers may want to watch for possible changes in disturbance-generating factors that operate on moderate time scales, e.g. generational shifts in land ownership or rural desertification, since these may lead into cessation of longer-term stationary disturbance patterns that have maintained habitat networks.

More profoundly, the approach we have introduced for modelling patch networks in dynamic landscapes distinguishes two processes behind the pattern and rates of patch emergence: the disturbance pattern and its coincidence with site suitability to patch emergence. Modelling disturbance intensities by using spatial random fields suits modelling disturbances over larger regions, where modelling of exact annual management schemes by property borders or management units is not needed (as e.g. in Wätzold et al., 2008, Hodgson et al., 2009), but the focus is rather in modelling regional variations and changes in mean disturbance frequencies or mean annual probabilities of local disturbance. These modelling choices enable the use of various kinds of social and environmental data for forecasting habitat availability for early-succession habitat specialists under alternative scenarios.

Data sets on anticipated changes in land ownership, density of active farmers, forestry practices, demands for agricultural products (Bryngelsson et al., 2016), or regional administrative differences in agri-environmental incentives (Kleijn and Sutherland 2003) may offer new avenues for forecasting regional disturbance intensities. Other potential data include those of anticipated changes in climatic factors that operate on regional scales, e.g. variations in the frequency of floods and windstorms (e.g. Wade et al., 2015), which are often used e.g. in studies of forest succession simulations (e.g. Scheller et al., 2007). Our model can be developed further to simulate either more deterministic,

directional shifts of disturbances, or gradual deterministic changes in disturbance intensities for these purposes. Our modelling approach could also be used to include gradual deterministic changes in the permanent site suitability factors while maintaining the current disturbance pattern. This could be used for instance to model the effects of climate change to dynamic habitat patch networks (Radchuk et al., 2013).

Utilization of our model also calls for consideration of how to reliably determine which proportion of spatial variation in patch locations is caused by factors other than disturbance intensity. In this study, we assumed that all unexplained spatial variation in patch locations was caused by regional differences in disturbance intensity. In future studies, the distinction of these factors should be developed further. In the case of habitat specialist species, modelling of the distributions of the target species and their key habitat resources, such as host plants, (Wisz et al., 2013, Pollock et al., 2014) may improve habitat suitability models. Moreover, site suitability and disturbance intensity could be modelled jointly (Iverson et al., 2011; Maire et al., 2012). Disturbance data could be acquired by recording not only the locations of currently suitable habitats, but also of the locations of overgrown, otherwise potential habitat sites during the field monitoring phase (Fabritius and McBride, 2017). Additionally, spatial data on current disturbance frequencies could be included in the joint modelling.

In conclusion, separating disturbance dynamics from site suitability for habitat emergence is an important object in the modelling of habitat availability and metapopulation dynamics for early-successional habitat specialists. Our study presents a method for the incorporation of wider-range variations in disturbance dynamics into these models, and can be developed further to accommodate social and environmental data for forecasting and scenario analysis.

Funding

This work was supported by the Academy of Finland [grant numbers 129,636 and 250,444], Emil Aaltonen Foundation, Societas Pro-Fauna et Flora Fennica and the South Ostrobothnia and Southwest Finland Centres for Economic Development, Transport and the Environment. OO was supported by the Academy of Finland (grants 284,601 and 309,581), Jane and Aatos Erkko Foundation, and the Research Council of Norway through its Centres of Excellence Funding Scheme (223,257) via Centre for Biodiversity Dynamics. Centres for Economic Development, Transport and the Environment participated in the design of data collection. No funding sources participated in the design of the data analysis.

Author contributions

HF coordinated the fieldwork, co-designed the study, created the dynamic SPOM simulations, fitted the patch location and area models, carried out result analyses and wrote the manuscript. HK estimated the Topographic Wetness Index for the study area landscape and wrote initial code used for raster creation and processing. OO defined the function for estimating the patch emergence rate from the patch occurrence probability, co-wrote the manuscript and supervised the study.

Appendices

Appendix 1: Patch network & visits to patches

An Excel file containing the survey data of the 2009–2012 false heath fritillary patch visits used in this study. Administrative regions OS & SA refer to the administrative regions of South Ostrobothnia and Satakunta, respectively. The coordinates are shown as per their deviance from mean value.

Appendix 2: Definition of the habitat patch emergence rate

A Word file.

Appendix 3: Technical details of the analyses and spatial covariate

layers

A Word file.

Appendix 4: Additional simulation results graphs

A Word file.

CRedit authorship contribution statement

Henna Fabritius: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. **Henrik de Knecht:** Conceptualization, Data curation, Methodology, Software, Writing – review & editing. **Otto Ovaskainen:** Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: HF carried out a conservation consultancy project for the Centre of Economic Development, Transport and the Environment (ELY centre) of South Ostrobothnia, Finland, in 2013.

Acknowledgements

We thank the regional environmental centres of South Ostrobothnia and Satakunta for false heath fritillary data and land tenure records, Tuomas Kankaanpää, Kalle Meller, Kaisa Torppa, Hanna Parri and Ninni Mikkonen for fieldwork in the false heath fritillary distribution survey and Jussi Jousimo for help with the INLA models.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.ecolmodel.2021.109738](https://doi.org/10.1016/j.ecolmodel.2021.109738).

References

- Avron, S., Burel, F., Baudry, J., Schermann, N., 2005. Carabid assemblages in agricultural landscapes: impacts of habitat features, landscape context at different spatial scales and farming intensity. *Agric. Ecosyst. Environ.* 108, 205–217.
- Ballinger, A., Lake, P.S., Nally, R.M., 2007. Do terrestrial invertebrates experience floodplains as landscape mosaics? Immediate and longer-term effects of flooding on ant assemblages in a floodplain forest. *Oecologia* 152, 227–238.
- Batáry, P., Dicks, L.V., Kleijn, D., Sutherland, W.J., 2015. The role of agri-environment schemes in conservation and environmental management. *Conserv. Biol.* 29, 1006–1016.
- Beaumont, M., 2010. Approximate bayesian computation in evolution and ecology. *Annu. Rev. Ecol. Syst.* 41, 379–406.
- Blangiardo, M., Cameletti, M., Baio, G., Rue, H., 2013. Spatial and spatio-temporal models with R-INLA. *Spat. Spatiotemporal Epidemiol.* 7, 39–55.
- Boughton, D., Malvadkar, U., 2002. Extinction risk in successional landscapes subject to catastrophic disturbances. *Conservation Ecology* 6, 1195–5449.
- Bryngelsson, D., Wirsén, S., Hedenus, F., Sonesson, U., 2016. How can the EU climate targets be met? A combined analysis of technological and demand-side changes in food and agriculture. *Food Policy* 59, 152–164.
- Chytrý, M., Tichý, L., Roleček, J., 2003. Local and regional patterns of species richness in central European vegetation types along the pH/calcium gradient. *Folia Geobot.* 38, 429–442.
- Cobben, M.M.P., Verboom, J., Opdam, P.F.M., Hoekstra, R.F., Jochem, R., Arens, P., Smulders, M.J.M., 2011. Projected climate change causes loss and redistribution of genetic diversity in a model metapopulation of a medium-good disperser. *Ecography* 34, 920–932.
- Cousins, S.A.O., Eriksson, O., 2008. After the hotspots are gone: land use history and grassland plant species diversity in a strongly transformed agricultural landscape. *Appl. Veg. Sci.* 11, 365–374.
- Csilléry, K., Blum, M.G.B., Gaggiotti, O.E., François, O., 2010. Approximate bayesian computation (ABC) in practice. *Trends Ecol. Evol. (Amst.)* 25, 410–418.

- De Roissart, A., Wang, S., Bonte, D., 2015. Spatial and spatiotemporal variation in metapopulation structure affects population dynamics in a passively dispersing arthropod. *J. Anim. Ecol.* 84, 1565–1574.
- Dormann, F., McPherson, C.M., Araújo, J.B., Bivand, M., Bolliger, R., Carl, J., Wilson, R., 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* 30, 609–628.
- Drechsler, M., Johst, K., 2010. Rapid viability analysis for metapopulations in dynamic habitat networks. *Proceedings. Proceedings of The Royal Society, Biological Sciences*, 277, 1889–1897.
- Drechsler, M., Watzold, F., Johst, K., Bergmann, H., Settele, J., 2007. A model-based approach for designing cost-effective compensation payments for conservation of endangered species in real landscapes. *Biol. Conserv.* 140, 174–186.
- Duesberg, S., Bogue, P., Renwick, A., 2017. Retirement farming or sustainable growth – land transfer choices for farmers without a successor. *Land use policy* 61, 526–535.
- Fabritius, H., 2021. *Simulation code from Fabritius et al.: Effects of a mobile disturbance pattern on dynamic patch networks and metapopulation persistence v1.0*. Zenodo. <https://doi.org/10.5281/zenodo.5510726>.
- Fabritius, H., McBride, M., 2017. Modelling habitat persistence and impacts of management on the habitats of an endangered butterfly. *Insect Conservation and Diversity* 10 (3), 200–210.
- Franklin, J., 2013. Moving beyond static species distribution models in support of conservation biogeography. *Divers. Distrib.* 19, 1217–1223.
- Gillespie, D.T., 1977. Exact stochastic simulation of coupled chemical reactions. *J. Phys. Chem.* 81, 2340–2361.
- Harper, G., 2007. Strategies for Managing Early Succession Habitat for Wildlife. *Weed Technology* 21 (4), 932–937.
- Harrison, P.J., Hanski, I., Ovaskainen, O., 2011. Bayesian state-space modeling of metapopulation dynamics in the Glanville fritillary butterfly. *Ecol. Monogr.* 81, 581–598.
- Greenberg, C., Collins, B., Thompson III, F., McNab, W.H., 2011. Introduction: What Are Early Successional Habitats, Why Are They Important, and How Can They Be Sustained? Sustaining Young Forest Communities. In: Greenberg, C., Collins, B., Thompson III, F. (Eds.), *In: Managing Forest Ecosystems*, 21. Springer, Dordrecht.
- Hanski, I., 1998. Metapopulation dynamics. *Nature* 396, 41–49.
- Hastings, A., 2003. Metapopulation persistence with age-dependent disturbance or succession. *Science* 301, 1525–1526.
- Hodgson, J.A., Moilanen, A., Bourn, N.A.D., Bulman, C.R., Thomas, C.D., 2009. Managing successional species: modelling the dependence of heath fritillary populations on the spatial distribution of woodland management. *Biol. Conserv.* 142, 2743–2751.
- Ingram, J., Gaskell, P., Mills, J., Short, C., 2013. Incorporating agri-environment schemes into farm development pathways: a temporal analysis of farmer motivations. *Land use policy* 31, 267–279.
- Iverson, L.R., Prasad, A.M., Matthews, S.N., Peters, M.P., 2011. Lessons learned while integrating habitat, dispersal, disturbance, and life-history traits into species habitat models under climate change. *Ecosystems* 14, 1005–1020.
- Johst, K., Brandl, R., Pfeifer, R., 2001. Foraging in a patchy and dynamic landscape: human land use and the white stork. *Ecol. Appl.* 11, 60–69.
- Johst, K., Brandl, R., Eber, S., 2002. Metapopulation persistence in dynamic landscapes: the role of dispersal distance. *Oikos* 98, 263–270.
- Johst, K., Drechsler, M., van Teeffelen, A.J., Hartig, F., Vos, C.C., Wissel, S., Wätzold, F., Opdam, P., 2011. Biodiversity conservation in dynamic landscapes: trade-offs between number, connectivity and turnover of habitat patches. *J. Appl. Ecol.* 48, 1227–1235.
- Kleijn, D., Sutherland, W.J., 2003. How effective are European agri-environment schemes in conserving and promoting biodiversity? *J. Appl. Ecol.* 40, 947–969.
- Larson, M., Thompson III, F., Mills, S., Dijk, W., Shifley, S., 2004. Linking population viability, habitat suitability, and landscape simulation models for conservation planning. *Ecol. Modell.* 180, 103–118.
- Latif, Q., Saab, V.A., Dudley, J.G., Hollenbeck, J.P., 2013. Ensemble modeling to predict habitat suitability for a large-scale disturbance specialist. *Ecol. Evol.* 3, 4348–4364.
- Lindgren, F., Rue, H., Lindstrom, J., 2011. An explicit link between gaussian fields and gaussian markov random fields: the SPDE approach (with discussion). *J. R. Stat. Soc. Series B* 73, 423–498.
- Maire, V., Gross, N., Börger, L., Proulx, R., Wirth, C., da Silveira Pontes, L., Soussana, J.-F., Louault, F., 2012. Habitat filtering and niche differentiation jointly explain species relative abundance within grassland communities along fertility and disturbance gradients. *New Phytol.* 196, 497–509.
- Marcot, B.G., Raphael, M.G., Schumaker, N.H., Galleher, B., 2012. How big and how close? habitat patch size and spacing to conserve a threatened species. *Nat. Resour. Model.* 26, 194–214.
- Matérn, B., 1960. Spatial variation. *Meddelanden fran Statens Skogsforskningsinstitut* 49. No. 5. Almaenna Foerlaget, Stockholm, p. 144.
- Mestre, F., Risk, B.B., Mira, A., Beja, P., Pita, R., 2017. A metapopulation approach to predict species range shifts under different climate change and landscape connectivity. *Ecol. Modell.* 359, 406–414.
- Midgley, G.F., Davies, I.D., Albert, C.H., Altwegg, R., Hannah, L., Hughes, G.O., O'Halloran, L.R., Seo, C., Thorne, J.H., Thuiller, W., 2010. BioMove – an integrated platform simulating the dynamic response of species to environmental change. *Ecography* 33, 612–616.
- Miller, B.W., Frid, L., Chang, T., Piekielek, N., Hansen, A.J., Morissette, J.T., 2015. Combining state-and-transition simulations and species distribution models to anticipate the effects of climate change. *AIMS Environ. Sci.* 2, 400–426.
- Moilanen, A., 1999. Patch occupancy models of metapopulation dynamics: efficient parameter estimation using implicit statistical inference. *Ecology* 80, 1031–1043.
- Moilanen, A., 2004. SPOMSIM: software for stochastic patch occupancy models of metapopulation dynamics. *Ecol. Modell.* 179, 533–550.
- Moilanen, A., Cabeza, M., 2002. Single-Species dynamic site selection. *Ecol. Appl.* 12, 913–926.
- Naujokaitis-Lewis, I.R., Curtis, J.M.R., Tischendorf, L., Badzinski, D., Lindsay, K., Fortin, M.-J., 2013. Uncertainties in coupled species distribution–metapopulation dynamics models for risk assessments under climate change. *Divers. Distrib.* 19, 541–554.
- Nicol, S.C., Possingham, H.P., 2010. Should metapopulation restoration strategies increase patch area or number of patches? *Ecol. Appl.* 20, 566–581.
- Ovaskainen, O., Hanski, I., 2001. Spatially structured metapopulation models: global and local assessment of metapopulation capacity. *Theor. Popul. Biol.* 60, 281–304.
- Ovaskainen, O., Hanski, I., 2004. Metapopulation dynamics in highly fragmented landscapes. In: Hanski, I., Gaggiotti, O. (Eds.), *Ecology, genetics, and Evolution of Metapopulations*. Academic Press Elsevier Science Pub, Burlington.
- Ovaskainen, O., Hanski, I., 2003. How much does an individual habitat fragment contribute to metapopulation dynamics and persistence? *Theor. Popul. Biol.* 64, 481–495.
- Panayotov, M., Kulakowski, D., Laranjeiro Dos Santos, L., Bebi, P., 2011. Wind disturbances shape old Norway spruce-dominated forest in Bulgaria. *For. Ecol. Manage.* 262, 470–481. <https://doi.org/10.1016/j.foreco.2011.04.013>.
- Pollock, L.J., Tingley, R., Morris, W.K., Golding, N., O'Hara, R.B., Parris, K.M., Vesik, P.A., McCarthy, M.A., 2014. Understanding co-occurrence by modelling species simultaneously with a joint species distribution model (JSDM). *Methods Ecol. Evol.* 5, 397–406.
- Radchuk, V., Johst, K., Groeneveld, J., Grimm, V., Schtickzelle, N., 2013. Behind the scenes of population viability modeling: predicting butterfly metapopulation dynamics under climate change. *Ecol. Modell.* 259, 62–73.
- Renwick, A., Jansson, T., Verburg, P., Revoredo-Giha, C., Britz, W., Gocht, A., McCracken, D., 2013. Policy reform and agricultural land abandonment in the EU. *Land use policy* 30, 446–457.
- Resetaritis Jr., W.J., Binckley, C.A., 2013. Patch quality and context, but not patch number, drive multi-scale colonization dynamics in experimental aquatic landscapes. *Oecologia* 173, 933–946.
- Rubin, D., 1984. Bayesianly justifiable and relevant frequency calculations for the applied statistician. *Ann. Stat.* 12, 1151–1172.
- Rue, H., Martino, S., Chopin, N., 2009. Approximate bayesian inference for latent gaussian models by using integrated nested Laplace approximations. *J. R. Stat. Soc. Series B* 71, 319–392.
- Rue H., S. Martino, F. Lindgren, D. Simpson & A. Riebler (2013). INLA: functions which allow to perform a full bayesian analysis of structured additive models using integrated nested laplace approximation. R Package Version 0.0. [<http://www.r-inla.org>]. Accessed 23 April 2016.
- Scheller, R.M., Domingo, J.B., Sturtevant, B.R., Williams, J.S., Rudy, A., Gustafson, E.J., Mladenoff, D.J., 2007. Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible temporal and spatial resolution. *Ecol. Modell.* 201, 409–419.
- Schippers, P., Verboom, J., Vos, C.C., Jochem, R., 2011. Metapopulation shift and survival of woodland birds under climate change: will species be able to track? *Ecography* 34, 909–919.
- Schuster, B., Diekmann, M., 2003. Changes in species density along the soil pH gradient – evidence from German plant communities. *Folia Geobot.* 38, 367–379.
- Siriwardena, G.M., 2010. The importance of spatial and temporal scale for agri-environment scheme delivery. *IBIS International Journal of Avian Science* 152, 515–529.
- Southwell, D., 2016. *Optimal Management of Metapopulations Across Space and time*. PhD Thesis. University of Melbourne. URL: <http://hdl.handle.net/11343/91796>.
- Southwell, D., Hauser, C.E., McCarthy, M.A., 2016. Learning about colonization when managing metapopulations under an adaptive management framework. *Ecol. Appl.* 2016, 279–294.
- Storkey, J., Meyer, S., Still, K.S., Leuschner, C., 2012. The impact of agricultural intensification and land-use change on the European arable flora. *Proc. of the Royal Society B Biol. Sci.* 279, 1421–1429.
- Templeton, A.R., Brazeal, H., Neuwald, J.L., 2011. The transition from isolated patches to a metapopulation in the eastern collared lizard in response to prescribed fires. *Ecology* 92, 1736–1747.
- van Teeffelen, A.J.A., Vos, C.C., Opdam, P., 2012. Species in a dynamic world: consequences of habitat network dynamics on conservation planning. *Biol. Conserv.* 153, 239–253.
- Verheyen, K., Vellend, M., Van Calster, H., Peterken, G., Hermy, M., 2004. Metapopulation dynamics in changing landscapes: a new spatially realistic model for forest plants. *Ecology* 85, 3302–3312.
- Wade S., M. Sanderson, N. Golding, J. Lowe, R. Betts, N. Reynard, & B. Harvey (2015). *Developing H++ climate change scenarios for heat waves, droughts, floods, windstorms and cold snaps*. Report Produced By the Met Office, University of Reading and CEH For the Adaptation Sub-Committee and to Support the Second Climate Change Risk Assessment (CCRA), UK. URL: <http://nora.nerc.ac.uk/id/eprint/512103/>.
- Wahlberg, N., 1997. The life history and ecology of *Melitaea diamina* (Nymphalidae) in Finland. *Nota Lepidoptera* 20, 70–81.
- Wahlberg, N., Klemetti, T., Hanski, I., 2002. Dynamic populations in a dynamic landscape: the metapopulation structure of the marsh fritillary butterfly. *Ecography* 25, 224–232.
- Wilson, J.P., 2012. Digital terrain modeling. *Geomorphology* 137, 107–121.
- Wilson, J.P., Gallant, J.C. (Eds.), 2000. *Terrain analysis: Principles and Applications*. John Wiley & Sons.

- Wisz, M.S., Pottier, J., Kissling, W.D., Pellissier, L., Lenoir, J., Damgaard, C.F., Dormann, C.F., Forchhammer, M.C., Grytnes, J.-A., Guisan, A., Heikkinen, R.K., Høye, T.T., Kühn, I., Luoto, M., Maiorano, L., Nilsson, M.-C., Normand, S., Öckinger, E., Schmidt, N.M., Tormansén, M., Timmermann, A., Wardle, D.A., Aastrup, P., Svenning, J.-C., 2013. The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biol. Rev.* 88, 15–30.
- Wätzold, F., Lienhoop, N., Drechsler, M., Settele, J., 2008. Estimating optimal conservation in the context of agri-environmental schemes. *Ecol. Econ.* 68, 295–305.
- Zwolak, R., 2009. A meta-analysis of the effects of wildfire, clearcutting, and partial harvest on the abundance of North American small mammals. *For. Ecol. Manage.* 258, 539–545. <https://doi.org/10.1016/j.foreco.2009.05.033>.