

# **Temporal habitat dynamics and conservation planning: the case of the false heath fritillary**

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“Our key points are that disturbances are a part of ecosystem development, and that all reserves sooner or later will be subjected to disturbances. Therefore, the ecological memory of these systems, situated inside or outside the disturbed area, is of crucial importance for recovery.”

Bengtsson *et al.* (2003)

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**The thesis constitutes of the following articles, which are referred to in the text by their Roman numerals:**

- I**      **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.  
Cabeza M, **Fabritius H**, Lehtomäki J, Ovaskainen O, Rönkä K, Wahlberg N (2015): Data from: The dual role of rivers in facilitating or hindering movements of the false heath fritillary butterfly. *Dryad Digital Repository*. [<http://dx.doi.org/10.5061/dryad.j54vv>]
- II**      **Fabritius H** & McBride M (Manuscript): Modelling habitat destruction and maintenance effects in highly dynamic moist meadows.
- III**      **Fabritius H**, de Knecht H & Ovaskainen O (Manuscript): The effect of spatio-temporal dynamics of patch emergence on metapopulation viability.
- IV**      **Fabritius H** & Cabeza M (Manuscript): Spatial conservation planning in a dynamic habitat patch network.
- V**      **Fabritius H**, Jokinen A & Cabeza M (Manuscript): Temporal fit of institutions in habitat maintenance: a case study on the false heath fritillary.

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## ABSTRACT

A noticeable fraction of the World's species inhabit disturbed or early-succession habitats. Extensively managed agricultural landscapes and disturbances of natural ecosystems have, however, declined in many parts of the World. This has caused population declines in many specialist species that inhabit early-succession habitats.

When conservation plans have to be designed for early-succession habitats and their species, specific complexities emerge due to their transitional nature. First, present and future habitat dynamics might be time-consuming to estimate and project with adequate realism. Yet, an understanding of habitat dynamics is a prerequisite to a reliable assessment of species persistence in dynamic landscapes and to the selection of useful conservation strategies.

An additional source of complexity to conservation planning in dynamic landscapes arises from the multitude of alternative strategies for conservation and from the socio-political dependencies related to arranging site maintenance. Besides the establishment of protected areas, species persistence may sometimes be better supported by altering the dynamics of their transitional habitats or by establishing new transient habitat sites. Protected areas are vulnerable to discontinuities in maintenance funding, and the establishment of protected sites usually requires landowner interest in site maintenance. Additionally, alternative strategies for site maintenance vary in terms of maintenance type, intensity and frequency, and the optimal strategy is not always self-evident.

My thesis focuses on the challenges of conservation planning that are related to the maintenance of specific successional stages or disturbance frequencies in dynamically changing environments. My study species is an endangered butterfly, the false heath fritillary (*Melitaea diamina*), an endangered Finnish butterfly. The false heath fritillary has the status of a *species of strict protection* in Finland due to the rapid shrinkage of its distribution during the past decades. Conservation planning for the false heath fritillary is complicated by

the species' dependence on disturbed habitats; either human-maintained (mowed, ploughed, or grazed) moist meadows as protected sites, or a dynamically changing network of suitable early-succession sites. The Finnish conservation legislation defines specific activities to be carried out by the conservation authorities to maintain a favourable conservation status of the species, but these activities are not directly linked with sources of funding for habitat maintenance.

Together with my collaborators, I have used the false heath fritillary and its habitats as a case study to develop methods to estimate habitat destruction rates, habitat maintenance effects and the spatial emergence pattern of dynamic habitats from field data. We use metapopulation models to study how changes in the patterns of patch emergence and destruction affect population viability and how habitat dynamics affect conservation success. Finally, we contrast our results against the institutional constraints in false heath fritillary conservation.

Our results show that false heath fritillary habitats, which occur on multiple land use types, have high destruction rates and reach their best quality 2-3 years since maintenance. In simulations, the habitat turnover rate and the spatio-temporal pattern of habitat patch emergence have a significant effect both on population viability and on the effectiveness of conservation actions. The institutional constraints of false heath fritillary conservation, as the conservation institutions do not properly account for temporal habitat dynamics, have led to unpredictability in habitat maintenance resourcing and thus complicate conservation planning.

Conservation planning for species that live in dynamic landscapes would benefit from the development of best practices for cost-efficient monitoring of habitat dynamics and for the prediction of changes in the future availability of habitat. Unless the potential institutional constraints of conservation cannot be solved, their existence and the limited availability of site maintenance funding should be taken into account already during the conservation planning phase for the attainment of realistic conservation plans.

# TIIVISTELMÄ

Merkittävä osa maapallon lajistosta asuu häiriytyissä tai alkuvaiheen suksession elinympäristöissä. Ihmisen maankäyttötoiminnan tehostuessa häiriyty, suksession alkuvaiheen elinympäristöt ovat kuitenkin vähentyneet. Tämä on johtanut monien häiriöriippuvaisten lajien populaatioiden pienentymiseen.

Alkuvaiheen suksession ympäristöjen lajiston suojeleminen sisältää monimutkaisia elementtejä, jotka johtavat lajien elinympäristöjen alati muuttuvasta luonteesta. Elinympäristöjen dynamiikan riittävän realistinen arvioiminen ja tulevan maisemadynamiikan ennustaminen on työlästä. Ymmärrys elinympäristöjen muutosdynamiikasta on kuitenkin myös edellytys sille, että voidaan arvioida lajien selviytymisen edellytyksiä ja valita hyödyllisiä suojelestrategioita.

Lisää suojelehaasteita syntyy myös siitä, että suojeleminen voi toteuttaa dynaamisissa maisemissa useita erilaisia strategioita noudattaen. Kaikissa tapauksissa paras suojelestrategia ei välttämättä ole pysyvien suojelekohteiden perustamisen, vaan tilapäisten elinympäristöjen dynamiikan muuttaminen tai uusien tilapäisten elinympäristöjen luominen voi joskus tuottaa paremman tuloksen. Koska alkuvaiheen suksession elinympäristöjen säilyminen edellyttää niiden jatkuvaa ylläpitoa, suojelealueet ovat haavoittuvia hoitorahoituksen katkoksille ja alueiden perustaminen edellyttää yleensä hoitotoimista kiinnostunutta maanomistajaa. Lisäksi alueiden optimaalinen hoitotapa, -intensiteetti ja -tiheys eivät ole aina itsestään selviä asioita.

Tutkimukseni käsittelee niitä suojele suunnittelun erityishaasteita, jotka liittyvät sopivien suksessiovaiheiden ja häiriötiheyksien ylläpitoon dynaamisesti muuttuvissa ympäristöissä. Käytän tutkimukseni tapaututkimuslajina tummaverkkoperhosta (*Melitaea diamina*), suomalaista uhanalaista perhoslajia. Tummaverkkoperhonen on luokiteltu luonnonsuojeleasetuksessa erityistä suojele vaativaksi lajiksi, sillä sen levinneisyysalue on maankäytön muutosten seurauksena kutistunut rajusti vuosikymmenien takaisesta. Lajin suojele vaikeuttaa lajin riippuvuus häiriytyissä elinympäristöistä; joko ihmisen ylläpitämistä (niitetyistä,

kynnetyistä, laidunnetuista tai kesannoiduista) kosteista niityistä tai dynaamisesti muuttuvasta suksession alkuvaiheen elinympäristöjen verkostosta. Suomen luonnonsuojelelain säädäntö velvoittaa määrittelle viranomaistoimia, joiden tarkoituksena on taata lajin suotuisa suojele taso, mutta se ei osoita resurssien lähdettä lajin elinympäristöjen ylläpitoon.

Kehitämme yhteistyökumppanieni kanssa tummaverkkoperhosen ja sen elinympäristöjen avulla menetelmiä arvioida maastoaineistosta lajin elinympäristöjen hoitovastetta ja tuhoutumisnopeutta sekä uusien elinympäristöjen ilmaantumisrakennetta. Käytämme metapopulaatiomalleja tutkiaksemme, kuinka muutokset elinympäristöjen ilmaantumisessa ja tuhoutumisessa vaikuttavat populaation selviytymiseen ja vertaamme näitä tuloksia tummaverkkoperhosen suojelele institutionaalisiin rajoitteisiin.

Tuloksemme osoittavat, että tummaverkkoperhosen elinympäristöillä, joita esiintyy monilla maankäyttötyypeillä, on nopea tuhoutumistahti, ja niiden laatu on parhaimmillaan 2-3 vuotta hoitotoimien jälkeen. Simulaatioissa elinympäristöjen vaihtuvuudella on suuri vaikutus populaatioiden elinvoimaisuuteen ja suojeletoimien tehokkuuteen. Tummaverkkoperhosen suojelele institutionaaliset rajoitteet, jotka eivät ota huomioon elinympäristöjen ajallista muutosta, johtavat ennaltaarvaamattomiin vaihteluihin suojeletoimien resursoinnissa, mikä monimutkaistaa suojele suunnittelua.

Häiriytyissä ympäristöissä elävien lajien suojele suunnittelu hyötyisi kustannustehokkaista käytännöistä seurata elinympäristöjen dynamiikkaa ja ennustaa elinympäristöjen saatavuuden muutoksia. Jos suojele instituutioiden mahdollisia rajoitteita ja hoitorahoituksen vähäistä saatavuutta ei saada ratkaistua, nämä suojele rajoitteet tulisi ottaa huomioon jo suojele suunnitelmia tehdessä realististen suojele suunnitelmien aikaansaamiseksi.





# SUMMARY

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## 1 INTRODUCTION

### 1.1 TEMPORAL HABITAT DYNAMICS AS A CONSERVATION CHALLENGE

Natural disturbances have shaped landscapes and ecosystems throughout history (Sousa 1984). Disturbances of ecosystems occur as a result of abiotic causes, such as fire (Bunnell 1995), windstorms and floods (Stelter *et al.* 1997, Ballinger *et al.* 2007, Lourival *et al.* 2011, Junk *et al.* 2012, Mclaughlin *et al.* 2013) or of biotic sources, such as insect outbreaks (Simard *et al.* 2012), landscape architects (DeGraaf & Yamasaki 2003) or packs of megafauna grazers that move as pulses across the landscape (Zimov *et al.* 1995, Lake 2000, Bengtsson *et al.* 2003, Brooks 2003, Estes *et al.* 2011, Banks *et al.* 2013). Such disturbances have created communities of species that belonged to various functional groups (Bonet 2004) and offered a variety of habitats for species (Cadotte 2007, Connell 1978, Swanson *et al.* 2011). As a result, a noticeable fraction of the Earth's species have adapted to utilise early-succession habitats.

Early human settlements did little to significantly alter the patterns of disturbance in ecosystems: agriculture was often practiced by using shifting cultivation and prescribed burning, and grazing sites for cattle varied in location (Bonet 2004, Pausas 1999, Levin *et al.* 2013). European heathlands emerged 7000-4000 years ago by forest clearance and small-scale land management activities of the early Europeans (Webb 1998). In Mediterranean landscapes, human disturbance produced diverse landscape mosaics and high biodiversity (Bonet 2004, Pausas 1999, Levin *et al.* 2013). Many landscapes in North America were regularly burned by Native Americans (Long 2009). However, the intensification of human land use has caused dramatic changes to disturbance regimes across ecosystems. Large proportions of unproductive land, such as wetlands, have been modified and converted to forestry or urban

areas, and human land use has reduced forest fires and floods (Hunter *et al.* 2001, Lytle & Poff 2004, Enck & Odato 2008, Lourival *et al.* 2011). Further, agricultural modernization has led to the abandonment of less productive agricultural land, to the cessation of grazing in natural pastures (Bolliger *et al.* 2011, Meulebrouck *et al.* 2009) and to the cessation of coppicing (Warren 1987).

The abandonment of farmland has led into a long-term decrease of recently disturbed, early-successional sites that are able to develop freely, leading into the endangerment of many species that inhabit early-successional habitats (Askins 2001, Thompson & DeGraaf 2001, Long 2009). In the 2007 assessment of the conservation status of habitat types in 25 EU countries, the status of agricultural habitats, which represent a large number of disturbed and early-successional habitats, was worse than the status of other habitat types (Halada *et al.* 2011). In the northeastern US in 1966-2000, greater proportions of grassland and shrubland species were decreasing compared to forest and wetland species (Dettmers 2003). Early-successional forests, which had historically high rates of disturbances in the North-Eastern United States due to fire (Zwolak 2009), flooding and beavers (DeGraaf & Yamasaki 2003, Johnson *et al.* 2006, Long 2009) have declined between 1950 and 2000 (Brooks 2003). In Finland, 23.3 % of the endangered species are species of traditional agricultural biotopes or otherwise human-modified habitats. These habitats are, after forests, the second most important habitat for endangered species in Finland (Rassi *et al.* 2010, Similä *et al.* 2010).

### 1.2 SPATIAL CONSERVATION PLANNING FOR DYNAMIC HABITATS: MANY OPTIONS

When conservation plans have to be designed for early-succession habitats and their species, specific complexities emerge due to their transitional nature.

The fundamental characteristic of early-successional or disturbance-dependent habitats is their rapid change in the course of time; the emergence of sites following disturbances or human-originated land use activities, temporal change in site qualities in the course of time (Harper 2007, Meulebrouck *et al.* 2009), and the eventual disappearance or re-emergence of sites caused by successional processes, site destruction or renewed disturbances (Bonet 2004). One of the complexities generated by these dynamics is the fact that, without habitat management, individual habitat sites are likely to rapidly develop unsuitable for the conserved species.

How should species of such dynamic habitats be conserved? The mainstream paradigm of the systematic conservation planning literature focuses on the identification and spatial prioritization of the establishment of conservation areas, and on the maintenance of their biodiversity assets, if necessary (Margules & Pressey 2000). For early-successional habitats, this model of conservation has been in principle implemented in the field of agri-environmental biodiversity conservation, where sites with high nature values are being maintained regularly at the same sites (European Commission 2005, Aviron *et al.* 2007, Arponen *et al.* 2013) with mixed results (Kleijn *et al.* 2006, Taylor & Morecroft 2009). However, such a solution—to remove habitat dynamics by maintaining habitats continuously in an early-successional stage—is not a panacea to solve the challenge of habitat dynamics. For instance, for the conservation of later successional stages that take longer to develop after disturbance, e.g. mid-successional forests (Fartmann *et al.* 2013), and for the conservation of species for which permanent habitat networks cannot be provided, other options are needed.

Another way of organizing the conservation of early-successional or disturbance-dependent habitats is the maintenance of disturbance regimes, which term refers to the mimicking of natural disturbances to provide landscapes of all successional stages (Long 2009). The complexity of this approach lies in the fact that different species benefit from different scales, frequencies and intensities of disturbance (van Teeffelen *et al.* 2008), such as the lengths and depths of flooding (Bunnell 1995, Litvaitis 2001, King *et al.* 2001, DeGraaf & Yamasaki 2003, Miller *et al.* 2011, Junk *et al.* 2012). Many studies have taken place to measure historic, natural rates of disturbances in specific ecosystems (Lorimer 1977, 2001, Bunnell 1995, Brooks 2003), to

help conservation managers to evaluate management frequencies that would maintain maximum diversities at conservation areas. Alternatively, successional processes have been modelled at study landscapes in order to estimate how the proportional availabilities of succession stages in the future change based on alternative management scenarios (Bonet 2004, Larson *et al.* 2004, van Teeffelen *et al.* 2008, Drechsler *et al.* 2009, Levin *et al.* 2013). This approach is limited by the limited size of conservation areas where such landscape-level planning could be performed (Hinsch & Poethke 2007).

Recent studies have looked at population viability in systems that consist of permanent conservation sites and of spontaneously arising temporary habitat patches (Bunnell 1995, Cousins & Eriksson 2002, Van Rossum 2009, Wilson *et al.* 2010, Bergsten *et al.* 2013). Systems of dynamic reserves, consisting of a fixed number of temporary conservation sites that change place according to landscape changes, have also been suggested (Pickett & Thompson 1978, Cumming *et al.* 1996, Bengtsson *et al.* 2003, Rayfield *et al.* 2008, Kattwinkel *et al.* 2009, Moilanen *et al.* 2014). Van Teeffelen *et al.* (2014) suggest that conservation banking, a legal mechanism designed for the compensation of habitat destruction by the creation of new corresponding habitats, might best work with rapidly generating ecosystem types. Permanent habitat patches in a dynamic landscape are thought to function as sources of dispersers, and therefore to increase the total population size and lower the probability of extinction (Pulliam *et al.* 1992, Hodgson *et al.* 2009b). Partly for this purpose, the persistence of individual species in dynamic habitats, and the interplay of species traits with habitat dynamics, have been studied using dynamic metapopulation models (Box 1; Litvaitis 2003, Hodgson *et al.* 2009a, Drechsler *et al.* 2007, Hinsch & Poethke 2007).

### 1.3 INSTITUTIONAL CHALLENGES

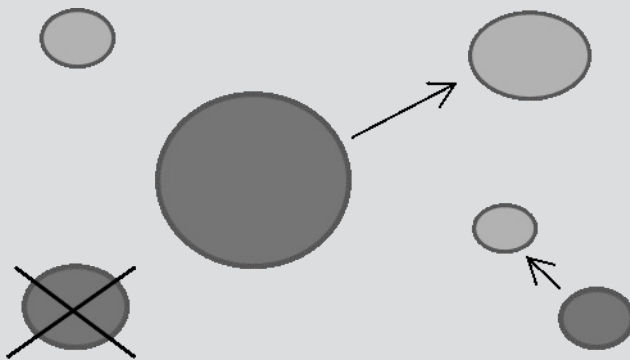
A specific complexity to conservation planning in dynamic landscapes arises from fact that disturbance-dependent habitats both emerge and disappear rapidly in the presence or absence of disturbances. Such rapid dynamics can lead into temporal fluctuations in habitat availability, which may impair the viability of populations that live in dynamic habitat networks (van Teeffelen *et al.* 2012). Therefore, continuous habitat availability relies on the existence of mechanisms that generate

## BOX 1: METAPOPOPULATION MODELS

Metapopulation models are used to study species' population dynamics in fragmented landscapes. A metapopulation consists of sub-populations, each living on a limited-sized habitat patch surrounded by a more hostile environment, the matrix. According to the theory, even if none of the sub-populations are large enough to survive as an independent population in the long term, the whole metapopulation may survive as an outcome of the extinction-colonization dynamics between habitat patches (Figure 1). A multitude of metapopulation models have been developed, varying from simple, spatially implicit models (Levins 1969, 1970) to spatially-realistic, individual-based models (Harrison *et al.* 2011). Metapopulation models have been used to study e.g. the effects of habitat fragmentation to species' viability.

Most of the developed metapopulation models have assumed that the habitat patch network inhabited by the studied species is temporally static. The effects of habitat fragmentation have been studied by comparing metapopulation persistence at differentiated landscapes. Some, however, have combined a model of species' extinction-colonization dynamics with models on the temporal change in habitat. Many such models have modelled habitat dynamics e.g. on a landscape grid of squares (Keymer *et al.* 2000, Johst *et al.* 2002, Kun *et al.* 2009, Meulebrouck *et al.* 2009) or hexagons (Pulliam *et al.* 1992, Johst & Drechsler 2003). Many spatially realistic models have been based on fixed locations of habitat patches across the landscape, each patch being either available or non-available or in one of multiple alternative states of habitat availability at any point of time (Hastings 2003, Ellner & Fussmann, 2003, Hinsch & Poethke 2007).

Studies on metapopulations living in dynamic landscapes have looked into the effects of the spatial-temporal dynamics of habitat patches to population viability. In such contexts, metapopulation models have been used to show e.g. that populations living in dynamic environments experience higher local extinction rates (Boughton & Malvadkar 2002, Johst *et al.* 2011) and lower habitat occupancy (Fahrig 1992, Keymer *et al.* 2000, Amarasekare & Possingham 2001, van Teeffelen *et al.* 2012, Cornell & Ovaskainen 2008, Hodgson *et al.* 2009a) and thus need higher long-term average population sizes for survival (Gyllenberg & Hanski 1997, Hanski 1999, Biedermann 2004, 2005) than similar populations living in stable environments.



**Figure 1. A schematic illustration of extinctions and colonizations in a habitat patch network.** Circles depict occupied and unoccupied habitat patches in dark grey and light grey, respectively. Circle sizes depict the sizes of the habitat patches. Arrows illustrate colonizations of unoccupied habitat patches by the species via dispersal events from nearby occupied habitat patches. A cross indicates a local extinction at an occupied habitat patch. Many spatially realistic metapopulation models assume that the probability (discrete-time models) or rate (continuous-time models) of colonization of an unoccupied habitat patch is a function of its size and connectivity to nearby occupied habitat patches. Likewise, the probability or rate of extinction of an occupied patch is often modelled as a function of patch size (e.g. Ovaskainen & Hanski 2003). Patch size is sometimes scaled based on patch quality.

disturbances and reset succession at overgrown sites (Harper 2007). Due to this rapid temporal response to changes in land use or disturbance patterns, protected areas established for early-successional species have a particular vulnerability to discontinuities in maintenance funding (Moilanen *et al.* 2014). This places emphasis on conservation institutions and their ability to guarantee continuity in the resourcing of site maintenance.

The maintenance of early-succession habitats usually requires co-operation with landowners and landowner interest and capability to maintain early-succession habitats (Harper 2007). Strategies for site maintenance vary in terms of maintenance type, intensity and frequency (Lytle & Poff 2004, Harper 2007, Toivonen *et al.* 2015), and therefore, the optimal maintenance strategy may vary between species and taxa (Pöyry *et al.* 2006, van Teeffelen *et al.* 2008). These factors complicate conservation planning and the types of data on habitat dynamics that are needed for making effective conservation choices (Box 2).

### 1.4 A CASE STUDY ON THE FALSE HEATH FRITILLARY (*MELITAEA DIAMINA*)

An example of a species that suffers from the decrease of processes that regenerate its habitat the false heath fritillary *Melitaea diamina* (Lang, 1789). The false heath fritillary is an endangered Finnish butterfly that has been listed as a species in need of special protection in Finland since 1989. The false heath fritillary is dependent on its larval host plant, *Valeriana sambucifolia*, a pioneering species of moist soils. The false heath fritillary has probably benefited from the age-old land use methods and patterns of traditional agriculture; small-scale tilling, harrowing and mowing probably used to create open, early-succession plots, which *V. sambucifolia* was then able to colonise (Liinalaakso 2000). Eventually, however, the modernisation of agriculture led to the cessation of cattle grazing in natural meadows and resulted into the forestation of remaining moist soils. This led to the rapid decline of the false heath fritillary population (Liinalaakso 2000, Wahlberg 1998). In the beginning of the 21st century, the species was known to have only three known metapopulations in the Pirkanmaa (Tampere) Region and another known, isolated distribution close to the city Kristiinankaupunki (Wahlberg 1998).

Conservation planning for the false heath fritillary is complicated by the species' dependence on disturbed habitats; either human-maintained (mowed, harrowed, or grazed) moist meadows as protected sites, or a dynamically changing network of suitable early-succession fallows. In the Pirkanmaa Region, where the species has been known to exist for decades, most of its historic habitat has disappeared, and much of the remaining habitat is in the process of being suffocated by excess vegetation (Liinalaakso 2000, Intke 2003, Kekkonen & Rönkä 2009). Sporadic habitat maintenance activities have taken place depending on the resources of the regional environmental (ELY) centre (Heliölä 2000). Population dynamics of the false heath fritillary have been studied in the Pirkanmaa Region by Wahlberg (1997), Wahlberg *et al.* (1996, 2002), Moilanen & Cabeza (2002), Ovaskainen (2004) and Cabeza *et al.* (2010).

During monitoring surveys in 2009 and 2010 around the Kristiinankaupunki area, the less well-known distribution region of the false heath fritillary at the West Coast of Finland proved wider than originally thought; the species was found to occupy a larger area along the West Coast of Finland that spanned over three administrative regions. The new findings posed questions on what had helped the false heath fritillary to survive in the West Coast distribution region without conservation activities, and where and how the species' habitats should possibly be conserved in the area

## 2 THESIS OUTLINE

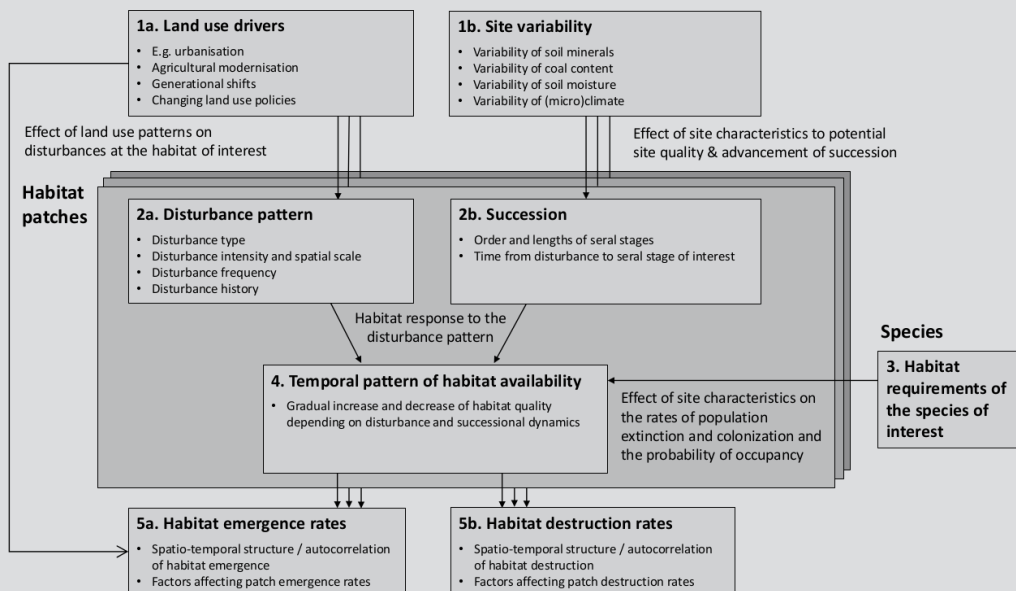
In this thesis, I present five articles that address the challenge of conservation planning in dynamic landscapes from various angles. By using the conservation planning of the false heath fritillary as a case study, I develop methods that increase the practical toolbox of methods for the study and estimation of both population viability and landscape dynamics. Specifically, I aim at answering the following questions:

1. Without the availability of long-term data on temporal habitat dynamics, how can habitat dynamics be cost-efficiently estimated to aid conservation planning? How could conservation managers record and monitor habitat dynamics cost-efficiently over time?

## BOX 2: WHAT KIND OF DATA ON HABITAT DYNAMICS ARE NEEDED FOR CONSERVATION PLANNING?

The empirical data required to study spatio-temporal patterns of habitat availability in dynamic landscapes depends on the questions being studied (Figure 2). In some cases, the question of interest is simply to understand the effect of landscape dynamics on species viability, or the interplay of landscape dynamics with species-specific traits. For instance, many metapopulation studies have looked at how changes in the rates (Fahrig 1992, Amarasekare & Possingham 2001, DeWoody *et al.* 2005, Johst *et al.* 2011) or spatio-temporal patterns of habitat emergence and destruction (Figure 2, boxes 5a-5b; Boughton & Malvadkar 2002, Wilcox *et al.* 2006, Radchuck *et al.* 2014) affect species in fragmented landscapes. Other studies have looked at the interplay of species' habitat requirements with landscape dynamics (Verheyen *et al.* 2004, Cizek & Kovicna 2005, Mortelliti *et al.* 2010, Heer *et al.* 2012, Pennekamp *et al.* 2014) and how such spatio-temporal changes in habitat suitability affect species occupancy and colonization and extinction rates (Figure 2, boxes 3-4; Jäkäläniemi *et al.* 2009, Caruso *et al.* 2010).

Studies that aim at providing useful data for habitat maintenance planning may be a need to tease apart the processes of habitat succession (Figure 2, box 2b) from those of habitat disturbance (Figure 2, box 2a) and site variability (Figure 2, box 1b; Cousins & Eriksson 2002, Bonet 2004, Harper 2007, Mclaughlin *et al.* 2013, Török *et al.* 2014), in order to identify which maintenance activities will help ensure adequate habitat availability for the species of interest. This might be particularly relevant in the case of meadow ecosystems, due to their differential responses to alternative maintenance methods (DeGraaf & Yamasaki 2003, Rook *et al.* 2004, Humbert *et al.* 2010) and to different maintenance histories (Cousins & Eriksson 2002, Johansson *et al.* 2008, Meulebrouck *et al.* 2009). In studies that attempt to make habitat availability projections into the future, information on land use drivers might also be required (Figure 2, box 1a).



**Figure 2. Dynamic habitats, disturbance patterns and their causes.** Disturbance-dependent habitats depend on either human land uses or natural disturbances in their provision. In the landscape level, (the spatio-temporal pattern of) habitat availability is an outcome of complex interactions of habitat succession, landscape variability, land use and disturbance patterns, and the habitat requirements of species. Chapter II of this thesis addresses 2a-2b, 3, 4 and 5b and Chapter III addresses 1a-1b and 5a using false heath fritillary field data.



2. How sensitive are population viability estimates and the best choices of spatial conservation plans and strategies to habitat network dynamics?
3. What are the consequences to conservation if conservation institutions fail to account for temporal habitat dynamics? How can such vulnerabilities in conservation institutions taken into account in conservation planning?
4. How should potential regional differences in habitat structure and dynamics be taken into account in conservation planning in dynamic landscapes?

In Chapter **I**, we build basis for answering the question 4 by studying the similarity of three false heath fritillary populations in Finland. In a case study, we compare the movement patterns of the false heath fritillary across a riparian landscape and a more mosaic-like inland landscape. We show that although the habitat-specific movement patterns of the false heath fritillary do not differ significantly across the distribution regions, the habitat-specific movement patterns result into more directional, longitudinal movement patterns in the riparian environment. More generally, we demonstrate how habitat-specific movement models can be used to compare species' movement patterns across structurally different landscapes. The results of Chapter **I** also lays the basis of the work carried out in the chapters **III** and **IV** by showing that the habitat-specific movement parameters of the false heath fritillary do not differ significantly across distribution regions, after which we utilise data from Pirkanmaa Region to model metapopulation dynamics in the West Coast.

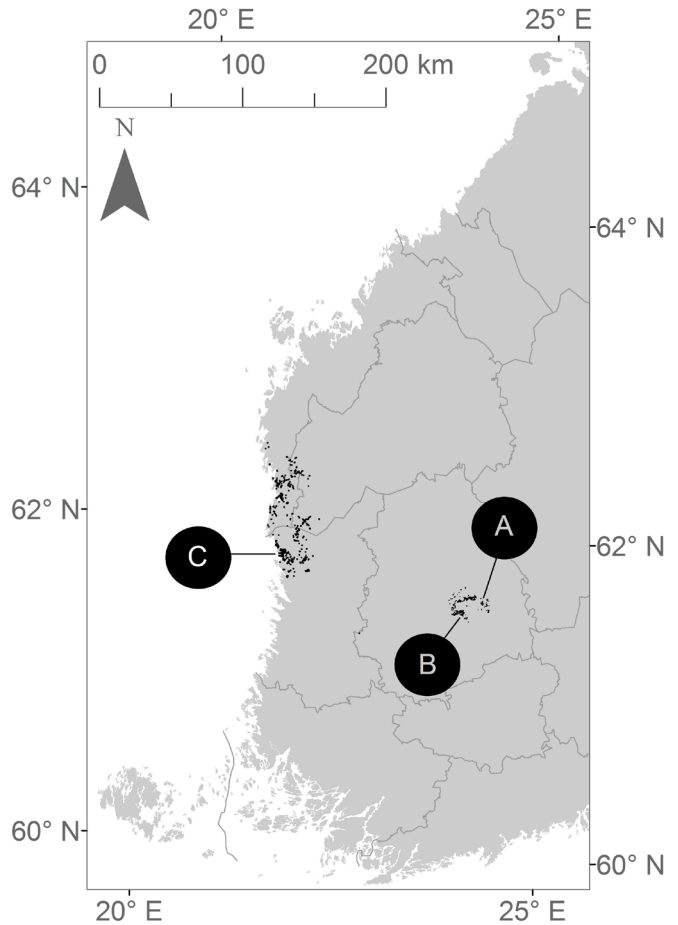
In Chapter **II**, we mainly address the study question 1 by using field surveys, site maintenance history data and expert elicitation to estimate habitat destruction rates and habitat maintenance effects at false heath fritillary habitat sites. As we collected habitat data on both distribution regions, we also address the study question 4 by studying the similarity of habitats and habitat destruction rates across the distribution regions. According to our results, the non-conserved false heath fritillary habitats covered 86 % of the study sites and were relatively dynamic with an expected patch lifetime of 16.8 years. Habitat site quality was maximized in 2-3 years after site maintenance both in the experts' estimates, which corresponded well with the field data. False heath fritillary habitats differed slightly between the regions and had a tendency towards

higher destruction rates in the West Coast distribution region. Field surveys, site maintenance history data and expert elicitation can provide a relatively fast and cost-efficient way to estimate temporal patterns in successional habitats.

In Chapter **III**, we continue to address question 1 by creating a landscape-scale habitat suitability model for the occurrence of false heath fritillary habitats and combine it with a metapopulation model with a model on habitat network dynamics. By doing this, we demonstrate a way to improve the spatial realism of modelling the emergence patterns of transient habitat patches. We also address question 3 by demonstrating how the spatio-temporal pattern of habitat emergence, which can be sensitive to changes in e.g. weather events, land use practices or generational shifts, affects population viability even when the total availability of habitat remains stable. In this work, we show how disturbance-generating events that act on moderate time scales, such as generational shifts in land use patterns, can have significant longer-term effects on the availability of transient habitats and population persistence.

In Chapter **IV**, we focus on the question 2 and demonstrate the crucial role of understanding habitat dynamics to the success of conservation scenarios in dynamic landscapes. We simulate the persistence of our study species, the false heath fritillary, in a dynamic network of habitat patches across a wide range of habitat destruction and emergence rates and across alternative conservation scenarios. Our results show that the optimal spatial configuration of conservation sites and the minimum number of sites needed to reach a pre-defined conservation target depend on the habitat dynamics of the system. Conservation plans for species living in dynamic habitats should, therefore, be based on an understanding of the dynamics of the species' habitat network and this understanding should be taken into account in reserve selection.

Chapter **V** is a study of the institutional setup of the conservation of the false heath fritillary in Finland. As such, it focuses on the study question 3 and reveals a temporal misfit in the conservation institutions that are responsible of conservation planning for the false heath fritillary. Additionally, the availability of maintenance funding varies according to the ownership category the sites to be maintained, the type of maintenance activities planned and other annual conservation priorities. These



**Figure 3. The false heath fritillary distribution in Finland.** False heath fritillary habitats are depicted in black. Regional administrative borders are depicted with grey borders. The three capture-recapture study areas (I) are depicted with capital letters A-C.

institutional restrictions should, and can, be taken into account in conservation planning by prioritizing or establishing protected areas at sites where the landowner is both interested in false heath fritillary conservation and eligible to apply for the most long-term available funding source of habitat maintenance, the agri-environmental support contract. An assessment of temporal fit (or, more generally, institutional fit) of conservation institutions can also point out ways on how conservation institutions could be improved to better take the habitat dynamics of successional habitats into account in their organization of activities.

### 3 MATERIAL AND METHODS

#### 3.1 STUDY AREAS

The false heath fritillary distribution in the Pirkanmaa Region (61.58°N, 24.05°E, 700 km<sup>2</sup>, Figure 3) was

located 10-20 km to the North of the city of Tampere in Finland. The known false heath fritillary distribution in the region consisted of 271 known present or historical habitat patches of for which the regional environmental centre had maintained records for decades, with the help of the local entomological society. Of the total 271 identified patches, 124 of the recorded sites had had records of false heath fritillary sightings in at least one year during irregular surveys conducted from 1995-2012, while 147 have remained without sightings. The oldest known habitat patches included 94 patches that were recorded in 1995, 59 of which were empty and 35 occupied at the time of recording, and 10 ten occupied patches that were recorded in 1997. 14 of these oldest patches have been officially demarcated as false heath fritillary habitats by environmental authorities in 2000-2007, which status forbids land use activities that would decrease the quality of the sites as false heath fritillary habitats. Population dynamics of the false heath fritillary had been studied in the Pirkanmaa Region by Wahlberg

(1997), Wahlberg *et al.* (1996, 2002), Moilanen & Cabeza (2002), Ovaskainen (2004) and Cabeza *et al.* (2010). Before the start of my project, successional patterns of false heath fritillary habitat patches had been studied in a M.Sc. project (Intke 2003), but knowledge or field data concerning habitat overgrowth had not been systematically collected nor integrated to the species-specific studies. A recent field survey report (Kekkonen & Rönkä 2009) indicated that a large number of known habitat sites were overgrown.

In the beginning of my thesis project in 2010, the false heath fritillary distribution along the West Coast of Finland (62.25°N 21.5°E) was less well known. A total of 70 (65 in South Ostrobothnia and Ostrobothnia, 5 in Satakunta) patches had been recorded in 1996-2004 by the regional environmental authorities and two of the sites had been acquired by the government to be maintained as false heath fritillary habitats. In 2009-2010, a university collaboration had revealed a larger distribution, covering a 3 200 km<sup>2</sup> area and including altogether 70 more habitat patches, but the area had not been entirely surveyed, the total extent of the distribution had not been studied and landowners of the sites were unknown. It was not known to which extent the false heath fritillary populations or their habitats in these two distribution regions were differentiated, and therefore, how well field data acquired in one of the distribution regions could represent the populations and habitats of the other. There was much more data available on false heath fritillary population dynamics and on habitat maintenance methods and histories in the Pirkanmaa Region. However, the need for conservation planning was more urgent in the West Coast region, where the new distribution areas had just been discovered.

### 3.2 CAPTURE-RECAPTURE DATA AND MOVEMENT ANALYSIS

We started the project by studying to which extent the false heath fritillary populations were differentiated across the distribution regions in terms of life history traits and movement patterns. In Chapter I, we utilized the existing capture-recapture data sets collected by Wahlberg (1996) and by Ovaskainen & Cabeza (2007) in the Pirkanmaa Region and compared the habitat-specific movement patterns to a third capture-recapture data set that we collected in 2011 at the Merikarvia river area in the newly discovered distribution region (Figure 3).

The work consisted of the estimation of habitat-specific movement parameters in the West Coast population, validation of the similarity of these parameters and movement patterns across study populations, and of simulations of false heath fritillary movements in real, modified and altered landscapes. We hypothesised that (H1) the coastal populations of the false heath fritillary are similar to the inland populations of the species in terms of habitat-specific movement parameters, but that (H2) the longitudinally structured riparian landscapes of the coastal distribution result into more directional, longitudinal movements than the mosaic-like landscapes of the inland populations. We assumed that the resulting connectivity across larger spatial scales could decrease metapopulation susceptibility to the effects of local climate variations, thus enforcing metapopulation persistence in the riparian landscapes.

### 3.3 FALSE HEATH FRITILLARY DISTRIBUTION SURVEY IN THE WEST COAST DISTRIBUTION

To be able to model false heath fritillary population dynamics in Chapters III-IV and to assess conservation scenarios in Chapter IV using the habitat patch network of the newly discovered West Coast distribution, we continued the habitat distribution survey in the West Coast distribution area in 2011-2012. During the survey, potential sites for habitat patches were first searched from aerial photographs across the region, after which promising sites were visited in the field. Sites were delineated as habitat patches 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. Patches were given a quality classification in the range of 0-3 (0 still classified as a patch) based on the above mentioned criteria and the number of false heath fritillary sightings. Each year of the survey, some of the previously identified habitat patches were revisited to reassess their habitat quality and occupancy. After the survey of year 2012, we concluded that the extent of the distribution was adequately well known (no new occupied habitat patches could be found anymore beyond the known distribution; Figure 3) and habitat patches within the distribution were adequately surveyed.



### 3.4 FIELD SURVEYS OF FALSE HEATH FRITILLARY MEADOWS AND LANDOWNER QUESTIONNAIRES

In Chapter II, we wanted to estimate habitat destruction rates and maintenance effects from field data, to better understand how time since site delineation (identification in the field) and time since last maintenance would affect meadow quality and persistence. For this purpose we collected data on the vegetation of 104 false heath fritillary meadows that had been delineated at different time points in the past. The data consisted of field surveys of the study sites and maintenance history data that we collected from ELY centre records and from study site landowners via questionnaires.

Fieldwork in the Pirkanmaa Region was carried out at 35 sites in 2012 and at the West Coast region at 69 sites in 2012-2013. At each study site, we marked clearly distinguishable destroyed areas as polygons in the map. Next, we recorded average false heath fritillary occupancy, host plant density, soil moisture, tree height and cover, willow height and cover, average height of grassy vegetation and forb cover in the remaining study site area. We approached study site landowners at their homes, or via phone calls or information sharing mails and asked them to define the current land use type of the study area and detail every maintenance activity that had been carried out at the study site during the past 15 years. We recorded the types and years of site maintenance activities carried out as free-form text. Maintenance activities were classified into four types: cultivation, grazing, mowing, and harrowing. From this maintenance history data we estimated the following parameters: *years since last maintenance*, *maintenance intensity*, and the number of years with cultivation, mowing, grazing or harrowing activities. We also estimated the *historical land use type* (oldest known land use type, preferably from pre-modern decades, using the following classification: meadow, pasture, field or clearcut) and the *current land use type* (conservation area, private meadow, tree sapling site, field, open area, abandoned or flooding area) for each site.

We used the field survey data and maintenance history data to create habitat overgrowth and maintenance effects models for the false heath fritillary and to estimate patch destruction rates in Chapter II. Since the false heath fritillary distribution survey raised interest in the regional ELY centres of the West Coast

distribution region in conservation planning of the false heath fritillary population, we also inquired the respondents in the West Coast on their interest in false heath fritillary conservation. Information on landowner willingness to conservation was used in Chapter IV to identify candidate conservation sites for conservation and to compare conservation scenarios in the South Ostrobothnia region.

### 3.5 EXPERT ELICITATION ON THE MAINTENANCE EFFECTS OF MEADOWS

Since the retrieved maintenance history data that we collected for Chapter II had a risk of being inaccurate because of the lack of written records on maintenance histories, we asked nine experts on meadow succession to provide estimates of false heath fritillary meadow succession and response to disturbance. We gave the experts descriptions of 20 imaginary hypothetical meadows that had the same environmental characteristics but varying maintenance histories for the past 15 years, such as different frequencies of field cultivation, grazing, mowing and harrowing activities. These combinations of land use histories were drawn from the types of maintenance histories elicited in the landowner interviews. We then used both the expert estimates and the field data (host plant densities at study meadows with respect to the site maintenance histories of the respective sites) to create a model of the habitat maintenance effects of false heath fritillary habitats.

### 3.6 METAPOPOPULATION MODEL WITH LANDSCAPE DYNAMICS AND A HABITAT SUITABILITY MODEL

To simulate the effects of habitat network dynamics and conservation scenarios to false heath fritillary population viability in Chapters III-IV, we created a continuous-time dynamic metapopulation model that incorporated the extinction-colonization dynamics of the false heath fritillary with the habitat emergence-destruction dynamics of its habitat patch network. To add spatial realism to the patch network dynamics, we modelled the present locations and areas of the false heath fritillary habitat patches in the West Coast region by using soil suitability, distance to fields, distance to rivers and Topographic Wetness Index as environmental covariates, and used the resulting prediction of patch

occurrence probabilities to control for habitat emergence rates across the study landscape. In Chapter **III**, we used spatial random fields to simulate disturbance-generating events of different temporal scales (characteristic decay times of 2, 15 and 50 years) across the landscape. We then simulated the metapopulation persistence of the false heath fritillary in a landscape in which habitat turnover rates and changes in the disturbance-generating patterns varied.

In Chapter **IV**, we used the data on the 18 available candidate conservation sites in the South Ostrobothnia region to assess alternative conservation scenarios across varying habitat emergence and destruction rates. We compared alternative candidate sets of conservation sites that were based on varying spatial configuration in terms of their effects to the resulting patch occupancy at the end of 50-year simulations. We then used the modelling outcomes to rank individual candidate sites, and tested how the number of protected sites affected patch occupancies across varying habitat emergence and destruction rates.

Not all of the field data collected in Chapter **II** on the habitat dynamics of the false heath fritillary were used in the simulations. Both of our metapopulation models (Chapters **III-IV**) modelled habitats in terms of their size, location and availability only, without incorporating a model on temporally changing habitat quality. The results on the maintenance response of false heath fritillary habitats was therefore not used in our analyses, but saved for future use. We also used a wider range of habitat destruction rates in Chapters **III** and **IV** than the confidence interval of habitat destruction rates estimated for the false heath fritillary in our field study in Chapter **II**. This was done partly for general interest, to study how a larger parameter space would affect model outcomes, but partly also because habitat destruction rates are prone to changes in land ownership or agricultural policies, which might also affect habitat dynamics of the false heath fritillary in the future.

### 3.7 THEMATIC INTERVIEWS OF POLICY INSTITUTIONS AND CONSERVATION PRACTICES

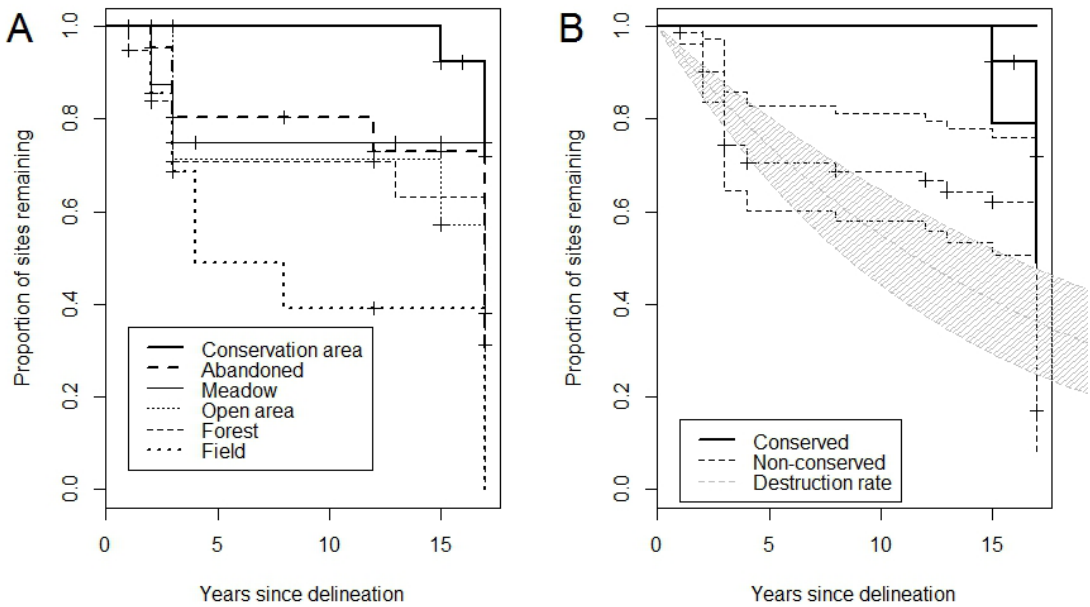
In Chapter **V**, we wanted to contrast the learnings from chapters **III-IV** against the reality of the conservation institutions that were used to conserve the false heath

fritillary in Finland. We studied the institutional setup of the conservation of the false heath fritillary in Finland. We carried out thematic interviews with six senior advisors or civil servants who work in the environmental administration to detail the decision-making processes, goals, collaborations and practices of false heath fritillary conservation in Finland. Based on the interviews, we outlined the collaboration structures and dependencies in the spatial conservation planning and funding allocation using the conceptual framework of temporal fit, which we used to assess the institutional performance of the related conservation institutions. We contrasted the interview outcomes against the annual funding of false heath fritillary conservation in the ELY centre of Pirkanmaa Region and against expert opinions on how many other endangered species faced similar conservation dilemmas in Finland.

## 4 RESULTS AND DISCUSSION

### 4.1 METHODS TO ESTIMATE LANDSCAPE DYNAMICS IN A COST-EFFICIENT MANNER

Understanding the habitat dynamics of early-successional species is important for reliable assessment of species persistence in dynamic landscapes and for the selection of useful conservation strategies. We demonstrate that maintenance effects, habitat overgrowth rates, habitat destruction rates (**II**) and a landscape-level model of habitat patch occurrence probabilities (**III**) can be estimated from snapshot data, even when data on habitat and landscape dynamics has not been purposefully recorded. In our case study on false heath fritillary habitat dynamics (**II**), 86 % of the studied sites belonged to the group of non-conserved habitats, which had an estimated average lifetime of 16.8 years (Figure 4). Habitat site quality was maximized 2-3 years after site maintenance in the experts' estimates, which correlated well with field data. False heath fritillary habitats had higher destruction rates at non-conserved sites in comparison to conserved sites, showed a tendency towards higher destruction rates in fields in comparison to other land use types and showed a tendency towards higher destruction rates in the West Coast distribution region in comparison to Pirkanmaa region. A GIS-based analysis on the locations of false heath fritillary habitats (**III**), on the other hand, demonstrated that the occurrence of false heath fritillary habitats depends on the right type of hydrology and nutrients in the soil, due to which habitats mostly



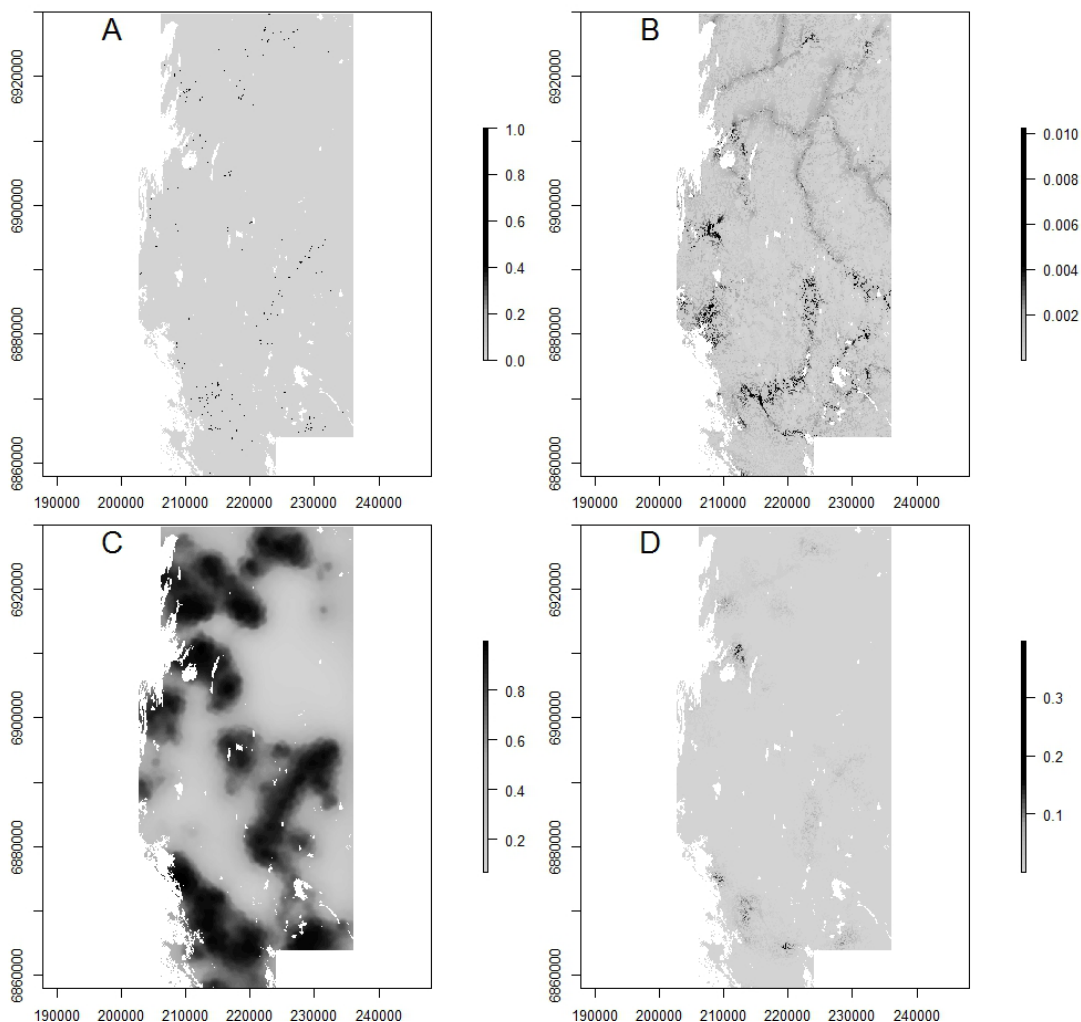
**Figure 4. Habitat patch destruction rates at conserved and non-conserved sites.** The graph depicts the proportion of remaining habitat patches as a function of years since the original delineation of the meadows. Study sites are classified based on their land use type (panel A) and based on their conservation status (panel B). The destruction curves are shown with confidence intervals for conserved and non-conserved sites (panel B). Panel B also depicts the estimated exponential patch destruction rate of non-conserved false heath fritillary habitats with 95 % confidence intervals. For details, see **II**.

occur along narrow stripes of calcareous soils across the landscape (Figure 5). Results such as these may prove useful in the assessment of the need for conservation actions in dynamic landscapes, taken that the sampling of study sites has been carefully planned to give accurate data on landscape dynamics.

Estimates of temporal habitat dynamics that have been comprised based on snapshot data come with a risk of being less accurate than estimates comprised based on long-term follow-up of experimental sites (see **II** for further discussion). Therefore, once a need for understanding habitat dynamics has been identified for a study case of interest, it becomes justified to develop monitoring practices in order to retrieve more accurate data of habitat dynamics in the course of time. Several parameters of temporal habitat dynamics, such as estimated tree height and cover and host plant density, could be regularly and systematically monitored during field surveys that are targeted for gathering data on the occurrences of species of interest. This would require detailed instructions on how to objectively estimate various measures of habitat quality in order to minimize the risk that estimates of temporal change would be

caused by differences in people's subjective estimation of study site characteristics. Maintenance activities and land use types should also be classified and systematically recorded.

Our case study (**II**) demonstrated that changes (e.g. extensions) in habitat site delineations may complicate the estimation of habitat dynamics unless properly recorded. One alternative for addressing this challenge could be to delineate habitat patches in at regular time intervals, which would then provide data on temporal change in the sizes of habitat patches, or to always maintain original site delineations, and record site extensions as adjacent sites and partial destructions as temporal developments of the original sites. It should also be noted that the retrieval of data on changes in habitat quality or on habitat destruction rates is easier than the retrieval of data on habitat emergence rates, since already identified habitat patches are at discrete locations and thus easier to follow. Therefore, in this study, we did not seek methods for the estimation of habitat emergence rates from field data, but rather we run our simulations using several alternative emergence rates (**IV**) to see how a range of emergence rates affected simulation outcomes.



**Figure 5. Prediction on the locations of habitat patches based on environmental covariates.** Panel A depicts the location of meadows in the West Coast study area landscape, panel B depicts the probability of meadow occurrence based on the linear component predictor of the chosen predictive habitat suitability model, panel C depicts the estimated random field generated by the chosen of the habitat suitability model predictive model and panel D depicts the probability of meadow occurrence based on the combined effect of the linear predictor and the random field. For details, see **III**.

#### 4.2 CONSERVATION OUTCOMES ARE SENSITIVE TO HABITAT DYNAMICS

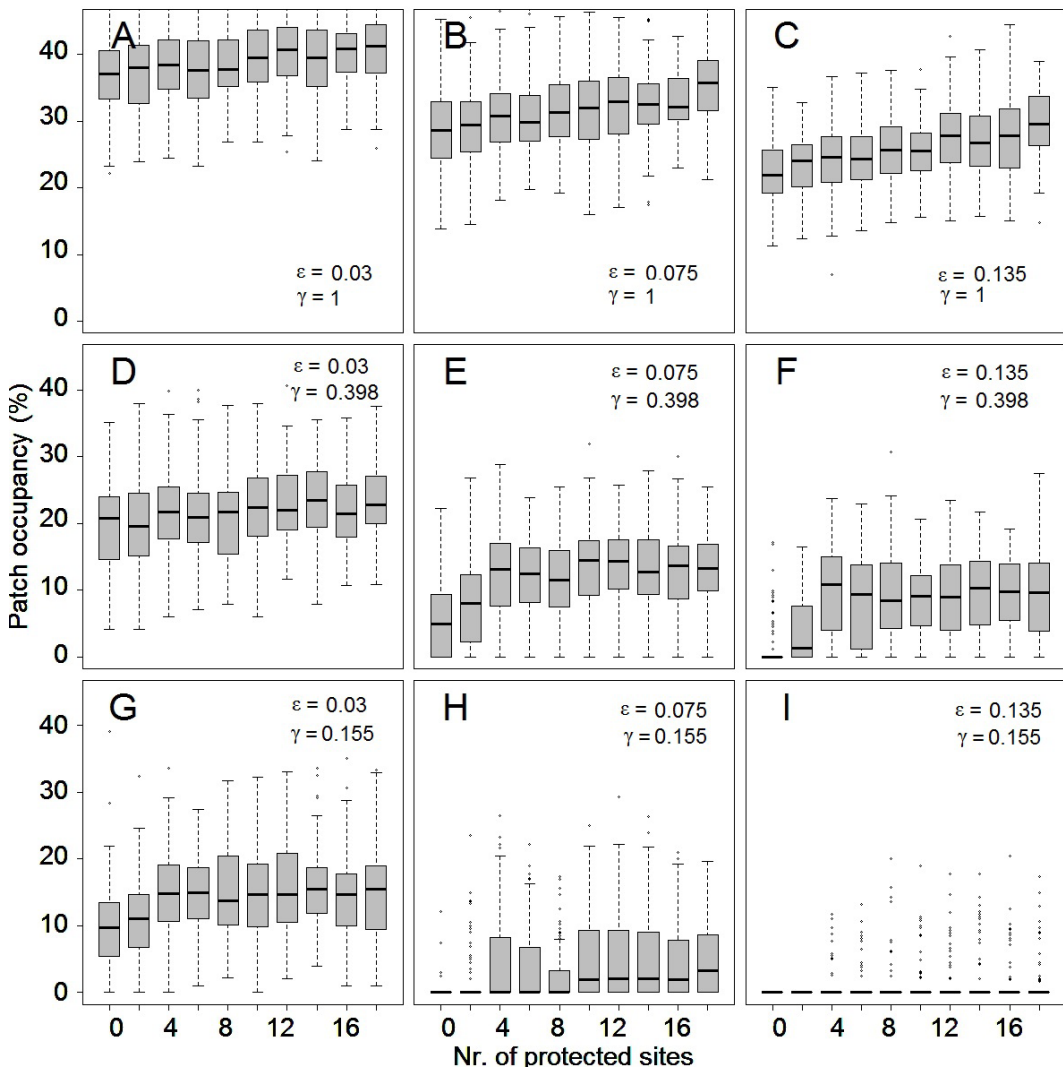
The value of methods for estimating habitat dynamics is emphasised by our findings that both population viability (**III**) and the conservation sites—number and spatial configuration—needed to reach pre-defined conservation targets (**IV**) may depend strongly on the habitat dynamics of the system. In other words, our study demonstrates that habitat network dynamics

have a significant impact on how much the spatial configuration and number of conservation sites affect population persistence. In our simulations, false heath frutillary populations were able to persist in very dynamic landscapes with high rates of patch destruction, as long as continuous habitat availability was ensured either by high emergence rate of transient habitat patches at the locations of the existing patch network (**III**) or by well-placed networks of protected sites (**IV**). In a comparison of conservation scenarios (**IV**), patch

occupancy either showed a clear threshold at the point of four highest-ranked candidate sites protected, after which patch occupancy could not be improved by protecting more of the available candidate sites, or patch occupancy increased in a linear manner with increasing number of protected sites, depending on patch network dynamics (Figure 6). An estimate of habitat network dynamics or that of the most likely locations of habitat patch emergence would therefore not only provide a better projections on population viability, but it would also allow a more realistic comparison of the costs and benefits of alternative conservation options and rule

out impossible landscape scenarios from conservation planning.

Many studies of spatial conservation planning do not take the emergence and availability of transient habitats into account when prioritizing potential habitat sites for conservation. Instead, they attempt at maximizing the probability of persistence of the targeted species within the network of conservation areas, regardless of the fate of habitats outside of the planned conservation network (e.g. Cabeza 2003, Moilanen & Cabeza 2007). Such spatial prioritization tools have favoured spatial



**Figure 6. The effect of the number of protected sites to patch occupancy.** Panels A-I depict the patch occupancies of the analyses based on increasing numbers of protected sites included in the simulations. In each panel, the results have been shown for a different combination of annual habitat patch destruction ( $\epsilon$ ) and emergence rates ( $\gamma$  scales patch emergence rates proportionally in relation to the patch destruction rates). Adopted from IV.



aggregation of protected sites for false heath fritillary conservation, since high connectivity between protected sites increases population persistence (Moilanen & Cabeza 2002). Our results imply that a set of protected sites that would have been selected using such an approach would most likely have performed well also in our dynamic study system, especially with such habitat dynamics where conservation would have made the greatest difference to species survival (i.e. when patch destruction rates were fast; **IV**). If conservation resources are abundant, a selection of protected sites that ensures self-sustained population persistence regardless of habitat dynamics would naturally be the safest conservation option. Choosing an aggregated cluster of protected sites in a dynamic system has also been found to increase population survival in other studies of dynamic landscapes (Litvaitis 2001, Drechsler *et al.* 2007, Hinsch & Poethke 2007, Hodgson *et al.* 2009b) and has been found to increase metapopulation persistence in dynamic landscapes (Johst *et al.* 2002, Johst & Drechsler 2003).

Three aspects in our analyses, however, suggest that understanding patch network dynamics may help to use conservation resources in a more cost-efficient manner in the conservation of early-successional species. One of them is the potential difficulty of identifying an adequate number of closely located sites where the landowner is interested in managing sites for conservation purposes. Further, false heath fritillary meadows require regular maintenance to retain good quality (**II**), and in Finland, such frequent maintenance of early-succession habitats is best organized via paying compensations to eligible landowners via agri-environmental schemes (European Commission 2005, Arponen *et al.* 2013). In such a case, an establishment of a well-connected network of conservation sites would require finding areas where many landowners are interested in managing sites for conservation purposes. We demonstrated such site selection (**IV**) by choosing candidate conservation sites based on landowner capability for site maintenance, but the low number of resulting candidate conservation sites (**IV**) and our organizational analysis (**V**) suggest that a large fraction of landowners are either not interested in, or not eligible for, support via agri-environmental schemes. Since early-successional habitats can be fast to develop in suitable environmental conditions, a potential workaround could be to look for areas where large enough clusters of conservation sites could be created with landowner consent and co-operation (Thompson &

DeGraaf 2001, Brooks 2003, DeGraaf & Yamasaki 2003, Rayfield *et al.* 2008, Ross *et al.* 2008). A well-designed habitat suitability model (**III**) could be of help in the planning where new protected sites could be created, as it would help to avoid using conservation resources at sites that have low probabilities of developing high-quality habitats for the species of interest.

Second, our analysis demonstrated that time lags until the destruction of non-conserved patches may affect population viability and the optimal placement of conserved patches within reasonable time scales (e.g. 50 years; **IV**). As conservation and land use policies change over time, and changes in land use practices might cause rapid changes in the availability of spontaneously arising early-successional sites (DeGraaf & Yamasaki 2003), it might be reasonable to define conservation targets within a limited time frame and then reassess the need of conservation (Moilanen *et al.* 2014). In our case study, a factor that could cause rapid changes in habitat dynamics is the fact that study sites that were in an active fallowing-cultivation cycle showed a tendency towards faster destruction rates than other types of non-protected habitats (**II**, Figure 4, panel A). It is possible that habitat destruction in the false heath fritillary study system might be modelled best by including three temporal classes of sites: permanent, successional and transient (sites that develop according to faster-than-normal successional dynamics due to human land use activities) sites, as in Wahlberg (2002). If different land use types were indeed associated with differentiated destruction rates, changes in land use patterns could rapidly change habitat dynamics without changing habitat availability, which would affect which kind of conservation actions were needed. Therefore, it would be beneficial for conservation managers to systematically record the land use types of habitat patches in order to track possible changes in land use culture that could quite straightforwardly affect habitat destruction rates of the whole system. Additionally, conservation managers working with specific early-succession habitat types should also follow up on disturbance-generating events that happen over moderate time scales, since they can have significant effects on the long-term availability of these habitat types (**III**).

Third, it is worth investigating whether permanent protected sites are the best use of conservation resources in a dynamic patch network, or if optimal locations of temporarily managed areas should be reassessed with

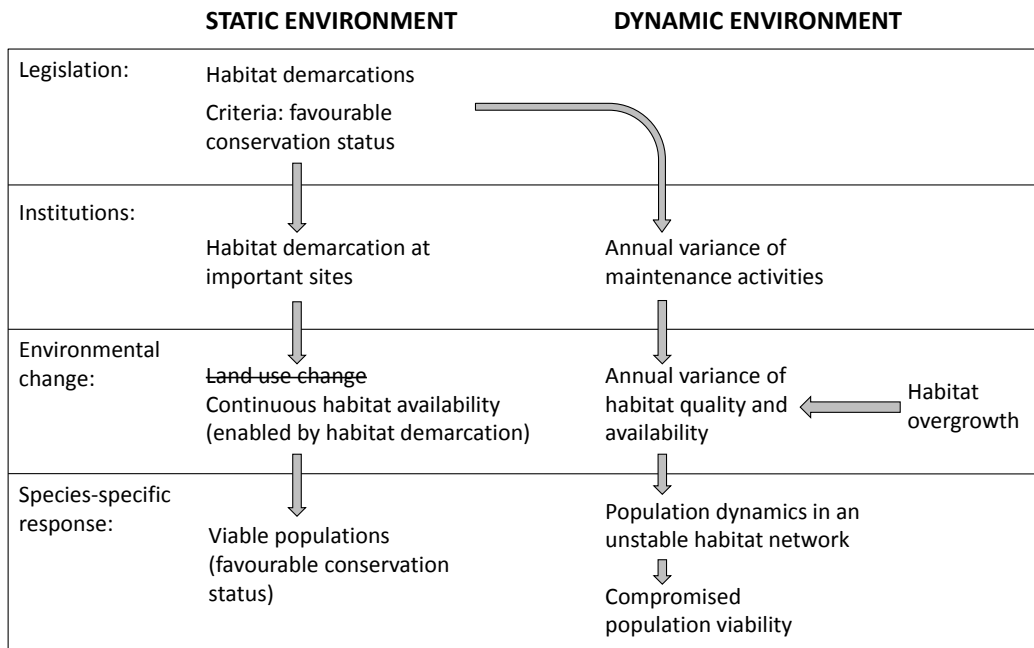
regular intervals (Cumming *et al.* 1996, Bengtsson *et al.* 2003, Kattwinkel *et al.* 2009, Moilanen *et al.* 2014). In our analysis of conservation scenarios (IV), site protection had an effect to the meeting of pre-defined patch occupancy targets only in very narrow parameter spaces of habitat dynamics, while being able to change the habitat dynamics would have had a larger effect to patch occupancies. Policy measures that would help to increase the lifetime of transient patches by a limited number of years, or to create new temporary patches altogether (Bunnell 1995, Ross *et al.* 2008, Bergsten *et al.* 2013) might be more acceptable to private landowners and therefore allow a larger selection of candidate sites where temporary conservation measures could be applied.

#### 4.3 IF CONSERVATION INSTITUTIONS FAIL TO ACCOUNT FOR HABITAT DYNAMICS, UNPREDICTABILITY INCREASES

The short time scales during which a habitat remains suitable for early-successional species make early-

successional habitat networks vulnerable to a number of factors, such as discontinuities in the funding mechanisms that enable the regeneration of early-successional habitats (Moilanen *et al.* 2014). We showed (V) that such discontinuities or fluctuations may be the outcomes of conservation institutions that have not been designed to take habitat dynamics into account, as such institutions are typically designed based on the assumption that endangered species' habitats are temporally static unless destroyed by land use change. As a result, they provide poorly performing tools for the maintenance of species persistence (Figure 7).

We use the conceptual framework of temporal (or, more generally, institutional) fit to demonstrate the root causes of poor institutional performance, with a goal of developing poorly performing conservation institutions into ones that are better in harmony with the ecological realities they deal with. For instance, mechanisms that would allow “banking” and buffering of species-specific maintenance budgets would allow the ELY centres to focus on long-term planning in their resource use. Field monitoring practices could



**Figure 7. Static assumptions and the dynamic reality in the habitat demarcation of successional sites.** The graph visualises the assumed consequences of habitat demarcation of species under strict protection in a landscape where habitats are static (left) versus the outcomes in cases where habitat sites are in reality dynamic and suffer from fast habitat overgrowth (right). For details, see V.

also be developed to include feedbacks that enable the initiation of maintenance planning or habitat network surveys before network habitat quality has dropped to a worrisome level. However, it is also possible to some extent for conservation planners to try to accommodate conservation plans into the real-life limitations of conservation institutions. For instance, since the most abundant and stable mechanism for habitat maintenance funding in Finland are the agri-environmental support contracts (V), a plausible way to approach false heath fritillary conservation would be to combine spatial conservation planning with data on landowner interest and eligibility to apply for agri-environmental support contracts.

#### 4.4 CONSERVATION PLANS OF DYNAMIC LANDSCAPES SHOULD BE ADJUSTED TO REGIONAL CONDITIONS

Landscape dynamics raise a question of how should local or regional differences in natural landscapes, land use cultures or landscape dynamics be taken into account in conservation planning. In our case study (I), the movement patterns of false heath fritillaries were affected by landscape structure, being more directional in longitudinal riverbank habitats than in more mosaic-like inland landscapes, even though the habitat-specific movement parameters of the species did not differ significantly across distribution regions. Additionally, there seemed to be slight differences in the vegetation structure of false heath fritillary habitats between distribution regions (II); study sites in the Pirkanmaa Region were smaller and had lower host plant abundance, higher percentage coverage of flowering plants and lower willow height than study sites in the West Coast distribution. Such differences were probably partially driven by climatic and hydrological differences between the regions, causing the fact that the host plant of the false heath fritillary, *Valeriana sambucifolia*, is generally more common in the West Coast of Finland (Kasviatlas 2015). The West Coast region also showed a tendency towards higher habitat destruction rates, perhaps due to a slightly differentiated structure of land use types, and perhaps due to a lower number of protected sites, in the habitat patch network.

Small-scale differences in landscape structure and dynamics might explain the originally perceived population viability differences between the West Coast

and Pirkanmaa regions. They might also call for slightly differentiated responses to the challenge of habitat dynamics, for instance in the planned number and configuration of permanent protected sites established. It is, for instance, possible that the wider-than-expected distribution of the false heath fritillary along the West Coast of Finland is partially caused by the abundance of rivers, which by their flooding dynamics create potentially the only naturally maintained wet meadow ecosystems for the false heath fritillary in Finland, and by slightly different agricultural land use practices in comparison to the Pirkanmaa region (I). Identification of such natural disturbance dynamics could be highly valuable for the regional conservation planning for a disturbance-dependent species, and it could induce regionally important conservation strategies, such as the establishment of meadow networks close to riverbanks.

## 5 CONCLUDING REMARKS

I have discussed many aspects of conservation planning in dynamic landscapes that are especially relevant in the conservation for early-succession species. A large amount of work still remains to be done, for a better integration of successional patterns and habitat dynamics into the general framework and practices of conservation planning. For instance, for the case of the false heath fritillary study, the next step would be to create a spatially realistic metapopulation model that incorporates the collected field data on patch destruction rates and maintenance response (II), and thus enables the analysis and comparison of alternative habitat maintenance schemes.

Early-succession habitats are often seen as independent, distinctive ecosystems with their distinctive needs from conservation point of view. Specifically, their conservation is seen to differ quite fundamentally from the conservation of late-successional habitats, such as old-growth forests. With a quick look, this might seem to be the case; whereas the conservation challenge of late successional habitats often focuses on their rarity, the challenge of conserving disturbance-dependent species is on overgrowth and rapid extinction. However, these two habitat types are still, after all, the two extremes of a continuum in which the dynamic characteristics of habitats develop from disturbance-dependent to disturbance-averse, and from short to long time lags from disturbances to habitat emergence. A wider adoption of



a temporal approach to spatial conservation planning could increase our understanding also on the needs and availability of the less studied mid-successional habitats.

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