DR. HENNA FABRITIUS (Orcid ID : 0000-0002-3886-3149)

AID: 12218

Article type : Techniques & Methodology

Accepted Date : 23-Dec-2016

Editor: Didham, Raphael

Associate editor: Oliver, Tom

Modelling habitat persistence and impacts of management on the habitats of an endangered butterfly

Henna Fabritius^{1,2,*}, Marissa McBride^{1,3}

¹Department of Biosciences, University of Helsinki, P.O. Box 65 (Viikinkaari 1), FI-00014 Helsinki, Finland

²Current address: Swedish Species Information Centre, Swedish University of Agricultural Sciences, P.O. Box 7007, SE-750 07 Uppsala, Sweden, henna.fabritius@slu.se, +46793349194

³Current address: Harvard Forest, 324 North Main Street, Petersham, MA 01366, United States

* Corresponding author

Email address:

HF: henna.fabritius@helsinki.fi

MM: marissamcbride@fas.harvard.edu

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1111/ICAD.12218](https://doi.org/10.1111/ICAD.12218)

This article is protected by copyright. All rights reserved

29 Abstract

- 30 1. In dynamic landscapes, effective species conservation requires an understanding of the
31 spatial and temporal dynamics of species' habitats.
- 32 2. In this study, vegetation data across differently aged sites, site management history data
33 and expert elicitation are used to estimate (i) expected habitat patch lifetimes and (ii)
34 the impacts of habitat management history on how habitat quality changes through
35 time for an early-successional habitat specialist, the endangered false heath fritillary
36 butterfly (*Melitaea diamina*).
- 37 3. Results demonstrate the accelerated temporal dynamics experienced by false heath
38 fritillary habitats, with the quality of false heath fritillary habitats peaking 2-3 years after
39 management, and a median-sized habitat patch initially without tree cover predicted to
40 become unsuitable 15 years after management due to overgrowth.
- 41 4. As a co-product of habitat management patterns, habitat succession and land use
42 changes, non-conserved false heath fritillary habitats had an expected lifetime of 13.1
43 years.
- 44 5. This study demonstrates a method that can be used to estimate habitat network
45 dynamics for an early-successional habitat specialists economically in situations where
46 the urgency of conservation challenges favours fast decision-making.

47

48 Keywords

49 Succession, habitat overgrowth, survival analysis, expert elicitation, chronosequence studies,
50 habitat management, false heath fritillary, *Melitaea diamina*

51

52 Introduction

53 Many open landscapes that are important insect habitats are characterised by continuous
54 changes in habitat structure due to habitat succession, destruction and emergence. Such
55 landscape dynamics may be caused by natural disturbances, such as fire (Harper 2007,
56 Zwolak 2009), storms (Panayotov *et al.* 2011), floods (Stelter *et al.* 1997, Ballinger *et al.*
57 2007) and succession (Wahlberg *et al.* 2002), or by anthropogenic land use changes (van de
58 Voorde *et al.* 2012). Past studies have shown that in these dynamic landscapes, species'
59 viability depends on the interplay between species-specific traits and the availability of

habitat through time; and in particular, whether or not species are able to colonize emerging habitats fast enough to compensate for extinctions that take place at disappearing habitats (Johst *et al.* 2011). For instance, rates of habitat destruction (DeWoody *et al.* 2005, Johst *et al.* 2011), the level of spatial aggregation of habitat destruction (Wilcox *et al.* 2006) and the average lifetime of a habitat patch (Boughton & Malvadkar 2002) may all have significant impacts on species viability in dynamic landscapes. As such, effective conservation of insects in these mutable landscapes depends on an understanding of the spatio-temporal dynamics of their habitats in order to effectively manage for species persistence (Prach & Walker 2011).

For species that rely on specific types of early-successional habitat, habitat availability through time is driven by multiple natural and anthropogenic processes, such as the lengths of seral stages (intermediate stages of vegetation communities found in ecological succession) in the landscape (Foster & Tilman 2000, Bowles & Jones 2006, Alexander *et al.* 2012), and as a result, rates of habitat overgrowth (degradation of site quality as habitat type of interest due to ecological succession towards the next seral stage). These processes can be influenced by environmental covariates such as hydrology (Bowles & Jones 2006), elevation (Moral & Chang 2015) and by the land use histories of sites, an issue which has been examined in the context of studies that predict species diversity or community structure based on information about either historical land uses (Cousins & Eriksson 2002, Johansson *et al.* 2008), or the methods and frequencies of past site management activities (Harper 2007, Lourival *et al.* 2011, Török *et al.* 2014). Additional anthropogenic impacts on habitat availability include human land use activities, such as habitat destruction due to land use change and various types of habitat management activities (e.g. mowing or grazing), which may slow down or reset the process of habitat overgrowth.

In attempting to characterize the impacts of these multiple, interacting processes for conservation planning purposes, an important emergent property of dynamic landscapes is the average ‘lifetime’ of a habitat patch (i.e. length of time that a habitat patch persists), which frequently depends not only on the rate of habitat overgrowth, but also on the frequency of habitat management and rates of habitat destruction caused by land use change. Estimating habitat patch lifetimes from field data is complicated by the fact that new habitats are often discovered only once they have already been in existence for some time, and their age as habitable patches at the time of discovery may be unknown. One

approach to overcome such a challenge is to model annual habitat disappearance (an umbrella term used here to refer to the combined effects of habitat patch overgrowth and destruction) rates using exponential decay models, which have been used, among other things, to estimate annual habitat loss (Puyravaud 2003), the expected lifetimes of populations (Öckinger & Nilsson 2010) and mineral weathering rates in the soils (Yonekura *et al.* 2012). An age-independent modelling approach has the benefit of not assuming that the age of modelled particles are known, which enables the modelling of the disappearance rates of habitats subsequent to their initial discovery during field surveys. Estimates of annual disappearance rates can then be turned into estimates of expected habitat lifetimes.

The study of these different, interacting processes, and thus habitat availability for early successional species through time, has been complicated by the fact that the times series data needed to quantify these processes is often not available. In the absence of such information, chronosequence data (sets of differently aged study sites that allow for the use of space-for-time substitution; Pickett 1989) has been considered suitable for the study of short-term temporal change in species-poor systems (Foster & Tilman 2000, Walker *et al.* 2010), and applied to things like the modelling of vegetation composition of sites with respect to time since natural site disturbance (Hirst *et al.* 2005), abandonment (van de Voorde *et al.* 2012, Ellis & Ellis 2013), and management activities (Selwood *et al.* 2009). They have the benefit of requiring less time to implement than alternatives like time series studies; a useful feature in situations where the urgency of conservation challenges favours expedient decision-making over time-intensive data collection (Grantham *et al.* 2009, Walker *et al.* 2010, Canessa *et al.* 2015), though at the risk of providing unreliable results where the study system contains multiple alternative successional trajectories (Johnson & Miyanishi 2008, Walker *et al.* 2010). To address these concerns, some studies have attempted to assess the reliability of chronosequence study estimates by comparing them to independent estimates derived from other types of data, such as dendrochronological data (Alberti *et al.* 2009, Brien *et al.* 2009).

This study investigates the potential for using vegetation data from a chronosequence of habitats discovered at different years in the past, complemented with information on the sites' management history and expert knowledge about the way habitat quality changes through time, to investigate two temporal patterns of successional meadow habitats: (i) expected habitat patch lifetimes, and (ii) the impact of habitat management history on the

development of habitat quality. To address the concerns related to the use of chronosequence data to estimate temporal habitat dynamics, we investigated the possibility of validating the results of chronosequence studies by comparing them against temporal habitat dynamics estimates elicited from experts (Martin *et al.* 2012, Perera *et al.* 2012).

As a case study, the habitats of an endangered Finnish butterfly, the false heath fritillary *Melitaea diamina* (Lang, 1789; Nymphalidae), were studied across two regions of its distribution. The false heath fritillary is a moist meadow specialist that has, like many butterfly species, suffered from agricultural modernization and drainage of moist soils in recent decades (van Swaay *et al.* 2006). Its habitat, moist *Valeriana sambucifolia* (J. C. Mikan; Caprifoliaceae) meadows (Wahlberg 1997), has a tendency to be rapidly overgrown by willows, and therefore often emerges at sites that are in transition from one land use to another (e.g. tree sapling sites). The study aimed at answering the following questions: (i) What is the expected lifetime of a false heath fritillary habitat patch? Does the expected lifetime differ across study regions, across land use types or depending on site conservation status? What are the causes of habitat disappearance and are patch disappearance events aggregated in space? (ii) How many years does a false heath fritillary habitat persist following management before it becomes overgrown? Does this time depend on the sites' past management intensity or on the management methods used? Results provide a demonstration of how multiple characteristics of a species' temporal habitat dynamics can be estimated for conservation purposes from the same set of chronosequence data.

Material and Methods

Study areas and the selection of study sites

The study areas consisted of false heath fritillary populations in two regions, the Pirkanmaa region, SD1 (61.58°N, 24.05°E, 700 km²), located 10-20 km to the north of the city of Tampere, Finland, and the West Coast region, SD2 (62.25°N 21.5°E, 1 600 km²), which spans over a 150-km wide strip along the West Coast of Finland. The two distribution regions, previously connected, have been separated due to habitat loss before the 1990s (Wahlberg 1996) and are now located 100 km apart. At the time of field study, SD1 consisted of 271 known habitat patches, half of which had been discovered and identified as suitable false heath fritillary habitat by the end of the 1990s. SD2 consisted of 459 habitat patches, 70 of which were discovered as suitable false heath fritillary habitat in 1996-2004 and the rest

over the course of 2009-2012. Habitat patches and their boundaries had been originally recorded on habitat network maps by local environmental authorities or their collaborators based on the following criteria: landscape openness, availability of *Valeriana sambucifolia*, availability of nectar plants for adult butterflies (e.g. *Ranunculus* sp.), and preferably, but not necessarily, false heath fritillary sightings. In SD1, 17 of the habitat patches had been officially demarcated as false heath fritillary habitats by local environmental authorities, a status which forbids land use activities that are harmful to the false heath fritillary, while the rest of the habitat patches have been recorded for monitoring purposes only. Population dynamics of the false heath fritillary have been studied in SD1 by Wahlberg (1997), Wahlberg *et al.* (1996, 2002), Moilanen & Cabeza (2002), Ovaskainen (2004), and Cabeza *et al.* (2010), and in both regions by Fabritius *et al.* (2015). In both regions, monthly mean temperatures vary from -8°C to 16.5°C, the mean annual rainfall is approximately 650 mm and a permanent snow cover lasts for 3-5 months (Kersalo & Pirinen 2009).

For the field study, 101 study sites were selected, with the aim of including as much variation in the time since the sites were first discovered and recorded by the environmental authorities (*time since discovery*) as possible, in order to assemble a chronosequence dataset capable of estimating the expected lifetime of a habitat patch since its initial discovery. The selected sites included 35 old study sites in SD1 (discovered in 1995-1997) and 66 study sites of various ages in SD2 (4, 7 and 3 sites discovered in 1996, 2000 and 2004, respectively, and 52 discovered in 2009-2012). These differences in the distribution of *times since discovery* across the two study regions is due to the alternate histories of false heath fritillary conservation at the two distribution regions.

Study site data

Site vegetation and false heath fritillary occupancy

Study site vegetation was estimated in order to model it against the study sites' management histories and their site age surrogate, time since discovery. Fieldwork in SD1 was carried out between 18-Jun-2012 and 12-Jul-2012 and in SD2 between 12-Jun-2012 and 30-Jun-2012 for 37 sites, and between 26-June-2013 and 12-Jul-2013 for 32 sites using the original site boundaries recorded by the local environmental authorities. During fieldwork, destroyed areas were marked as polygons in the study site maps (Fig. 1): this included areas that had either been converted into other land uses (e.g. field cultivation) or in which the

soil, moisture or light conditions had changed so that the herbal layer was dominated by species untypical to meadows (e.g. *Calluna vulgaris* or *Vaccinium myrtillus*). For the remaining (non-destroyed) study site area, the following parameters were estimated based on visual observation, using 2-meter long measurement bars as aids in the visual estimation of heights: average tree height (m), tree cover (%), average willow height (m), willow cover (%), average height of grassy vegetation (cm) and forb cover (%). In eight cases of large-size study sites (mean size 1.8 ha) that had thick vegetation or rough terrain due to habitat overgrowth, parts of the study sites (less than half of the total area) were excluded from detailed estimation and vegetation parameters were estimated based on the visited area.

Since the host plant of the false heath fritillary, *V. sambucifolia*, typically grows in the false heath fritillary meadows in aggregates, a host plant density estimate for the non-destroyed study site area was created as follows. First, host plant aggregates were marked based on visual observation as polygons on the study site map and the resulting polygons were classified into host plant density classes (Fig. 1). Next, at least one 15 m transect line was placed randomly within each host plant density class, four transects altogether per each study site, and the number of individual host plant ramets was counted within 50 cm on each side of the transect. The transect counts were used to estimate host plant densities for each density class and, finally, the host plant density of each study site was estimated by using an area-weighted average of the class-specific host plant densities.

Records of false heath fritillary occupancy (the existence of sightings of adult false heath fritillary butterflies) were compiled for sites across both study regions in order to permit modelling of site occupancy based on key vegetation parameters. In SD1, false heath fritillary occupancy was monitored at 32 sites during vegetation surveys. This monitoring was undertaken during good weather conditions by surveying the entire area of a study site once by maintaining a slow but steady walking pace. In SD2, false heath fritillary occupancy data from a monitoring survey that took place in 2012 was used for 18 study sites in order to allow for carrying out vegetation surveys regardless of weather conditions.

Finally, to compare the relative importance of patch connectivity versus vegetation composition in determining site occupancy, Incidence Function Model patch connectivity measures were calculated for each study site using the Harrison *et al.* (2011) formula

$$S_i = \sqrt{A_i} \sum_{j \neq i} \{ \exp(-\alpha d_{ij}) \sqrt{A_j} \}, \quad (1)$$

where A_i is the area of the study site i , A_j is the area of a remote patch j , d_{ij} is the distance between the study site i and other patches j of the studied patch network in kilometres, and α measures the spatial scale of connectivity. The value of α was set to 0.7 for the false heath fritillary based on a variation of estimates in Moilanen (1999), Moilanen & Cabeza (2002) and Ovaskainen (2004).

Management history data

Data on current and historical land use types and management histories for the study sites were collected over the past 15 years from the records of the environmental centre and by approaching site landowners via door-to-door visits, phone calls or mailed questionnaires. In the few cases where a site had several landowners or clearly distinguishable alternate land use types, or if the study site had been extended to cover a larger area since its original discovery, the sites were split into two sites with separately defined *times since discovery* and site management histories.

Site management activities were classified into four types, cultivation, grazing, mowing and harrowing, and for each study site, the following parameters were estimated: the *historical land use type* (oldest known land use type: meadow, pasture, field or a clearcut), *current land use type* (Table 1), *time since last management*, *management intensity* over the past 15 years (the sum of years during which a site has been maintained during the 15-year management histories assembled) and the number of years with cultivation, mowing, grazing or harrowing activities. Sites with a current land use type of “Conservation area” were classified as conserved and sites under all other land use types were classified as non-conserved. Finally, differences between regions in terms of vegetation characteristics and the distribution of land use types were also tested for in order to ensure the comparability of data across study regions.

Estimation of expected patch lifetimes

Identification of overgrown sites

Habitat overgrowth at study sites was modelled using logistic regression models that had false heath fritillary occupancy (a binary variable) as the response variable and site area,

connectivity, time since discovery, host plant abundance (counted as the estimated host plant density x area) and the six vegetation parameters as covariates. Following a forward selection procedure, covariates were added to the model in the order of decreasing statistical significance until the model AIC value could not be improved by including additional factors. During the process, factors that had been rendered non-significant were dropped out in the order of least statistical significance. Region was included as a covariate in the final model to see if it was significant and whether it rendered some of the other covariates insignificant. All analyses were performed using the software R 3.1.1 (R Core Team 2013).

The resulting habitat occupancy model was used to predict the probability of false heath fritillary occupancy for study sites. Sites were defined as overgrown if the predicted probability of the site occupancy based on the habitat occupancy model was below a threshold β . The threshold parameter β was chosen so that the resulting prediction of habitat occupancy had the highest possible predictive precision for the habitat occupancy model.

Estimation of habitat disappearance rates and expected patch lifetimes

Survival analysis (Kleinbaum & Klein 1996) was used to estimate annual habitat disappearance rates for false heath fritillary habitats and whether annual disappearance rates differed per land use type or region. Survival analysis has rarely been used to model the persistence of habitats, but has often been applied within ecology to estimating the individual survival of animals (e.g. Blay & Cote 2001). For the survival analysis, site age was defined based on *time since discovery* and study sites were classified as having disappeared if they were either classified as at least 50 % destroyed in the field surveys, or as overgrown by the habitat occupancy model. Survival analysis was conducted using the *survival* package (Therneau & Lumley 2011) of the R 3.1.1 programming environment (R Core Team 2013).

Kaplan-Meyer survivor curves were created for the study sites (Kaplan & Meier 1958), to plot the proportion of study sites remaining against years since site discovery. Right-censored data were used with an exponential survival model (*survreg*) to test site persistence against land use type, conservation status and region. Expected patch lifetimes were estimated by calculating inverses of the estimated disappearance rates and their confidence intervals. The spatial clustering of the destroyed and overgrown sites was tested

by estimating the Moran's I for the destroyed or overgrown status of study sites based on the 10 nearest neighbours. Moran's I was tested using the library *spdep* in the R 3.1.1 programming environment.

Estimation of the impact of habitat management history on habitat quality

Expert elicitation of the impact of habitat management history on habitat quality

Nine experts in meadow succession were asked to provide estimates of how false heath fritillary meadow habitat quality develops through time following different management histories. The experts included four early-career biologists involved with false heath fritillary related fieldwork, a civil servant biologist and an amateur Lepidopterist, both with at least ten years of experience in false heath fritillary conservation planning, and three experienced meadow ecosystem researchers, each with over ten years of meadow research experience. The experts were emailed a questionnaire (Appendix S1) that included an overview of the study system and descriptions of 20 hypothetical meadows with equal environmental characteristics but varying management histories for the past 15 years. Based on these management histories, the experts were asked to estimate the quality of each hypothetical meadow as a false heath fritillary habitat (measured primarily in terms of host plant abundance and secondarily in terms of forb cover) for 1, 2, 3, 5, 10 and 20 years after the last management operation. The experts were also asked to self-evaluate their expertise in estimating the differences of alternative meadow management methods and the speed of habitat overgrowth.

Habitat quality model and comparison with study site data

Individual expert estimates were combined into equal-weighted average estimates of habitat quality for each hypothetical meadow (e.g. Clemen & Winkler 1999, Winkler 2015). These averaged expert estimates were used to model the impact of habitat management history on how habitat quality changes through time. A generalized additive model (GAM) was fitted with a Gaussian distribution using the *gam* function in the *mgcv* package (Wood 2006). In this model, site quality was used as the response variable and six independent variables (historical land use type, time since last management, management intensity and the number of years with cultivation, harrowing, grazing and mowing activities) were tested as covariates. Prior to fitting, the habitat quality scores (ranging from 0-100) were transformed into proportions (ranging from 0 to 1) using the arcsine transformation

appropriate for use with proportional data. Because there were insufficient data points to fit variables for the impact of grazing and mowing separately, these were removed from testing. The degree of smoothing for each GAM fit was determined by the GAM function's default method. GAMs were used in a backwards stepwise procedure using AIC for model selection. The model with the lowest AIC was selected as the most suitable.

The fitted habitat quality model was used to generate habitat quality predictions for the study sites based on their management histories. Since host plant abundance proved to be the most significant predictor of habitat occupancy, the correlation between habitat quality predictions and estimated log-transformed host plant densities at study sites with different management histories was tested. The rationale of testing the correlation of habitat quality predictions against host plant densities, rather than abundances, was the expectation that similar habitat management histories would result in different host plant abundances depending on the size of the managed area. Habitat quality models based on each of the nine experts' individual response sets were fitted in a similar manner and the respondents' individual estimates were compared against field data (using the same process as above).

Given the significant correlation between habitat quality predictions of the model based on averaged expert estimates and estimated log-transformed host plant densities, the habitat quality predictions of the habitat quality model were scaled to their corresponding log-transformed host plant densities, to enable prediction of how host plant abundances would change over the course of time at a median-sized habitat patch (for which predicted host plant abundances could be calculated based on predicted host plant density and patch area) and when a median-sized patch would be predicted to become overgrown according to the habitat occupancy model. The habitat quality model was scaled using the formula

$$\sum_{i=1}^n (\gamma_i - a\beta_i + b)^2 \quad (2)$$

in which γ_i is the log-transformed host plant density at a study site i , β_i is the predicted habitat quality at a study site i and a and b are scalars. Parameters a and b were adjusted to values that minimized the sum of squares of the differences between the habitat quality predictions and the log-transformed host plant densities. Next, the scaled habitat quality model predictions were used to predict changes in host plant abundance at a median-sized habitat patch initially without tree cover, and expecting an annual 15 cm increase in tree

height; an approximate rate of increase that fits well within the standard range annual tree growth of spruce trees in Scandinavia (e.g. St. Clair JB & Kleinschmit 1986, Örlander & Karlsson 2000 and Eerikäinen *et al.* 2014). With the resulting predictions of host plant abundances, the habitat occupancy model was used to predict after how many years the median-sized habitat patch without tree cover would become unoccupied due to habitat overgrowth. To test whether management histories varied across land use types, which could lead to differences in habitat lifetimes, ANOVA models were fitted in which land use type was a predictor variable and the significant predictors of the GAM model were predicted values.

Results

Study site data

Vegetation data were collected at 100 of the 101 study sites (Appendix S2), one site being classified as entirely destroyed. Study sites in SD1 and SD2 differed slightly in terms of structure and vegetation, with study sites in SD1 being smaller (Welch.t = -2.33, $P = 0.024$ *) and better connected (Welch.t = 2.61, $P = 0.011$ *) in comparison to SD2 (Appendix S2). Additionally, study sites in SD1 had lower willow height (Welch.t = -3.28, $P = 1.5e-3$ ***), lower percentage forb cover (Welch.t = 2.77, $P = 0.0070$ **) and lower host plant abundance (Welch.t = -2.47, $P = 0.016$ *; Appendix S2).

Full or partial management history data were retrieved for 50 and 41 of the 101 study sites, respectively. Six of these study sites were split into two ($n=5$) or three ($n=1$) sites due to different land use types and four sites were split into two sites due to extensions since the sites' original discovery. Land use types ($n=83$; Table 1) differed between distribution regions (Pearson's chi-sq. test: $X^2 = 15.18$, $df = 6$, $P = 0.02$), but not when the larger number of conservation areas in SD1 was not accounted for (Pearson's chi-sq. test: $X^2 = 4.82$, $df = 5$, $P = 0.44$). Historical land use types ($n=82$) consisted of 46 fields, 23 meadows, six pastures and seven forest clearcuts. Study sites had been maintained on average 5.6 (SD=5.5, $n=48$) times within the past 15 years, and time since last management was on average 6.2 years (SD=10.05, $n=61$).

Annual habitat disappearance rates and expected patch lifetimes

False heath fritillary occupancy at study sites was best predicted by host plant abundance and tree height ($n = 65$, AIC: 79.65; Table 2). Site age, region or connectivity were not significant when added to the full model. The predictive precision of the habitat occupancy model was highest when the threshold prediction level of habitat occupancy was set to $\beta = 0.71$, for which the model predicted habitat occupied and unoccupied patches correctly in 45 % ($n = 40$) and 92 % ($n = 25$) of the cases, respectively. Based on the habitat occupancy model, 77.8 % ($n = 35$) and 46.7 % ($n = 21$) of the study sites in SD1 and SD2, respectively, were predicted to be overgrown (Appendix S2).

Out of the 91 study sites with management history data, 13.2 % ($n = 12$) and 19.8 % ($n = 18$) were classified as fully or partially destroyed, respectively. The causes of patch disappearance were field cultivation ($n = 13$, 56.1 % of the destroyed area) and forest growth ($n = 17$, 43.9 % of destroyed area). The proportion of at least partially destroyed sites did not differ between distribution regions (Pearson's chi-sq. test: $X^2_1 = 0.35$, $P = 0.55$). There was no significant spatial aggregation of patch disappearance in SD1 (Moran's $I_{k=10} = 1.17$, $n = 35$, $P = 0.88$) or in SD2 (Moran's $I_{k=10} = 0.68$, $n = 63$, $P = 0.25$).

Survival analysis did not reveal differences in annual disappearance between land use types ($n = 88$, $X^2_1 = 4.88$, $P = 0.43$; Fig. 2A), but did indicate a trend ($n = 91$, $X^2_1 = 3.17$, $P = 0.075$) towards site conservation having a decelerating effect on the annual disappearance rate for sites, and that site disappearance was fastest during the first years since site discovery (Fig. 2B). Additionally, non-conserved study sites had a faster annual disappearance rate in SD2 in comparison to SD1 ($n = 78$, $X^2_1 = 15.88$, $P = 6.8e-5$ ***). The overall estimated annual disappearance rate of non-protected meadows was 0.076 (95 % CI 0.058-0.10), which corresponds to an average patch lifetime of 13.1 (95 % CI 9.9–17.3) years.

The impact of management history on habitat quality

Based on averaged expert estimates, time since last management was the most influential predictor of habitat quality, and site quality was expected to peak 2-3 years since last management (Fig. 3A). Additionally, the number of years of harrowing and cultivation were expected to have a positive impact on site quality ($n = 120$, $R^2 = 0.868$, AIC: - 283.97, Table 3). Habitat quality predictions for study sites, which were based on the habitat quality model

fitted using averaged expert estimates, correlated positively (Pearson correlation: 0.45, $n = 56$, $P < 0.001$ ***) with the estimated host plant density at study sites (Fig. 3B). Based on the predictions of the habitat occupancy and habitat quality models, the latter ones scaled to their corresponding log-transformed host plant densities with scalars $a = 5.81$ and $b = -5.58$, a median-sized (1.41 ha) habitat patch without tree cover would become unoccupied due to habitat overgrowth 15 (10-20) years since last management. Time since last management of fields (median: 0, range: 0–2, $n = 13$) differed significantly from that of forests (median: 5, range: 0–35, $n = 13$, pairwise t-test Bonf. corr.: $P = 2.9e-05$ ***) and abandoned sites (median: 6.5, range: 2–45, $n = 12$, pairwise t-test Bonf. corr.: $P = 0.14e-06$ ***)).

The experts self-evaluated their expertise to estimate differences between alternative meadow management methods with a mean of 2.9 (range: 2–4), and the speed of habitat overgrowth with a mean of 3.25 (range: 2–5). Habitat quality models based on individual expert estimates predicted host plant density with similar degrees of correlation as the average response model for five experts, while models for four experts failed to correlate with host plant density. While not significant, there was a slight suggestion that experts who rated their abilities more highly actually tended to perform less well in providing estimates that corresponded with observed host plant densities.

Discussion

This study distinguishes and models two different temporal parameters of dynamic habitats: the length and successional pattern of the seral stage of interest, and its average lifetime at a discovered habitat patch. In early-successional habitats, these parameters can differ depending on land use practices, since habitat management can reset succession back to the onset of the seral stage of interest. In this study case, the average lifetime of a habitat patch was of a similar magnitude to the time for which a median-sized habitat patch would remain habitable following management, as some temporary habitats were managed by landowners more than once before they disappeared due to overgrowth or land use changes, and others were converted to other land uses before they became overgrown. Estimating each of these parameters can therefore be useful in informing conservation efforts: the average lifetime of a non-conserved habitat patch provides information about the landowner-driven dynamics of habitat disappearance in the system and helps to

estimate species viability in the absence of management interventions (Prach & Walker 2011), and the successional pattern of the seral stage provides information about optimal management frequencies for conservation managers.

This work also demonstrates the potential for expert elicitation to act as a validation tool to address the concerns associated with the use of chronosequence data (Johnson & Miyanishi 2008, Walker *et al.* 2010). The model developed using this approach aligned well with the chronosequence data, giving greater support to the results. Past studies have found experts to possess useful knowledge for conservation decision-making in the absence of empirical information, but to also be less accurate than models developed from empirical data (e.g. Cerquiera *et al.* 2013, McConnachie & Cowling 2013, Aizpurua *et al.* 2015, Drolet *et al.* 2015), which could be seen in the variation of the responses of individual experts in our study. Though not significant, the negative association observed here between experts' expectations of their knowledge and actual performance reflects a common finding in studies assessing expert performance (e.g. McKenzie *et al.* 2008, Burgman *et al.* 2011). The implications for conservation decision-makers looking to use expert knowledge are to avoid relying on self-ratings of expertise in selecting and weighting opinions from experts. Instead we recommend consulting a group of at least five, diverse experts and using an average of their responses, as was done here. If time permits, allowing the experts to view the responses of others in the group and to share their knowledge and reasoning could also reduce inter-expert variation and help to improve response quality (e.g. Burgman *et al.* 2011, Kerr and Tindale 2011).

Several practical conservation guidelines for false heath fritillary habitats arise from the habitat quality model. These results suggest that the host plant *V. sambucifolia* benefits from intermediate management frequencies that better enable the growth and seeding of the biannual *V. sambucifolia* than do annual management frequencies. Harrowing and cultivation also increase host plant densities, which suggests that *V. sambucifolia* benefits from decreased root competition against stronger competitors such as *Anthriscus sylvestris*, *Angelica sylvestris*, nettles (*Urticaria*), and a variety of grasses. These findings are in line with past studies of meadow ecosystems, which have demonstrated differential responses to alternative management methods (DeGraaf & Yamasaki 2003, Rook *et al.* 2004, Humbert *et al.* 2010) and to different management histories (Cousins & Eriksson 2002, Johansson *et al.* 2008, Meulebrouck *et al.* 2009). Management requirements may differ between the two

distribution regions, as indicated by the slight differences between the study sites' vegetation and the faster habitat disappearance rates estimated in SD2.

The identification of seven different land use types under which false heath fritillary habitat patches occurred highlights the degree to which different habitat patches may have different annual disappearance rates depending on their current land use type. This is in line with the argument of Wahlberg *et al.* (2002), who suggested that habitat patches may include successional and transient patches, the latter of which may have shorter lifetimes than normal successional patches as a result of an increased risk of destruction due to human land use. Even though we failed to demonstrate differentiated annual disappearance rates across land use types, the time since last site management differed between land use types, and Kaplan-Meyer plots indicated faster site disappearance rates at younger sites. The use of a more equal distribution of study sites across regions, land use types and times since discovery might better enable the identification of differences in land use specific disappearance rates in future studies. Providing data on the linkages between land use types and annual site disappearance rates can help with conservation planning efforts by providing more detailed information on the dynamics of the habitat patch network.

A major challenge in the study of habitat patch dynamics lies in estimating habitat overgrowth. Metapopulation theory (Hanski 1994) predicts that the proportion of unoccupied, suitable habitat patches in a habitat patch network depends on the spatial structure and extinction-colonization dynamics of the system (Hanski & Ovaskainen 2001), but in dynamic landscapes the links between patch occupancy and connectivity may be masked by the changing structure of the patch network (Hodgson *et al.* 2009). Ideally, links between succession and habitat occupancy should be estimated within the context of the spatio-temporal dynamics of the patch network (as e.g. as in Snäll *et al.* 2005, Caruso *et al.* 2010, Donner *et al.* 2010). The method used here of estimating the number of overgrown sites based on the predictive precision of the habitat occupancy model is a necessary simplification when carrying out a retrospective study for which data on the past patch network dynamics are typically not available. Inconsistency across studies in the definition of patches and patch disappearance (Cizek & Konvicka 2005) also means that the estimates of patch overgrowth rates calculated here should be interpreted with caution.

While the spatial structures of endangered species' habitat networks are increasingly well recorded in the form of GIS (Geographic Information System) data sets, temporal changes in habitat networks often go unrecorded. Our method of utilizing such GIS data sets as a basis for a retrospective study offers a means for developing a quick understanding of habitat lifetimes and factors behind habitat disappearance for early-successional habitat specialists. The applicability of our method to other systems will depend on whether it can be assumed that (i) all recorded habitats were in a habitable condition for the species of interest at the time of their identification, and that (ii) all study sites are sufficiently connected to populations of the study species, to allow for site overgrowth to be modelled based on a lack of site occupancy. Modelling the impacts of habitat management history on habitat quality either requires that the study sites' management history can be obtained or that experts with sufficient knowledge on the study system are available. While the obtained estimates of expected habitat lifetimes can be used to simulate habitat availability given, for example, alternative conservation scenarios, the data produced by our method can also be used to justify and set time intervals for more systematic site monitoring in the future.

Acknowledgements

We thank Aki Suzuki, Tuomas Kankaanpää, Hanna Parri and Iina Ollikainen for fieldwork, Henrik de Knecht and Dimitri Stucki for help with survival analysis and Jenny Hodgson for comments on the manuscript.

References

- Aizpurua, O., Cantú-Salazar, L., San Martín, G., Biver, G., Brotons, L. & Titeux, N. (2015) Reconciling expert judgement and habitat suitability models as tools for guiding sampling of threatened species. *Journal of Applied Ecology*, **52**, 1608-1616.
- Alberti, G., Peressotti, A., Piussi, P. & Zerbi, G. (2009) Structure and stand development of secondary forests in Eastern Prealps (Italy). *Dendrochronologia*, **27**, 173-181.
- Alexander, H.M., Foster, B.L., Ballantyne, F., Collins, C.D., Antonovics, J. & Holt, R.D. (2012) Metapopulations and metacommunities: combining spatial and temporal perspectives in plant ecology. *Journal of Ecology*, **100**, 88-103.

- 556 Ballinger, A., Lake, P.S. & Nally, R.M. (2007) Do terrestrial invertebrates experience flood-
557 plains as landscape mosaics? Immediate and longer-term effects of flooding on ant
558 assemblages in a floodplain forest. *Oecologia*, **152**, 227-238.
- 559 Blay, N. & Cote, I.M. (2001) Optimal conditions for breeding of captive Humboldt penguins
560 (*Spheniscus humboldti*): a survey of British zoos. *Zoo Biology*, **2**, 545-555.
- 561 Boughton, D. & Malvadkar, U. (2002) Extinction risk in successional landscapes subject to
562 catastrophic disturbances. *Conservation Ecology*, **6**, 1195-5449.
- 563 Bowles, M. & Jones, M. (2006) Testing the efficacy of species richness and floristic quality
564 assessment of quality, temporal change, and fire effects in tallgrass prairie natural
565 areas. *Natural Areas Journal*, **26**, 17-30.
- 566 Brienien, R.J.W., Lebrija-Trejos, E., van Breugel, M., Pérez-García, E.A., Bongers, F., Meave,
567 J.A. & Martínez-Ramos, M. (2009) The potential of tree rings for the study of forest
568 succession in Southern Mexico. *Biotropica*, **41**, 186-195.
- 569 Burgman, M.A., McBride, M., Ashton, R., Speirs-Bridge, A., Flander, L., Wintle, B., Fidler, F.,
570 Rumpff, L. & Twardy, C. (2011) Expert status and performance. *PloS ONE*, **6**, e22998.
- 571 Cabeza, M., Arponen, A., Jäättelä, L., Kujala, H., van Teeffelen, A. & Hanski, I. (2010)
572 Conservation planning with insects at three different spatial scales. *Ecography*, **33**, 54-
573 63.
- 574 Canessa, S., Guillera-Arroita, G., Lahoz-Monfort, J., Southwell, D.M., Armstrong, D.P.,
575 Chadès, I., Lacy, R.C. & Converse, S.J. (2015) When do we need more data? A primer
576 on calculating the value of information for applied ecologists. *Methods in Ecology &*
577 *Evolution*, **6**, 1219-1228.
- 578 Caruso, A., Thor, G. & Snäll, T. (2010) Colonization-extinction dynamics of epixylic lichens
579 along a decay gradient in a dynamic landscape. *OIKOS*, **119**, 1947-1953.
- 580 Cerqueira, M.C., Cohn-Haft, M., Vargas, C.F., Nader, C.E., Andretti, C.B., Costa, T.V.V., Sberze,
581 M., Hines, J.E. & Ferraz, G. (2013) Rare or elusive? A test of expert knowledge about
582 rarity of Amazon forest birds. *Diversity & Distributions*, **19**, 710-721.
- 583 Cizek, O. & Konvicka, M. (2005) What is a patch in a dynamic metapopulation? Mobility of an
584 endangered woodland butterfly, *Euphydryas maturna*. *Ecography*, **28**, 791-800.
- 585 Clemen, R.T. & Winkler, R.L. (1999) Combining probability distributions from experts in risk
586 analysis. *Risk Analysis*, **19**, 187-203.
- 587 Cousins, S.A.O. & Eriksson, O. (2002) The influence of management history and habitat on
588 plant species richness in a rural hemiboreal landscape, Sweden. *Landscape Ecology*,
589 **17**, 517-529.

- DeGraaf, R. & Yamasaki, M. (2003) Options for managing early-successional forest and shrubland bird habitats in the northeastern United States. *Forest Ecology & Management*, **185**, 179-191.
- del Moral, R. & Chang, C.C. (2015) Multiple assessments of succession rates on Mount St. Helens. *Plant Ecology*, **216**, 165-176.
- DeWoody, Y.D., Feng, Z. & Swihart, R.K. (2005) Merging spatial and temporal structure within a metapopulation model. *American Naturalist*, **166**, 42-55.
- Donner, D.M., Ribic, C.A. & Probst, J.R. (2010) Patch dynamics and the timing of colonization-abandonment events by male Kirtland's Warblers in an early succession habitat. *Biological Conservation*, **143**, 1159-1167.
- Drolet, D., Ocke, A., Lewis, M. & Davidson, J. (2015) Evidence-based tool surpasses expert opinion in predicting probability of eradication of aquatic nonindigenous species. *Ecological Applications*, **25**, 441-450.
- Eerikäinen, K., Valkonen, S. & Saksa, T. (2014) Ingrowth, survival and height growth of small trees in uneven-aged *Picea abies* stands in southern Finland. *Forest Ecosystems*, **1**, 5.
- Ellis, C.J. & Ellis, S.C. (2013) Signatures of autogenic epiphyte succession for an aspen chronosequence. *Journal of Vegetation Science*, **24**, 688-701.
- Fabritius, H., Rönkä, K. & Ovaskainen, O. (2015) The dual role of rivers in facilitating or hindering movements of the false heath fritillary butterfly. *Movement Ecology* **3**, 4.
- Foster, B.L. & Tilman, D. (2000) Dynamic and static views of succession: testing the descriptive power of the chronosequence approach. *Plant Ecology*, **146**, 1-10.
- Grantham, H.S., Wilson, K.A., Moilanen, A., Rebelo, T. & Possingham, H.P. (2009) Delaying conservation actions for improved knowledge: how long should we wait? *Ecology Letters*, **12**, 293-301.
- Hanski, I. (1994) A practical model of metapopulation dynamics. *Journal of Animal Ecology*, **63**, 151-162.
- Harper, C.A. (2007) Strategies for managing early succession habitat for wildlife. *Weed Technology*, **21**, 932-937.
- Harrison, P.J., Hanski, I. & Ovaskainen, O. (2011) Bayesian state-space modeling of metapopulation dynamics in the Glanville fritillary butterfly. *Ecological Monographs*, **81**, 581-598.
- Hirst, R., Pywell, R.F., Marrs, R.H. & Putwain, P.D. (2005) The resilience of calcareous and mesotrophic grasslands following disturbance. *Journal of Applied Ecology*, **42**, 498-506.

- 624 Hodgson, J.A., Moilanen, A. & Thomas, C.D. (2009) Metapopulation responses to patch
625 connectivity and quality are masked by successional habitat dynamics. *Ecology*, **90**,
626 1608-1619.
- 627 Humbert, J.-Y., Ghazoul, J., Sauter, G.J. & Walter, T. (2010) Impact of different meadow
628 mowing techniques on field invertebrates. *Journal of Applied Entomology*, **134**, 592-
629 599.
- 630 Johansson, L.J., Hall, K., Prentice, H.C., Ihse, M., Reitalu, T., Sykes, M.T. & Kindström, M.
631 (2008) Semi-natural grassland continuity, long-term land-use change and plant species
632 richness in an agricultural landscape on Öland, Sweden. *Landscape & Urban Planning*,
633 **84**, 200-211.
- 634 Johnson, E.A. & Miyanishi, K. (2008) Testing the assumptions of chronosequences in
635 succession. *Ecology Letters*, **11**, 419-431.
- 636 Johst, K., Drechsler, M., van Teeffelen, A.J., Hartig, F., Vos, C.C., Wissel, S., Wätzold, F. &
637 Opdam, P. (2011) Biodiversity conservation in dynamic landscapes: trade-offs
638 between number, connectivity and turnover of habitat patches. *Journal of Applied*
639 *Ecology*, **48**, 1227-1235.
- 640 Kaplan, E.L. & Meier, P. (1958) Nonparametric estimation from incomplete observations.
641 *Journal of American Statistical Association*, **53**, 457-481.
- 642 Kerr, N.L. & Tindale, R.S. (2011) Group-based forecasting? A social psychological analysis.
643 *International Journal of Forecasting*, **27**, 14-40.
- 644 Kersalo, J. & Pirinen, P. (2009) Suomen maakuntien ilmasto. *Ilmatieteen laitos: Raportteja*, **8**,
645 1-185. Yliopistopaino, Helsinki.
- 646 Kleinbaum, D.G. & Klein, M. (1996) *Survival analysis*. Springer-Verlag, NY.
- 647 Lourival, R., Drechsler, M., Watts, M.E., Game, E.T. & Possingham H.P. (2011) Planning for
648 reserve adequacy in dynamic landscapes; maximizing future representation of
649 vegetation communities under flood disturbance in the Pantanal wetland. *Diversity &*
650 *Distributions*, **17**, 297-310.
- 651 Martin, T.G., Burgman, M.A., Fidler, F., Kuhnert, P.M., Low-Choy, S., McBride, M.F. &
652 Mengersen, K. (2012) Eliciting expert knowledge in conservation science. *Conservation*
653 *Biology*, **26**, 29-38.
- 654 McConnachie, M.M. & Cowling, R.M. (2013) On the accuracy of conservation managers'
655 beliefs and if they learn from evidence-based knowledge: a preliminary investigation.
656 *Journal of Environmental Management*, **128**, 7-14.

- 657 McKenzie, C.R.M., Liersch, M.J. & Yaniv, I. (2008) Overconfidence in interval estimates: what
658 does expertise buy you? *Organizational Behavior and Human Decision Processes*, **107**,
659 179-191.
- 660 Meulebrouck, K., Verheyen, K., Brys, R. & Hermy, M. (2009) Metapopulation viability of an
661 endangered holoparasitic plant in a dynamic landscape. *Ecography*, **32**, 1040-1050.
- 662 Moilanen, A. & Cabeza, M. (2002) Single-species dynamic site selection. *Ecological*
663 *Applications*, **12**, 913-926.
- 664 Moilanen, A. (1999) Patch occupancy models of metapopulation dynamics: Efficient
665 parameter estimation using implicit statistical inference. *Ecology*, **80**, 1031-1043.
- 666 Öckinger, E. & Nilsson, S.G. (2010) Local population extinction and vitality of an epiphytic
667 lichen in fragmented old-growth forest. *Ecology*, **91**, 2100-2109.
- 668 Örlander, G. & Karlsson, C. (2000) Influence of shelterwood density on survival and height
669 increment of *Picea abies* advance growth. *Scandinavian Journal of Forest Research*, **15**,
670 20-29.
- 671 Ovaskainen, O. & Hanski, I. (2001) Spatially structured metapopulation models: global and
672 local assessment of metapopulation capacity. *Theoretical Population Biology*, **60**, 281-
673 304.
- 674 Ovaskainen, O. (2004) Habitat-specific movement parameters estimated using mark-
675 recapture data and a diffusion model. *Ecology*, **85**, 242-257.
- 676 Panayotov, M., Kulakowski, D., Laranjeiro, Dos Santos, L. & Bebi, P. (2011) Wind disturbances
677 shape old Norway spruce-dominated forest in Bulgaria. *Forest Ecology &*
678 *Management*, **262**, 470-481.
- 679 Perera, A.H., Drew, C.A. & Johnson, C.J., editors. (2012) *Expert knowledge and its application*
680 *in landscape ecology*. Springer, New York.
- 681 Pickett, S.T.A. (1989) Space-for-time substitution as an alternative to long-term studies.
682 *Long-term studies in ecology* (ed. by Likens G.E.), pp 71-88. Wiley, Chichester.
- 683 Prach, K. & Walker, L.R. (2011) Four opportunities for studies of ecological succession.
684 *Trends in Ecology & Evolution*, **26**, 119-23.
- 685 Puyravaud, J.P. (2003) Standardizing the calculation of the annual rate of deforestation.
686 *Forest Ecology & Management*, **177**, 593-596.
- 687 R Core Team (2013) *R: A language and environment for statistical computing*. R Foundation
688 for Statistical Computing, Vienna, Austria.

689 Rook, A.J., Dumont, B., Isselstein, J., Osoro, K., WallisDeVries, M.F., Parente, G. & Mills, J.
690 (2004) Matching type of livestock to desired biodiversity outcomes in pastures - a
691 review. *Biological Conservation*, **119**, 137-150.

692 Selwood, K., Mac Nally, R. & Thomson, J.R. (2009) Native bird breeding in a chronosequence
693 of revegetated sites. *Oecologia*, **159**, 435-46.

694 Snäll, T., Ehrlén, J. & Rydin, H. (2005) Colonization-extinction dynamics of an epiphyte
695 metapopulation in a dynamic landscape. *Ecology*, **86**, 106-115.

696 St. Clair, J.B. & Kleinschmit, J. (1986) Genotype-environment interaction and stability in ten-
697 year height growth of Norway spruce clones (*Picea abies* Karst.). *Silvae Genetica*, **35**,
698 177-186.

699 Stelter, C., Reich, M., Grimm, V. & Wissel, C. (1997) Modelling persistence in dynamic
700 landscapes: lessons from a metapopulation of the grasshopper *Bryodemus tuberculata*.
701 *Journal of Animal Ecology*, **66**, 508-518.

702 Therneau, T. & Lumley, T. (2011) *Survival analysis, including penalised likelihood*. R package
703 version 2.36-9. <[http://ftp.uni-](http://ftp.uni-bayreuth.de/math/statlib/R/CRAN/doc/packages/survival.pdf)
704 [bayreuth.de/math/statlib/R/CRAN/doc/packages/survival.pdf](http://ftp.uni-bayreuth.de/math/statlib/R/CRAN/doc/packages/survival.pdf)> 29th May 2016

705 Török, P., Valkó, O., Deák, B., Kelemen, A. & Tóthmérész, B. (2014) Traditional cattle grazing
706 in a mosaic alkali landscape: effects on grassland biodiversity along a moisture
707 gradient. *PloS ONE*, **9**, e97095.

708 van de Voorde, T.F.J., van der Putten, W.H. & Bezemer, T.M. (2012) The importance of plant-
709 soil interactions, soil nutrients, and plant life history traits for the temporal dynamics
710 of *Jacobaea vulgaris* in a chronosequence of old-fields. *OIKOS*, **121**, 1251-1262.

711 van Swaay, C., Warren, M. & Lois, G. (2006) Biotope use and trends of European butterflies.
712 *Journal of Insect Conservation*, **10**, 189-209.

713 Wahlberg, N. (1996) Suomen uhanalaisia lajeja: Tummaverkkoperhonen (*Melitaea diamina*)
714 *Suomen Ympäristö*, **168**. Suomen ympäristökeskus, Oy Edita Ab, Helsinki.

715 Wahlberg, N. (1997) The life history and ecology of *Melitaea diamina* (Nymphalidae) in
716 Finland. *Nota Lepidopterologica*, **20**, 70-81.

717 Wahlberg, N., Klemetti, T., Selonen, V. & Hanski, I. (2002) Metapopulation structure and
718 movements in five species of checkerspot butterflies. *Oecologia*, **130**, 33-43.

719 Wahlberg, N., Moilanen, A. & Hanski, I. (1996) Predicting the occurrence of endangered
720 species in fragmented landscapes. *Science*, **273**, 1536-1538.

- Walker, L.R., Wardle, D., Bardgett, R.D. & Clarkson, B.D. (2010) The use of chronosequences in studies of ecological succession and soil development. *Journal of Ecology*, **98**, 725-736.
- Wilcox, C., Cairns, B.J. & Possingham, H.P. (2006) The role of habitat disturbance and recovery in metapopulation persistence. *Ecology*, **87**, 855-63.
- Winkler, R.L. (2015) Equal versus differential weighting in combining forecasts. *Risk Analysis*, **35**, 16-18.
- Wood, S. (2006) *Generalized additive models: an introduction with R*. CRC Press, Boca Raton, FL.
- Yonekura, Y., Ohta, S., Kiyono, Y., Aksa, D., Morisada, K., Tanaka, N. & Tayasu, I. (2013) Soil organic matter dynamics in density and particle-size fractions following destruction of tropical rainforest and the subsequent establishment of *Imperata* grassland in Indonesian Borneo using stable carbon isotopes. *Plant Soil*, **372**, 683-699.
- Zwolak, R. (2009) A meta-analysis of the effects of wildfire, clearcutting, and partial harvest on the abundance of North American small mammals. *Forest Ecology & Management*, **258**, 539-545.

Figures

Fig. 1 Host plant density and habitat disappearance at a representative false heath fritillary habitat study site. Grey areas depict areas classified as destroyed as they have been taken back into crop cultivation. Numbers depict host plant density classes (class 0: no host plant, class 1: average distance of host plant ramets >5 m, class 2: 1–5 m, class 3: <1 m) and straight lines depict the locations of transect lines.

Fig. 2 Proportion of remaining false heath fritillary habitat study sites as a function of years since discovery, depicted as Kaplan-Meier estimator plots for a) current land use types (excluding flooded areas; see Table 1) and for b) conserved and non-conserved patches and for the estimated exponential patch disappearance rate of non-conserved sites. Median estimates (medians $\pm$ 95 % CI) are depicted for current land use types (conserved vs. non-conserved patches and the estimated exponential patch disappearance rate of non-conserved sites).

Fig. 3 Comparison of a) the fitted model for the experts' estimates of how habitat quality varies in relation to time since last management (in years; solid line) with b) the estimated host plant density at study sites against time since last management (circles) and the scaled management model impact predictions (dashed line). The grey shaded region in panel a indicates 95% confidence intervals and black dots represent the average (group) expert estimate for the different hypothetical land use histories elicited. The black dots in panel b indicate habitat sites without identified harrowing or cultivation events, to which the habitat quality model predictions were scaled. Note that a log scale was used in panel b.

Table 1 Land use type categorisation of study areas

Current land use type	Description	Number of study sites	
		SD1	SD2
Conservation area	Areas demarcated as conservation areas for the false heath fritillary by environmental authorities.	11	2
Private meadow	Meadows managed by landowners within agri-environmental schemes due to their natural value.	4	4
Tree sapling site	Tree plantation areas that are managed for commercial forest production.	9	11
Field	Areas that were under crop or fodder cultivation or as temporary fallows at the time of field study.	7	9
Open area	Areas that are otherwise not being used, but for which trees and willows are being managed to keep the site open, e.g. for aesthetic reasons or under powerline rights-of-ways. This category was not used for fields, meadows or conservation areas located under powerline areas.	5	3
Abandoned	Areas that do not have any active or planned land use e.g. due to the aging of the landowners.	9	14
Flooded area	Riverbank area that is not actively managed, but stays open due to the flooding dynamics of the river.	-	3
Total		45	46

Table 2 Parametric coefficients of the best-fitting habitat occupancy model created using normalized covariates. The significance codes have been classified as *** ($p < 0.001$), ** ($p < 0.01$), * ($p < 0.05$) and . ($p < 0.1$).

Coefficients:	Estimate	St. error	z-value	P-value	Significance code
Intercept	0.76	0.31	2.45	0.014	*
Log host plant abund. (no.)	0.82	0.33	2.50	0.012	*
Log(x+1) Tree height (m)	-0.85	0.38	-2.22	0.027	*

Table 3 Parametric coefficients and smooth terms of the best-fitting habitat quality GAM model, fitted using equal-weighted averages of individual expert estimates. For the parametric coefficients, the table shows the covariates, their coefficient estimates, standard error, t-values and p-values. For the smooth terms, the table shows estimated degrees of freedom (edf), reference degrees of freedom (ref.df), the F values and p-values. The significance codes have been classified as *** (p<0.001), ** (p<0.01), * (p<0.05) and (p<0.1).

Parametric coefficients:	Estimate	St. error	t-value	p-value
Intercept	0.763	0.0066	115	< 2e-16 ***
Smooth terms:	Edf	ref.df	F	p-value
s(Year)	4.55	4.85	114.02	< 2e-16 ***
s(Harrowing)	4.81	4.97	31.27	< 2e-16 ***

icad_12218_f1.eps

icad_12218_f2.eps

icad_12218_f3.eps

Minerva Access is the Institutional Repository of The University of Melbourne

Author/s:

Fabritius, H;McBride, M

Title:

Modelling habitat persistence and impacts of management on the habitats of an endangered butterfly

Date:

2017-05-01

Citation:

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), pp.200-210. <https://doi.org/10.1111/icad.12218>.

Persistent Link:

<http://hdl.handle.net/11343/292397>