Birds and butterflies at the forest-farmland interface

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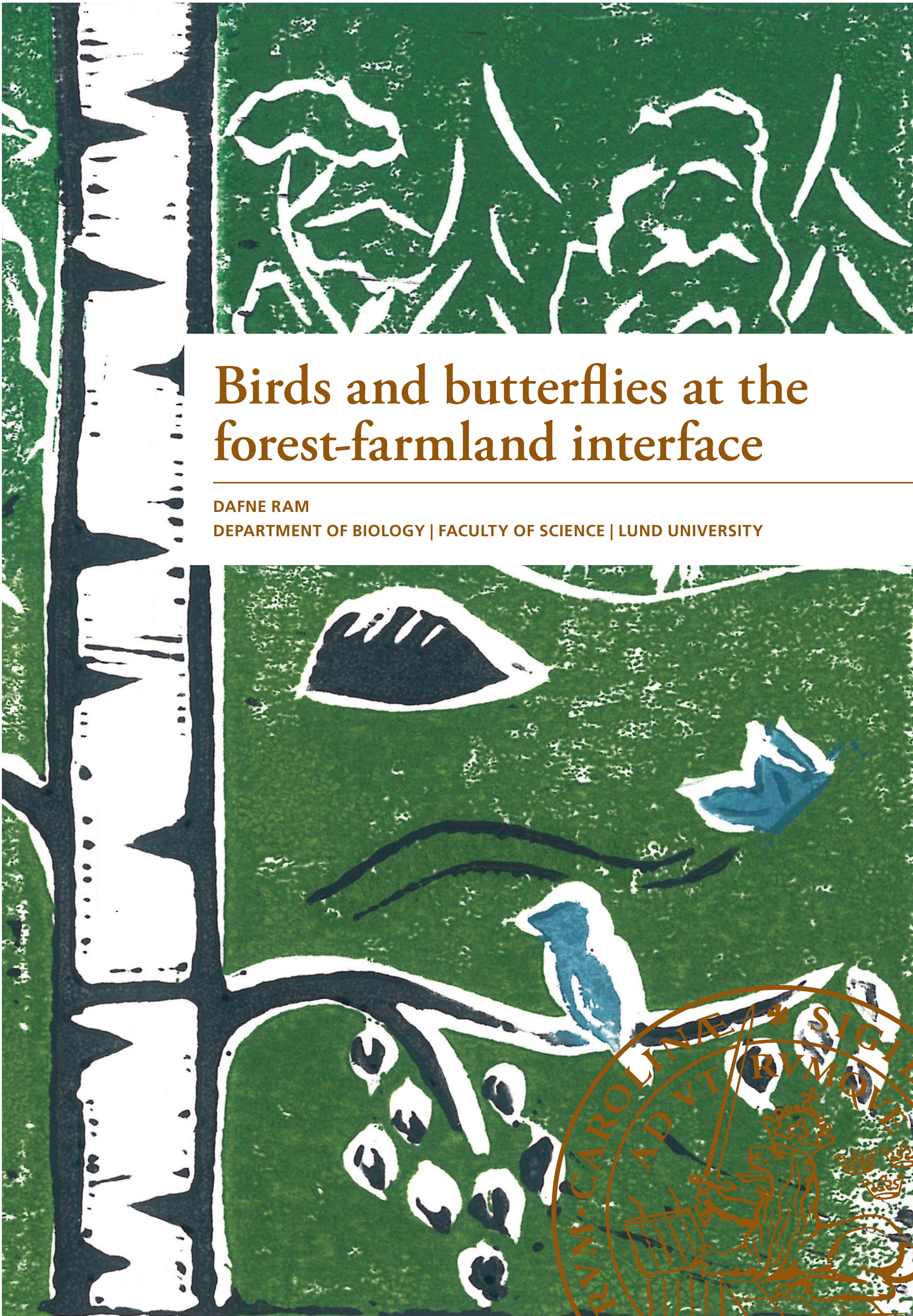

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DOCTORAL DISSERTATION

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Abstract
Land-use change is thought to be one of the greatest threats to biodiversity. Through intensification of land-use, the agricultural landscape has become more homogenous and a result, many species associated with traditional farmland or other semi-natural open habitats have declined. To be able to improve biodiversity conservation we need to be able to track components of biodiversity and understand how they respond to environmental changes. Biodiversity indicators can be very helpful in tracking such changes. However, species categorized as an indicator species for a certain habitat, might not exclusively occur in that habitat. In an intensely used landscape, with low amounts of natural and semi-natural habitats, some species may turn to use anthropogenic habitats such as forest clear-cuts. While these habitats might not categorize as grassland or farmland in our eyes, in some cases they seem to provide similar resources to farmland and grassland species. In this thesis, we compared multi-species indicators of farmland, grassland and forest butterflies and birds (Paper I) and found that indicators based on different taxa may send different signals even though they are based on the same habitat. Additionally, national trends might mask regional variation in trends. The literature review (Paper II) showed that farmland and grassland birds and butterflies do indeed occur on clear-cuts but the exact conditions that they need are often unclear. We then further explored the occurrence patterns of birds and butterflies in forest-clear cuts (Paper III and IV). We found that bird communities on clear-cuts changes with clear-cut age, size, vegetation height, the proportion of farmland in the near surroundings, and region. 10 out of 15 farmland bird indicator species occur on clear-cuts. They responded differently to environmental variables suggesting some might use clear-cuts as primary habitat in some regions and some might use clear-cuts more as complementary habitat while still depending on farmland in the surroundings. Clear-cuts are, however, not suitable for all farmland birds, most likely for reasons related to nesting sites, food, and predation risk. Butterfly communities on clear-cuts differ between the two surveyed counties as well as with clear-cut age and the proportion of open habitat and broadleaf forest in the surrounding landscape. Of the 20 farmland and grassland butterfly indicator species, 17 were observed on clear-cuts. While birds mostly responded to open habitat within a 200 m buffer of the clear-cuts, the butterflies more strongly responded to the larger scale 5 km landscape variables. Farmland bird abundance was often positively affected by clear-cut size while farmland and grassland butterflies, in the clear-cut centroids, were negatively affected by clear-cut size. This effect on butterflies was not seen in the edge of the clear-cuts, and this might indicate that butterflies either have a preference for the edges of the clear-cuts or use these lines in the landscape for orientation. While further studies are needed to expand our knowledge on how species, not least the currently declining grassland and farmland species, use these habitats to form more detailed management advice, the results in this thesis emphasize the importance of a landscape scale approach to conservation of both birds and butterflies. Forest clear-cuts could contribute to a green infrastructure for farmland and grassland birds and butterflies, however, the negative effect of forest clear-cuts on forest biodiversity as well as the climate needs to be taken into account when making conservation decisions.

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II. Ram, D., Lindström, Å., Pettersson, L.B., Caplat P. 2020. Forest clear-cuts as habitat for farmland birds and butterflies. *Forest Ecology and Management* 473:118239.

III. Ram, D., Lindström, Å., Pettersson, L.B., Caplat P. Farmland birds on forest clear-cuts: liked by some, avoided by others. *Submitted.*

IV. Ram, D., Pettersson, L.B., Lindström, Å., Caplat P. Landscape composition explains butterfly use of clear-cuts in contrasting forest-farmland mosaics. *Manuscript.*

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Additional published papers not included in the thesis

Ram, D., Axelsson, A.L., Green, M., Smith, H.G., Lindström, Å. 2017. What drives current population trends in forest birds – forest quantity, quality or climate? A large-scale analysis from northern Europe. *Forest Ecology and Management* 385: 177–188.

Bakx, T.R.M., Lindström, Å., Ram, D., Pettersson, L.B., Smith, H.G., van Loon, E.E., Caplat, P. 2020. Farmland birds occupying forest clear-cuts respond to both local and landscape features. *Forest Ecology and Management* 478: 118519.

Author contributions

I. DR, ÅL and LP conceived the idea of the study, with input from PC; KOB, EC, ÅL and LP supplied the data; DR, ÅL and LP analyzed and visualized the data; DR wrote the first draft with help from PC, ÅL and LP; all authors read and commented upon a final draft; PC, EC, NJ, ÅL and LP acquired the funding.

II. DR, ÅL, LP and PC conceived the idea of the study; DR surveyed and analyzed the literature; DR wrote the first draft; all authors read and commented upon a final draft; PC contributed with funding.

III. DR, ÅL and PC conceived the idea of the study, with input from LP; DR and ÅL organized the gathering of the data; DR analyzed the data, with help from PC and LP; DR and ÅL wrote the first draft; all authors read and commented upon a final draft; ÅL and PC acquired funding.

IV. DR, LP and PC conceived the idea of the study; DR and LP organized the gathering of the data; DR analyzed the data, with help from PC and LP; DR and LP wrote the first draft; all authors read and commented upon a final draft; PC acquired the funding.

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Abstract

Land-use change is one of the greatest threats to biodiversity. Through intensification of land-use, the agricultural landscape has become more homogenous and a result, many species associated with traditional farmland or other semi-natural open habitats have declined. To be able to improve biodiversity conservation we need to be able to track components of biodiversity and understand how they respond to environmental changes. Biodiversity indicators can be very helpful in tracking such changes. However, species categorized as an indicator species for a certain habitat, might not exclusively occur in that habitat. In an intensely used landscape, with low amounts of natural and semi-natural habitats, some species may turn to use anthropogenic habitats such as forest clear-cuts. While these habitats might not categorize as grassland or farmland in our eyes, in some cases they seem to provide similar resources to farmland and grassland species.

In this thesis, we compared multi-species indicators of farmland, grassland and forest butterflies and birds (*Paper I*) and found that indicators based on different taxa may send different signals even though they are based on the same habitat. Additionally, national trends might mask regional variation in trends.

The literature review (*Paper II*) showed that farmland and grassland birds and butterflies do indeed occur on clear-cuts but the exact conditions that they need are often unclear. We then further explored the occurrence patterns of birds and butterflies in forest-clear cuts (*Paper III* and *IV*). We found that bird communities on clear-cuts changes with clear-cut age, size, vegetation height, the proportion of farmland in the near surroundings, and region. 10 out of 15 farmland bird indicator species occur on clear-cuts. They responded differently to environmental variables suggesting some might use clear-cuts as primary habitat in some regions and some might use clear-cuts more as complementary habitat while still depending on farmland in the surroundings. Clear-cuts are, however, not suitable for all farmland birds, most likely for reasons related to nesting sites, food, and predation risk.

Butterfly communities on clear-cuts differ between the two surveyed counties as well as with clear-cut age and the proportion of open habitat and broadleaf forest in the surrounding landscape. Of the 20 farmland and grassland butterfly indicator species, 17 were observed on clear-cuts. While birds mostly responded to open habitat within a 200 m buffer of the clear-cuts, the butterflies more strongly responded to the larger scale 5 km landscape variables. Farmland bird abundance

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While further studies are needed to expand our knowledge on how species, not least the currently declining grassland and farmland species, use these habitats to form more detailed management advice, the results in this thesis emphasize the importance of a landscape scale approach to conservation of both birds and butterflies. Forest clear-cuts could contribute to a green infrastructure for farmland and grassland birds and butterflies, however, the negative effect of forest clear-cuts on forest biodiversity as well as the climate needs to be taken into account when making conservation decisions.

Popular summary

Many populations of farmland and grassland birds and butterflies have been declining for several decades, a trend observed in several countries as well as on a European scale. To be able to improve biodiversity conservation we need to be able to track components of biodiversity and understand how they respond to environmental changes. Biodiversity indicators, and multi-species indicators in particular, are a useful tool for this. Multi-species indicators combine trend information of a selected group of species into one summarizing index. Often multi-species indicators are based on a group of species that are associated with the same type of habitat, such as forest or farmland. In some cases, such as the Farmland Bird Index and the Grassland Butterfly Indicator, these indicators are adopted at the national and EU level to inform management and policy decisions. Biodiversity indicators help us detect large-scale patterns, but it is important to keep in mind that their trends depend on the species that are included and that they might mask smaller scale patterns.

Large parts of Europe, including Sweden, consist of mosaic landscapes of forest and farmland. Many farmland and grassland species depend on the heterogeneity present in traditional farmland landscapes. Historically, farmland consisted of a patchwork of smaller agricultural fields, grazed pastures and woodlands but during the 20th century, agriculture intensified and, consequently, the agricultural landscape changed dramatically. Fields have become larger and many semi-natural habitats have strongly declined, resulting in a more homogenous landscape and habitat loss for many farmland and grassland species. At the same time, forest management has also intensified. While previously selective cutting of mature trees was the most common method of felling, currently, clear-cutting is the standard in Swedish forestry. Clear-cut forestry, where all or nearly all trees in a site are felled and new trees replanted in the next two to five years, results in even-aged tree plantations of a single tree species, with generally negative effects on forest biodiversity. Nevertheless, farmland birds and butterflies have been shown to occur on forest clear-cuts, and this fact is a key aspect of this thesis.

In paper I of this thesis, we compared biodiversity indicators of birds and butterflies on different scales. We found that regional trends do not always follow the national trend and that there is quite some variation between regions. We also found that indicators of butterflies and birds did not give the same signal even if they were

based on the same habitat classification such as farmland, grassland or forest. Over the investigated period, butterflies generally seemed to be doing better in Sweden than birds, especially those associated with farmland and grassland. A possible explanation for this could be that butterflies respond faster to climate change, which in Sweden might benefit many butterfly species. It is therefore important to use different biodiversity indicators complementarily and to be aware of potential regional differences when informing management and policy decisions. An important explanation to regional differences in trends and distributions of species are differences in the landscape and its configuration. In an intensely used landscape, with low amounts of natural and semi-natural habitats, some species may turn to use anthropogenic habitats such as power-line corridors, road verges and forest clear-cuts. While these habitats might not categorize as grassland or farmland in our eyes, in some cases they seem to provide similar resources to farmland and grassland species. Many farmland and grassland species have been shown to use habitats other than farmland and grassland. In paper II of this thesis, I reviewed the literature on farmland and grassland birds and butterflies and their use of forest clear-cuts. Many species do indeed use forest clear-cuts but the exact conditions that they need are often unclear. We further investigated the occurrence patterns of birds and butterflies in clear-cuts in papers III and IV. To accomplish this we performed bird and butterfly surveys on forest clear-cuts with the help of many volunteers and field assistants. We surveyed nearly 300 clear-cuts throughout Sweden for birds and 120 clear-cuts in Dalarna and Skåne for butterflies. We found that 10 out of 15 farmland indicator bird species and 17 out of 20 farmland and grassland indicator butterfly species occurred on clear-cuts. Different species responded differently to environmental variables suggesting some might use clear-cuts as primary habitat in some regions (for example, Whinchats *Saxicola rubetra* in the north of Sweden) and some might use clear-cuts more as complementary habitat while still depending on farmland in the surroundings (for example, Greater Whitethroat *Sylvia communis* and Yellowhammer *Emberiza citronella*). Clear-cuts are, however, not suitable for all farmland birds and butterflies most likely for reasons related to nesting sites, food, host-plant availability, and predation risk.

Forest-clear-cuts might contribute to a green infrastructure for declining grassland and farmland species, and help them survive in an intensely used landscape. However, it is important to note that while we do know many species occur on clear-cuts, we often do not know to what extent they use them and if they can successfully reproduce there. Therefore, before we can draw conclusions about the importance of these habitats to certain species, further studies are needed to look at resource availability and reproductive success. I am no advocate of clear-cutting in general, but while clear-cutting remains a common feature of forestry, we should consider managing them so they may contribute to a green infrastructure for open habitat species. However, any such measures must be balanced against the potential effects clear-cuts and their management may have on forest biodiversity.

Thesis aims

Large parts of Europe consist of mosaic landscapes of forest and farmland. During the 20th Century, land-use has intensified, resulting in more homogenous landscapes and the decline of many natural and semi-natural habitats. Although Sweden is dominated by forest, the forests are more or less interspersed by areas of open land (e.g., farmland, grassland, clear-cuts, mires, power lines) forming mosaic landscapes. These landscapes are in a state of continuous change: when forests are fragmented into mosaics of open and forested patches, the suitability for forest animals may decrease, while at the same time the suitability for open-land animals will increase. Today, the opposite processes dominate in many parts of Sweden; open areas close and the forest cover increases. How these changes affect species distribution patterns is a key question in biodiversity conservation.

The aim of my thesis is to use two well studied taxa, butterflies and birds, as a case study. Butterfly and bird populations have been monitored on a national scale for quite some time (butterflies 13 years now, and birds more than 20 years) by the two national monitoring schemes: the Swedish Butterfly Monitoring Scheme and the Swedish Bird Survey. By combining the national butterfly monitoring data with other, smaller scale, monitoring schemes I formed the longest and most complete time series of butterfly monitoring data in Sweden to date. I used this newly combined butterfly dataset together with the national bird monitoring data to look at large scale temporal and spatial patterns of birds and butterflies in Sweden (*Paper I*).

Butterflies and birds have both been used as proxies for changes in biodiversity and have been adopted as indicators for forest and farmland biodiversity both on a national scale in Sweden and in Europe. However, the reliability of biodiversity indicators depends greatly on the sensitivity and habitat associations of the species they include. Many farmland and grassland species depend on the heterogeneity that was present in traditional farmland landscapes, including smaller scale, less intensive farmed crop fields and grazed pastures and patches or edges of forest. While the amount of forest in Sweden has been increasing, modern forestry has also created new habitats in the form of clear-cuts, power-line corridors and forest roads, which have been shown to have potential value for farmland and grassland species.

To further investigate the importance of forest clear-cuts for farmland and grassland species, I first conducted a literature review on farmland and grassland birds and butterflies in forest clear-cuts (*Paper II*). I then investigated bird and butterfly communities in Swedish forest clear-cuts using field surveys (*Paper III* and *IV*). I focused on both local site characteristics (size, age, vegetation height) as well as landscape characteristics (proportion farmland, clear-cut forest and broadleaf forest), to gain a better understanding of when and where grassland and farmland species can utilize clear-cuts.

If many farmland and grassland birds and butterflies use other habitats, such as forest clear-cuts, the habitat-based indicators may not necessarily reflect changes in the focal habitat specifically. While many farmland and grassland species are declining, better understanding their habitat association and distribution in the landscape can help make conservation efforts more effective. How tightly farmland and grassland indicator species are associated with the habitat they supposedly represent, and what determines their occurrence on anthropogenic habitats outside of traditional farmland and grassland, are therefore important questions. Using monitoring data to analyze large scale temporal and spatial patterns of two taxa, and clear-cuts as a model of smaller scale changes in the forest-farmland interface I aim to help answer these questions.

More specifically, the questions addressed in the individual papers were:

Paper I: Do habitat-based indicators of different taxa send the same signal? And consequently, can indicators of one taxon be used to indicate the state of other taxa?

Paper II: What is the current knowledge base on the occurrence of farmland birds and butterflies on clear-cuts and what are important gaps in this knowledge?

Paper III: How do bird communities on forest clear-cuts differ with varying local and landscape characteristics? Under what circumstances do farmland species and red-listed species in particular occur on clear-cuts? Which farmland bird species do, or do not, occur on clear-cuts?

Paper IV: How do butterfly communities on forest clear-cuts differ with varying local and landscape characteristics? Under what circumstances do farmland and grassland species in particular occur on clear-cuts? Which farmland and grassland butterfly species do, or do not, occur on clear-cuts?

Introduction

Land-use change is thought to be one of the greatest threats to biodiversity (Walther et al. 2002, Parmesan & Yohe 2003, Pereira et al. 2012, IPBES 2018). Through intensification of land-use, many semi-natural habitats in Europe have declined or become fragmented (Cousins et al. 2015, Hooftman & Bullock 2012). Agriculture has intensified while less-productive land was abandoned or afforested (Stoate et al. 2001) resulting in more homogeneous landscapes (Tscharntke et al. 2005). As a result, strong declines of many species associated with farmland or other semi-natural open habitats have been reported, including birds (Krebs et al. 1999, Donald et al. 2001, Berg et al. 2015, Hallmann et al. 2017), insects (Benton et al. 2002, Goulson et al. 2005, Winfree et al. 2009) and plants (Luoto et al. 2003, Thomas et al. 2004, Dahlström et al. 2006). Long-term monitoring and detailed analyses are needed to understand these biodiversity trends (Gonzalez et al. 2016, Simmons et al. 2019, Thomas et al. 2019). Habitat-based (and other) biodiversity indicators have been widely used for this purpose, both at a national scale in Sweden (and many other countries) as well as on a European scale.

Large parts of Europe, including Sweden, consist of mosaic landscapes of forest and farmland. Many farmland and grassland species depend on the heterogeneity that was present in traditional farmland landscapes, including smaller scale, less intensive farmed crop fields and grazed pastures (Berg 2002, Benton et al. 2003). Heterogeneous mosaic landscapes are important for many bird species with nesting sites in forests but main feeding habitats in farmland (Pitkänen & Tiainen 2001). Similarly for butterflies, forests and forest edges are beneficial (Marini et al. 2009, Krämer et al. 2012, Villemey et al. 2015, Toivonen et al. 2017, Bergman et al. 2018) especially when semi-natural grasslands are scarce (Kuussaari et al. 2007). During the same period of agricultural intensification, forest management has intensified as well. However, modern forestry also creates new habitats in the form of clear-cuts, power-line corridors and forest roads which have been shown to have potential value for farmland and grassland species (Fuller et al. 2004, Paquet et al. 2006, Berg et al. 2011, Söderström & Karlsson 2011, Stjernman et al. 2013, Blixt et al. 2015, Percival & Dale 2016, Viljur & Teder 2016, Żmihorski et al. 2016, Milberg et al. 2021).

In this introduction, I first describe how habitat-based biodiversity indicators were developed and their trends in Sweden and Europe. Then I describe the habitat that grassland and farmland birds and butterflies are associated with and how this has changed with intensified land use. Finally, I describe forest management and clear-cutting in Europe and how this can be a potential habitat for farmland and grassland species.

Habitat-based biodiversity indicators

Development of biodiversity indicators

An ideal indicator quantifies the state of the species included in the indicator, as well as related species and habitats and ecosystem health in general (Gregory et al. 2005). Multi-species indicators integrate data from a group of species to present a simple but representative summary (Gregory 2006). Species are chosen based on different traits, such as habitat preference or dispersal ability, and therefore constructing and interpreting indicators requires substantial knowledge of the life history and ecology of species. Species selection is often based on expert opinion, although quantitative assessments are becoming more common (Fraixedas et al. 2020). The quality of the indicator will depend very much on the species selection and therefore the knowledge of species ecology (Butler et al. 2012).

Birds, composing one of the most studied and extensively monitored taxon, are good candidates to be biodiversity indicators (Gregory & van Strien 2010, Schmeller et al. 2012). Since birds are often high in the food chain they could serve as proxies for lower trophic levels as well (Gregory et al. 2005). The Pan-European Common Bird Monitoring Scheme (PECBMS, www.pecbms.info) was initiated in 2002 to coordinate a Europe-wide effort of bird monitoring and calculating population trends and indicators (Gregory et al. 2005). The indicators used by the PECBMS are multi-species indicators, focusing on common bird species in different habitat preference groups and have been adopted by the Streamlining European Biodiversity Indicators (Butler et al. 2010, EEA 2012).

Butterflies are, after birds, the second most studied group, as well as the only invertebrate group where extensive monitoring exists (Thomas 2005, van Swaay et al. 2008). Their high reproductive rate and sensitivity to small environmental changes makes their response relatively fast and therefore a very suitable indicator (Thomas 2005, Devictor et al. 2012). Although, ideally, monitoring of other taxa should be increased, butterflies can also be used as indicators for other terrestrial insects (Thomas 2005). The European Grassland Butterfly Indicator was developed in 2005 and consists of several common grassland species and some grassland-specialists (van Swaay & van Strien 2005). Since then, multiple other butterfly indicators have been developed including woodland and urban butterfly indicators (van Swaay et al. 2020). The European Grassland Butterfly Indicator was adopted by the Streamlining European Biodiversity Indicators as one of the status indicators on biodiversity (EEA 2012).

In Sweden, there are several biodiversity indicators incorporated in the national environmental objectives used to monitor the progress towards national targets (www.sverigesmiljomal.se). Butterfly and bird indicators used in the Swedish national environmental goals include a forest bird indicator, mountain bird indicator, farmland bird and butterfly indicator (farmland indicators are based on the same species as the European indicators), and an indicator for red-listed species.

Butterfly and bird indicator trends in Europe and Sweden

While there are several more butterfly and bird indicators calculated both on European level as well as nationally in Sweden, I focus here on the indicators for farmland, grassland and forest.

Butterfly indicator trends

The most recent update of the European Grassland Butterfly Indicator was published in 2020 and includes data from butterfly monitoring schemes from 22 countries over a time-period of 29 years (1990-2018)(van Swaay et al. 2020). The indicator includes 17 butterfly species typical of grasslands, seven widely occurring species and ten specialists, and were selected by experts. The indicator shows that, since 1990, grassland butterflies in Europe have declined by 22%, although the decline has slowed down in the last five to ten years. Of the seventeen species included, eight have declined, five remained stable and four have uncertain trends (van Swaay et al. 2020).

The Swedish Butterfly Monitoring Scheme uses the subset of the seventeen grassland species that occur in Sweden to calculate the national grassland butterfly indicator, including data from 2010 and onwards (Pettersson et al. 2022). The Swedish grassland butterfly indicator consists of twelve species, all seven of the widely occurring species and five of the specialist species. The indicator showed a dip in 2012, followed by some recovery in the years after and is now considered stable. However, abundance numbers are still significantly lower than at the start of the monitoring.

In addition to the grassland butterfly indicator, the Swedish Butterfly Monitoring Scheme calculates three other butterfly indicators on a national level (Pettersson et al. 2022). The farmland butterfly indicator (based on species selection of a UK farmland indicator, Gilburn et al. 2015), forest butterfly indicator (based on expert opinion, Eliasson et al. 2005 and Bink 1992) and the 20 most common species in Sweden. The farmland butterfly indicator has been declining while the forest butterfly indicator and the common species indicator are both stable (Pettersson et al. 2020).

Bird indicator trends

The European wild bird indicators are calculated by the Pan-European Common Bird Monitoring Scheme (PECBMS, www.pecbms.info) and include both a common farmland bird indicator (39 species) and a common forest bird indicator (34 species). The latest update of the European wild bird indicators includes data from monitoring schemes from 29 countries over a time-period of 40 years (1980–2019). Species are selected according to their predominant regional habitat (farmland, forest or other). The PECBMS takes into account that species can have different habitat associations in different bio-geographical regions. If a species was assigned the same habitat association in multiple regions, this classification was adopted at the European level. If habitat association differed between regions, species were classified as "other". The European Common Farmland Bird Indicator has declined dramatically (more than 50%) over 36 years, however, the decline seemed to have slowed down gradually. The European Common Forest Bird Indicator is quite stable.

A subset of the European indicator species is included in the Swedish Farmland Bird Indicator and the Swedish Forest Bird Indicator (Green et al. 2022). The national indicators are calculated from data from standardized survey routes, the "Fixed routes", of the Swedish Bird Survey. The Swedish common farmland bird indicator includes 15 species and the Swedish common forest bird indicator includes 26 species. The Swedish common farmland bird indicator is declining as well, not as strong as the European indicator, but around 18% in 23 years. The Swedish common forest bird indicator has increased with about 20%, although this increase has levelled off in recent years, and the last couple of years show signs of decline.

Farmland and grassland birds and butterflies

Habitat requirements of farmland and grassland butterflies and birds

The general habitat requirement for this group of species is that they traditionally have been found in, and connected to, farmland, grassland or other forms of open habitat (Ottvall et al. 2008, Solonen 1994, Tucker & Evans 1997, van Swaay et al. 2006). Specific habitat requirements differ between species, but there are general components and similarities within this group.

Most grassland and farmland butterflies prefer early-successional vegetation such as semi-natural grasslands (Emmet 1991, Bink 1992, Van Swaay et al. 2006, Dennis 2010). In addition to open habitat, many species depend on edges. Some species prefer edges such as field borders and edges of shorter vegetation (e.g., Large white *Pieris brassicae*, Essex skipper *Thymelicus lineola*, Small tortoiseshell *Aglais urticae* and Wall brown *Lasiommata megera*) and some species prefer forest edges and higher vegetation (e.g., Comma *Polygonia c-album* and Orange-tip *Anthocharis cardamines*). Habitat descriptions of farmland and grassland butterflies often mention mosaic landscape, emphasizing the importance of heterogeneity for many of the butterfly species. Adult farmland and grassland butterflies feed on nectar from flowers of herbs or, as most farmland butterflies do, on shrubs. However, the hostplants and food sources for the caterpillars are more specific and include grasses, sedges, nettles, legumes and mustards (Emmet 1991, Bink 1992, Van Swaay et al. 2006, Dennis 2010).

While some farmland birds prefer completely open terrain (e.g., Lapwing *Vanellus vanellus*, Skylark *Alauda arvensis*) many species also require woodland, forest edges, hedges, bushes or shrubs near the open areas (Cramp et al. 1977-1994). Some species are also known to occur in young conifer or tree plantations (e.g., Winchat *Saxicola rubetra*, Meadow Pipit *Anthus pratensis*, Linnet *Linaria cannabina*, and Yellowhammer *Emberiza citrinella*). Several species use some sort of elevated perch to sing from or hunt from, like fence posts, power lines, single trees, tree stumps or stone walls. Most farmland birds have a mixed diet of plant (mostly seeds) and animal material (mostly invertebrates), while some feed exclusively on insects (e.g., Barn Swallow *Hirundo rustica*). The majority of farmland birds have their nest on the ground or close to the ground in low vegetation (Cramp et al. 1977-1994). Some exceptions however are Rook *Corvus frugilegus* (nesting in tall trees), Barn Swallow (nesting against vertical structures under ledges, beams etc.), Tree Sparrow *Passer montanus* and Starling *Sturnus vulgaris* (nesting in holes).

Farmland species in the modern forest-farmland landscape

Whereas farmland and grassland species traditionally have been found in farmland and grassland, the way farmland looks like has changed quite dramatically. Traditional farmland landscapes consisted of small fields in addition to hedges, shrubs, forest edges and pastures resulting in a heterogeneous mosaic landscape. As many grassland and farmland species do not solely depend on open, low vegetation but also need structures such as shrubs, hedges, forest edges, trees or other high points, mosaic landscapes are important (Pitkänen & Tiainen 2001, Villemey et al. 2015, Toivonen et al. 2017, Bergman et al. 2018). Some species use open vegetation for foraging and shrubs or forest edges for breeding for example. Agricultural intensification has resulted in larger fields, smaller amounts of semi-natural habitats and overall a more homogenous farmland landscape (Ihse 1995, Tscharntke et al. 2005, Fig. 1). In addition to intensification, abandonment of less productive farmland and afforestation has caused further loss of diverse farmland (Stoate et al. 2009). For farmland and grassland species that often depend on an open but heterogeneous landscape, the process of agricultural intensification and abandonment therefore often causes loss and fragmentation of suitable habitat (Raven & Wagner 2021), especially for specialist species (Ekroos et al. 2010).

Although “farmland species” traditionally have been found predominately in farmland, they have not evolved in farmland and would probably be more accurately described as open habitat or early-successional species. Furthermore, “farmland” as a habitat category is based on the human perception of the landscape. The species that we categorize as farmland or grassland species likely perceive the landscape quite different from us (Van Dyck 2012). A species will need the right resources and conditions to survive which may be found elsewhere than farmland. Many farmland species indeed also occur outside of farmland, for example, in bogs, mires, forest clear-cuts, power-line corridors and road verges (Berg et al. 2011, Stjernman et al. 2013).

Figure 1. Modern farmland with large agricultural fields and little to no natural or semi-natural habitats, and forest in the distance, in Skåne, southern Sweden. (Photo: Author)

Forest clear-cuts

Forest clear-cutting management in Europe

Until the mid-18th century, most of European forests were exploited through a procedure called “selective cutting”, by which only a small proportion of trees are felled every year. With the beginning of the industrial revolution, forestry practices intensified, which led to the use of clear-cutting methods, by which all trees in an area are cut at the same time followed by natural regeneration or replanting (Lundmark et al. 2013). In Sweden, the introduction of clear-cutting came at the end of the 1800s, but took some time to establish more extensively (Lundmark et al. 2013). Currently, even-aged forest management with clear-cutting as a main harvesting method is the most common forestry method in Sweden, Finland and Austria, and occurs throughout other parts of Europe as well (McDermott et al. 2010). However, forest management strategies and intensity often depend on whether forest is private or state owned. Additionally, regulations differ between countries as well as regions or provinces (McDermott et al. 2010). The majority of Sweden’s productive forest (forest land suitable for forestry with a production rate of at least 1 m^3 ha^{-1} $year^{-1}$) has been clear-cut at some point during the last 40 years (Fig. 2).

Figure 2. Black polygons indicate areas that have been clear-cut in Sweden during the last 40 years. A zoomed in section is shown to further illustrate the density and extent of clear-cutting. Data: Swedish Forestry Agency 2022.

Most European countries have some sort of obligation for regeneration in their forest laws (Bauer et al. 2004). In the case of clear-cutting, several countries require regeneration to be done within two to five years of final felling (McDermott et al. 2010). However, detailed requirements or time frames for regeneration are often not stated. While clear-cuts could previously be quite large (Simonsson et al. 2015), most countries now also limit the size of the clear-cut area. Limits range from 5 ha to 20 ha, often depending on soil or forest types (McDermott et al. 2010).

Traditionally the practice of clear-cutting means to clear the felled area completely. Approximately 30 years ago, a new approach was introduced called retention forestry (Gustafsson et al. 2012). Retention forestry aims to retain structures valuable for biodiversity conservation during harvesting and other forestry operations, to closer resemble natural disturbances. In the last 25 years, voluntary forest certification (FSC and PEFC) has introduced some measures to benefit biodiversity as well, such as increasing the amount of broadleaved trees in production stands and the creation of high stumps, but thresholds for certification are low (Johansson et al. 2013). Therefore, nowadays while in most cases clear-cutting is stated as the practice used, sometimes this is only partial clear-cutting with some retention of valuable structures. Retention forestry can be applied in a variety of ways and extents, from retaining patches of forest to single trees or dead wood (Gustafsson et al. 2012).

Figure 3. A modern forest landscape in Sweden, consisting of even-aged plantation forest and clear-cuts (Photo: Åke Lindström)

Clear-cuts as habitat

About 58% of Sweden is production forest (SLU 2021) and even-aged forestry with clear-cutting is the main management practice. With rotation times ranging from as short as 45 years to 100+ years, most forest is regularly clear-cut, resulting in a significant proportion of the land being in a recent clear-cut state. The total amount of clear-cuts cut within the last 10 years makes up about 5–6% of the total land area. This is almost as much as the total amount of farmland in Sweden (7–8%, Statistics Sweden 2019). Forest clear-cuts are therefore a common habitat in Sweden (Fig. 3).

Clear-cutting creates temporary patches of early successional vegetation in the landscape. Forest clear-cuts can resemble shrubby grassland as found in semi-natural farmland before growing trees turn it into forest again. Grassland and farmland bird and butterfly species have been shown to occur on clear-cuts (Berg et al. 2011, Blixt et al. 2015, Fuller et al. 2004, Lundberg 2009, Paquet et al. 2006, Percival & Dale 2016, Söderström & Karlsson 2011, Stjernman et al. 2013, Viljur & Teder 2016, Żmihorski et al. 2016). These man-made habitats thereby potentially contribute to higher connectivity of habitat for farmland and grassland species. In light of the strong declines seen in farmland and grassland species, a better understanding of their use of the landscape will aid conservation efforts. However, conservation decisions should always be made with consideration to the negative effects of forest clear-cutting on forest biodiversity as well as the effect on climate.

Methodology

Monitoring data

The Swedish Bird Survey

The Swedish Birds Survey (SBS) is a volunteer-based national monitoring program, which was initiated in 1969 (Green et al. 2022). In 1998, the fixed route surveys started (Lindström & Green 2021), which is the data that I have worked with. The fixed route scheme consists of 716 routes, each 8 km long, distributed evenly over Sweden in a grid of 25 km (Fig. 4). Due to the grid-wise even distribution, birds are sampled within a representative sample of Sweden's different habitats. Routes consists of 8 line transects of 1 km, and 8 point counts, and are surveyed yearly as far as surveyor availability allows. The surveyor counts all birds seen and heard while walking the line transects. Point counts consists of a 5-minute count, where all birds seen and heard are counted. The routes are surveyed clockwise, preferably starting at the south-west corner point. Surveys should start 04.00 (+/- 30 min.) but not before sunrise. Surveys are done within different periods depending on the relevant breeding season on location, all between the 15th of May and 5th of July. Since 2002, around 400–500 routes have been surveyed annually.

The Swedish Butterfly Monitoring Scheme

The Swedish Butterfly Monitoring Scheme (SeBMS) is a volunteer-based national monitoring program, which was initiated in 2010 (Pettersson et al. 2021). The scheme includes 880 sites which are visited 3 to 7 times annually, between April 1st and September 30th (Fig. 4). Counts are done using two standardized methods; point counts and fixed-route Pollard walk transects (Pollard & Yates 1993). Point counts are 15-minute counts covering a circular area with a radius of 25 m. Fixed-route Pollard walk transects are transect counts of 0.5 to 3 km in length under which a surveyor records all butterflies seen 2.5 m to their right, 2.5 m to their left, 5 m ahead of them and 5 m above them. Survey sites are chosen by volunteer surveyors but remain constant once chosen. Conditions for surveying include temperature over 13 °C, low wind speeds and at least half-clear or sunny sky. Surveys are done between 11:00 and 17:00. Each year, around 450 sites are surveyed.

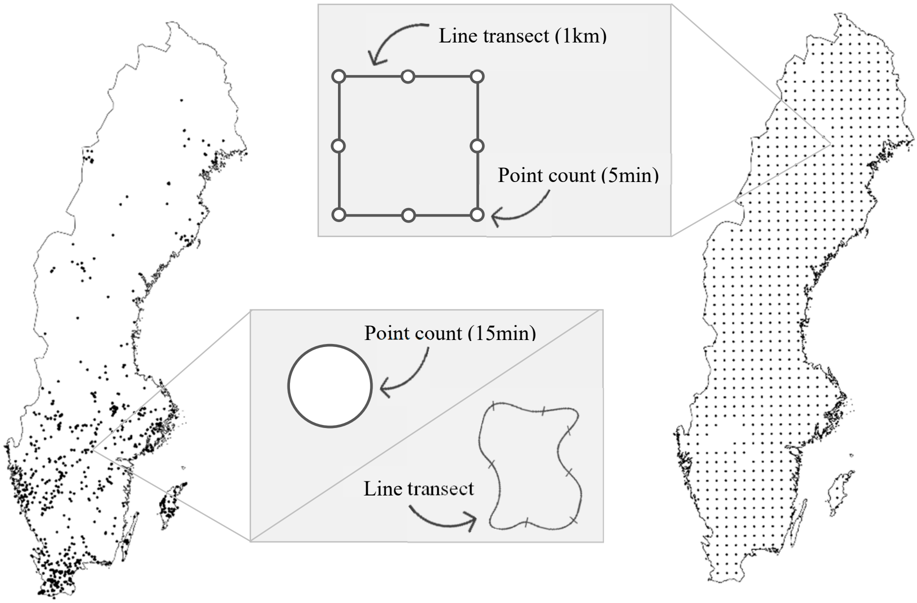

Figure 4. Maps of the national monitoring schemes survey routes for butterflies (left) and birds (right). Butterfly surveys consists of either point counts or transect walks. Bird surveys consist of a combination of 8 point counts and 8 segments of line transects.

Merging butterfly databases

I combined data from three different sources into one database, thereby forming the longest and most complete time series of butterfly monitoring data in Sweden to date (Fig. 5). The Swedish Butterfly Monitoring Scheme contributed 10 years of monitoring data (2010–2019), the Swedish University of Agricultural Sciences contributed 14 years of data (2006–2019) and the county administrative boards contributed 11 years of data (2009–2019).

Swedish University of Agricultural Sciences (SLU)

Since 2006 the Swedish University of Agricultural Sciences coordinates monitoring of 700 meadow and pasture sites for butterflies (and bumblebees) (Cronvall 2017). Every year around one-fifth of the sites are surveyed, resulting in total coverage every 5 years. Surveys consists of transects, placed at least 20 meters apart, either in north-south or east-west direction on the site. The transects are surveyed by a surveyor who records butterflies seen 5 meter to their right, 5 meter to their left and 5 meter ahead of them. Conditions for surveying include temperature over 17 °C, low wind speeds and sunny weather. Surveyed sites are visited two to three times within a season between 09:00 and 16:30. Some sites have only been surveyed one year (N=61), most two years (N=503) and some three years (N=171).

County administrative boards

Since 2009, seven counties in south and middle Sweden combine their survey effort in a collaborative monitoring scheme (Bergman et al. 2015). Every county monitors between 30 and 70 meadow and pasture sites. Sites are surveyed every fifth year with surveys consisting of three visits per year. Surveys consists of transects, placed in the same parallel manner as in the SLU transects, as well as a series of additional point counts in habitat surrounding the meadow/pasture site. Transects are surveyed in the same manner as in the SeBMS transects (Fixed-route Pollard walk) and point counts are surveyed in the same manner as SeBMS point counts. Conditions for surveying include temperature over 17 °C, low wind speeds and sunny weather. Surveys are done between 09:00 and 16:30.

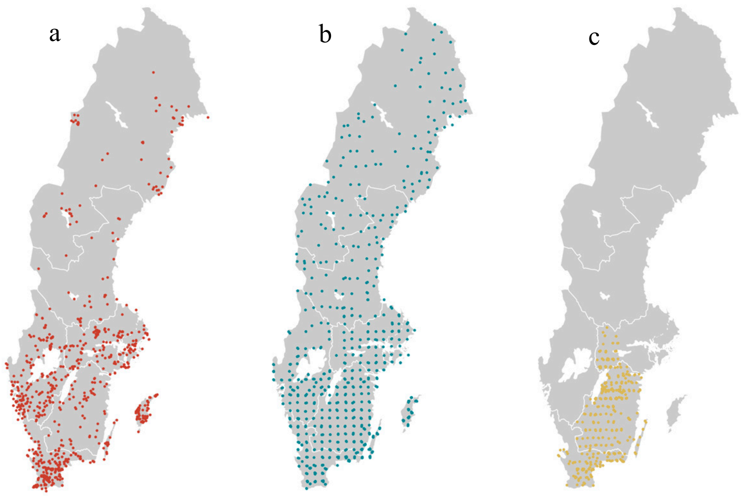

Figure 5. Distribution of butterfly monitoring survey sites (colored dots) for (a) the National Butterfly Monitoring Scheme, (b) the Swedish University of Agricultural Sciences meadow and pasture surveys and (c) the county administrative boards butterfly surveys.

Trends and multi-species indicators

Trends and indices

Bird trends with TRIM

To analyze bird species trends over time from the monitoring data, we calculated TRIM indices. TRIM (Trends & Indices for Monitoring data) is the standard analysis tool used in the Pan-European Common Bird Monitoring Scheme (Gregory et al. 2007, www.pecbms.info/methods/software/trim) and is available as an R package (*rtrim*, Bogaart et al. 2018, Pannekoek et al. 2018). TRIM uses Poisson Generalized Linear Models (GLM) to estimate species-specific yearly indices and temporal trends of annual abundance, while controlling for serial correlation and overdispersion. TRIM handles missing data, when sites have not been surveyed, by imputation. There are three different models that TRIM uses to calculate indices. We only used model 2 'Linear (switching) trend'. In model 2 the expected count is a linear function with a site-effect and a linear effect of time. The model allows for the slope parameter to change at some time points (i.e., "switch").

Butterfly trends with rbms

To analyze butterfly species trends over time we used the Generalized Abundance Index approach by Dennis et al. (2016) and the R package *rbms* (Schmucki et al. 2019). While TRIM was previously also used by many butterfly monitoring schemes, the Generalized Abundance Index and *rbms* is a newer development of this approach which takes into account the seasonal nature of butterfly data (Schmucki et al. 2016). Following this method, first seasonal flight curves are calculated for each species based on our count data. Missing data is then imputed using the flight curves and the count data, and thereby taking into account the different flight periods of the species. Collated indices were then estimated using Poisson Generalized Linear Models (GLM) with site and year as factors, and the proportion of the flight curve surveyed as a weight for the GLM (Schmucki et al. 2019).

Multi-species indicators

Using the TRIM and rbms indices, we calculated Multi-Species Indicators (MSIs). A MSI is a combined index including the indices for several species. They are calculated according to Soldaat et al. (2017) by combining the geometric mean of the indices of the species included. We used the R package 'BRCIndicators' (August et al. 2017) that implements these methods. We used a recently developed Monte Carlo method to account for sampling error in trend estimation in the MSIs (Soldaat et al. 2017). This method also allows for testing differences between indicator trends.

We calculated MSIs for specific species groups, based on their habitat requirements. For birds, we used three indicators; the forest bird indicator, the farmland bird indicator and the common species indicator. For butterflies, we used four indicators; the forest butterfly indicator, farmland butterfly indicator, the grassland butterfly indicator as well as an indicator built from the 20 most common species in Sweden. The species selection for the bird indicators is based on the indicators used for the Swedish environmental objectives and the European indicators (www.sverigesmiljomal.se, www.pecmbs.info).

The grassland butterfly indicator is based on the European Grassland Butterfly Indicator (van Swaay et al. 2020). The farmland butterfly indicator is based on species selected by Gilburn et al. (2015). The forest butterfly indicator is based on expert selection from the encyclopedia of Swedish flora and fauna (Eliasson et al. 2005) and the butterfly atlas of north-west Europe (Bink 1992). For species lists per indicator see suppl. files Paper I.

All MSIs were calculated in the six regions as well as nationally (Fig. 6). By calculating MSI trends both on a regional scale and a national scale we were able to compare trends in different biogeographical zones as well as see how different regions influence the national trends. Some patterns might not be visible on a national scale that will be apparent on smaller scales.

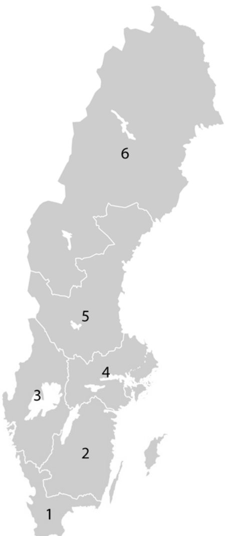

Figure 6. Map of Sweden outlining the six regions used to calculate regional indicator trends. Each region consists of several counties, listed in parentheses: (6) Northern Norrland (Jämtland, Västerbotten, Norrbotten), (5) Southern Norrland (Dalarna, Gävleborg, Västernorrland), (4) Eastern Svealand (Södermanland, Örebro, Västmanland, Stockholm, Uppsala), (3) Western Göta- and Svealand (Västra Götaland, Värmland), (2) Eastern Götaland (Kronoberg, Kalmar, Jönköping, Gotland, Östergötland). (1) Southern Götaland (Skåne, Halland, Blekinge).

Literature review

To synthesize what is currently known about farmland and grassland birds and butterflies utilizing forest clear-cuts, I did a literature review. All known literature on the occurrence of grassland and farmland birds and butterflies in clear-cuts was collected and I included all case-studies that were done in Europe in my review. Most articles were found during a broad systematic literature search on drivers of butterfly and bird population trends at the temperate/boreal forest-farmland interface. This systematic search resulted in over 6000 papers of which first titles and, in a next step, abstracts were scanned for relevance. Additionally, I did a non-systematic, more targeted search on clear-cut case studies to supplement the broader search. A total of 19 scientific articles were included in the review, of which 8 analyze butterflies in clear-cuts and 11 analyze birds in clear-cuts.

Clear-cut surveys

Clear-cut bird surveys on the Fixed routes

In 2017, 2018 and 2019, we asked surveyors of the Swedish Bird Survey Fixed routes to do an additional point count on one or two clear-cuts along their route (Fig. 7a). Selected clear-cuts where not older than 10 years, not directly bordering other clear-cuts, and overlapping with the fixed route line transect. Surveyors received a map with the selected clear-cuts on their route marked out and results were reported on a separate protocol together with the regular Fixed route results. Point counts were conducted in a similar way to the other point counts included in the standard route surveys. During 5 minutes, the surveyor counted all birds seen or heard that to their judgement were on the clear-cut. Birds seen in the forest edge, not obviously making use of the clear-cut, were excluded in the count. In order to minimize the interference with the ordinary fixed route counts, the surveyor did not leave their original route. Accordingly, the point counts were sometimes done from the edge and sometimes more towards the center of the clear-cut. In addition to the point count, the surveyors were also asked to take a photo of the clear-cut where they did the count.

Clear-cut butterfly surveys in Dalarna and Skåne

In 2018, 2019 and 2020 we organized butterfly surveys on clear-cuts in Dalarna and Skåne (Fig. 7b). In both regions, clear-cuts were surveyed twice, once in June and once in July to cover flight times of different species. Selected clear-cuts were not older than 5 years in 2018, and not within one kilometer of each other. Clear-cuts intersecting with power lines were excluded to avoid areas cut as a maintenance of the power line corridors. The surveys consisted of one to three point counts per clear-cut, depending on the size of the clear-cut, arranged from the center to the edge of the clear-cut (only the centroid and edge point counts were used in *Paper IV*). Surveys were only done with a minimum temperature of 17°C with clear skies or 25°C with partially clouded skies, and no strong winds. Points were also positioned on the sunny side of the clear-cut. A point count was done by counting every butterfly seen while walking around for 15 minutes within a 50 meter diameter circle (Fig. 8). A photo was also taken of the surveyed clear-cut.

As Silver-studded Blue *Plebejus argus* and Idas Blue *P. idas* as well as Green-veined White *Pieris napi* and Cabbage White *P. rapae* are difficult to distinguish in the field these species were combined and treated as one species respectively.

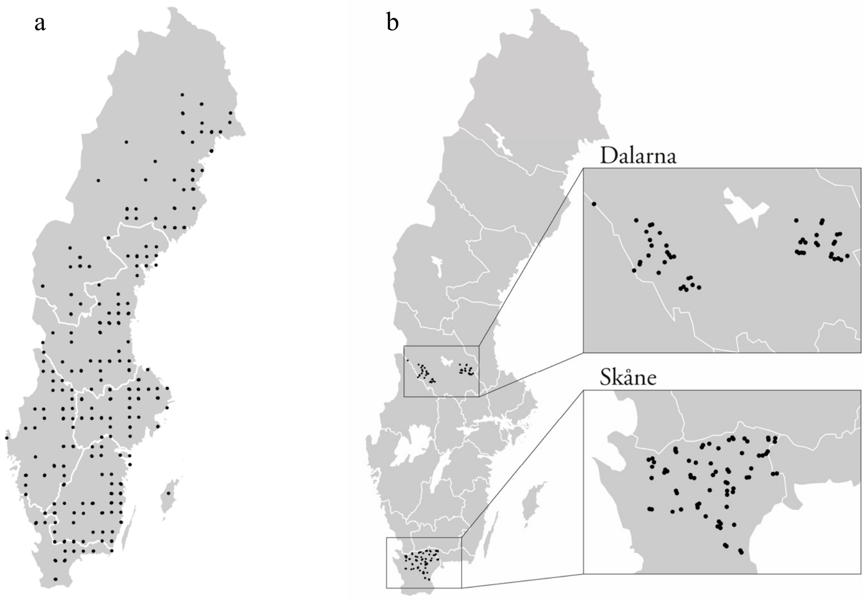

Figure 7. Black dots indicate clear-cut birds surveys done along Swedish Bird Survey Fixed routes (a) and clear-cut butterfly surveys done in Dalarna and Skåne (b). Details in paper III and IV.

Community analysis and species associations

We used distance-based redundancy analysis (dbRDA) based on Bray-Curtis dissimilarities (Legendre & Anderson 1999) to investigate the structure of bird and butterfly communities on clear-cuts. We included environmental constraint variables for clear-cut size, age, vegetation height (bird analysis) and region or county, as well as the proportion of recent clear-cut forest, the proportion of farmland and the proportion of broadleaf forest (butterfly analysis) in a 200 meter buffer and a 5 kilometer buffer around the surveyed clear-cut. All variables were included in the full model, after which we performed model selection to find the best model.

Poisson generalized linear models (GLM) were fitted on a species level as well as for several species' groups (farmland species, grassland species and red-listed species) to further investigate the relationship between their abundance on clear-cuts and the environmental variables. The full models included all variables, after which we performed model selection based on AICc and model averaging including the models in the lowest 0.05 quantile of ΔAICc.

For birds, we calculated the regional relative frequency of species in the clear-cuts and compared them to the regional relative frequency of the respective species in the Swedish Bird Survey. This comparison puts the occurrence of a species in clear-cuts in perspective with to what extent they occur in the region in general. This comparison of relative frequencies with the national monitoring scheme was not done for butterflies, since there were not enough survey points in Dalarna to compare to our clear-cut surveys.

Figure 8. The author during a butterfly survey on a clear-cut in north-eastern Skåne. (Photo: Michael Simmonds)

Results and discussion

Habitat-based indicators

Habitat-based multi-species indicators, comprising of common and specialist species in a habitat, are used to indicate the state of these species and to evaluate current management and policy of the habitat (Butler et al. 2010, Gregory et al. 2019). Commonly used habitat-based indicators include farmland and grassland indicators and forest indicators, some of which are already used as indicators of ecosystem health (i.e. the European Farmland Bird Index, Gregory et al. 2005, Butler et al. 2010, the Grassland Butterfly Indicator, van Swaay et al. 2020). When using indicators to inform habitat-wide policy it is important that the indicator is representative of the majority of organisms it supports. If this would be the case, indicators of different taxa for the same habitat, would be expected to give a similar signal.

Comparing habitat-based indicators

In *Paper I,* we compared farmland, grassland and forest indicators of birds and butterflies in Sweden, both on a national as well as a regional scale. As a reference for how the taxa is doing in general, we also calculated common species indicators for both taxa. We found that at the national scale, the butterfly indicator trends were positive or stable. However, the national bird indicator trends varied and had declining (Farmland bird indicator), increasing (Forest bird indicator) and stable results (Common species indicator). Within indicators there was also regional variation, confirming that national indicators might not be representative of the entire country (Fig. 9).

Can taxon-specific indicators represent other taxa?

While habitat-based biodiversity indicators are sometimes used to represent more taxa than they include or even used as indicators of ecosystem health (Gregory & van Strien 2010, Renwick et al. 2012, van Swaay et al. 2020), we found that indicators based on one taxon may not reliably predict responses in indicators based on other taxa. Considering the differences in ecology between birds and butterflies this result may not be surprising, as they are likely responding to different aspects of the landscape (Ekroos et al. 2013).

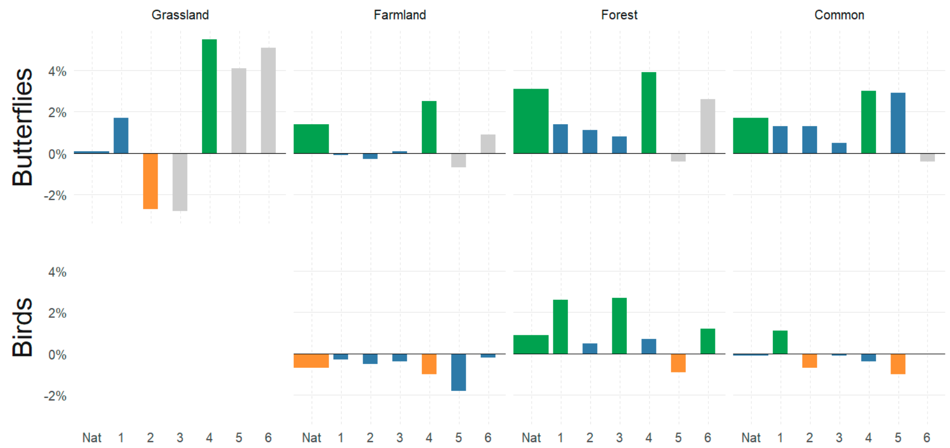

Figure 9. National (wide bars) and regional (narrow bars) multi-species indicator trends for 2006-2019 for the butterfly indicators (upper) and bird indicators (lower), for the grassland and farmland, forest, and common species indicators. Colors indicate the significance of the trend direction where orange is significantly declining, green is significantly increasing, blue is stable and light grey indicates an uncertain trend. Details in Paper I.

Are butterflies doing better than birds?

The most notable differences include the stable or positive trends in grassland and farmland butterflies (with the exception of one region) compared to the negative trends in farmland birds. Agricultural intensification and abandonment are known to have negatively affected both farmland and grassland birds and butterflies (Nilsson et al. 2013, Butler et al. 2010) and both groups have been declining since before the time period we analyzed (Gregory et al. 2019, van Strien et al. 2019, Warren et al. 2020). Devictor et al. (2012) showed that butterflies in Europe respond more rapidly to climate warming than birds, which could be a possible explanation to the differences in trends we see here. The forest indicators have mostly positive trends for both butterflies and birds, but even here butterflies show more positive slopes (Fig. 10). Additionally, the common species indicator of butterflies has more positive trends than the common bird indicator suggestion that butterflies are doing better in general.

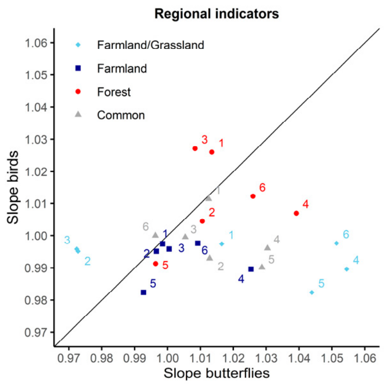

Figure 10. The relationship between the slopes of regional bird and butterfly indicator trends. The black solid line indicates the 1:1 relation. Points below this line indicate that butterflies are doing better than the birds in a given region. More details in Paper I.

Interpreting multi-species indicators

When intepreting multi-species indicators (MSIs) it is important to keep several things in mind. As an MSI consists of trends of several species, it is a summary of these trends. This means that declining species can be included in MSIs that show positive trends, as is the case for example with the declining Willow tit *Poecile montanus* and Pied flycatcher *Ficedula hypoleuca* which are included in the forest bird indicator showing a positive trend. National trends can also mask regional patterns both on species as well as indicator level.

How well an indicator represents a specific habitat also depends greatly on the species selected. Some species are more specialized or strongly associated with a specific habitat than others (O'Reilly et al. 2022). Furthermore, our course classification of habitat in "farmland" or "forest" neglects variation within these habitat, such as the difference between broadleaf and coniferous forest or smaller scale differences in the niches occupied by species in the landscape. Additionally, many species traditionally associated with a certain type of habitat might also use alternative habitats. Farmland birds and butterflies, for example, have been shown to also occur to a large extent outside of farmland in habitats such as bogs, power-line corridors and forest clear-cuts (Stjernman et al. 2013, Berg et al. 2011).

Clear-cuts as habitat for farmland and grassland species

Forest clear-cuts are open patches in an otherwise often forest dominated landscape, and can be potential habitat for farmland and grassland bird and butterfly species. With literature on this subject growing, I performed a literature review synthesizing factors and characteristics of clear-cuts that affect farmland and grassland bird and butterfly occurrence (*Paper II*). I found 19 studies in total, of which 11 studies analyze bird occurrence and 8 studies analyze butterfly occurrence in clear-cuts. The findings can be divided into two main categories: clear-cut characteristics and landscape characteristics (Fig. 11).

Clear-cut characteristics include clear-cut age and vegetation height, clear-cut size, the food resources available in the clear-cut and retention trees and other structures. Within two to five years after clear-cutting, trees are often replanted or otherwise regenerated, as many countries in Europe have an obligation for regeneration in their forest laws (Bauer et al. 2004). Besides tree regeneration, the herb layer recovers in the first one to five years as the site starts the stages of succession into forest (McDermott et al. 2010). Clear-cut age, or time since clear-cutting, can be used as an indicator of regeneration and vegetation height. While one would expect younger clear-cuts to be more similar to farmland or grassland and therefore richer in butterflies, we did not find this supported in the literature.

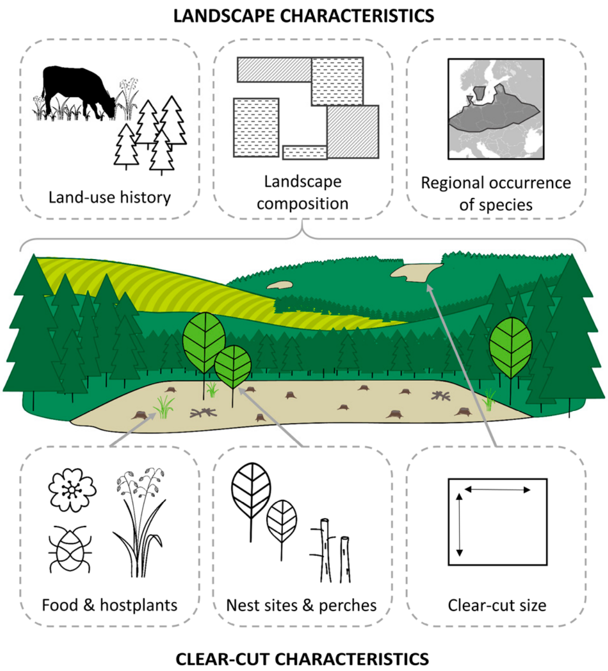

Figure 11. Conceptual illustration of variables affecting farmland bird and butterfly occurrence in forest clear-cuts on a local scale (clear-cut characteristics) and a larger scale (landscape characteristics). From Paper II.

However, species composition might shift with clear-cut age (Ibbe et al. 2011) as species can prefer clear-cuts of a certain age (e.g., Marsh fritillary *Euphydryas aurinia*, Wahlberg et al. 2002). An effect of clear-cut age was found on farmland birds, with communities shifting from early successional species to more forest dependent species (Baguette et al. 1995). However, a higher abundance and species richness of farmland birds was found on older (6-10 years old) clear-cuts in Poland (Żmihorski et al. 2016). Additionally, some species use clear-cuts many years after clear-cutting (e.g., Ortolan bunting *Emberiza hortulana*, Percival & Dale 2016). The extent of how long a clear-cut is suitable for farmland species will depend on other local and landscape factors as well as the species considered, but there is evidence of a large time frame in which these species can use clear-cuts as habitat. The effects of clear-cut size were mixed and while some species preferred larger clear-cuts (e.g., Ortolan bunting, Percival & Dale 2016) the range of sizes included in the studies was relatively small.

Retention forestry, the retaining of dead or live trees on clear-cut areas, has been shown to positively affect forest species but could potentially be beneficial for farmland species as well (Söderström & Karlsson 2011, Percival & Dale 2016, Bakx et al. 2020). Retained structures could provide nest sites, perches or food resources.

However, some farmland species were negatively affected by the amount of retention trees (Söderström 2009). Studies looking at food resources, especially host plants for butterflies, are scarce (but see Söderström & Karlsson 2011, Hollander et al. 2015, Viljur & Teder 2018) and direct measures of food availability would greatly improve the understanding of suitability of clear-cuts as habitat.

Land-use history, for example if clear-cuts were previously meadows or forest, significantly impacts the current plant communities (Jonason et al. 2014, Blixt et al. 2015). As a result, grassland butterflies were positively affected, causing communities in clear-cuts with meadow-history to be more abundant and species rich. In addition to land-use history, the surrounding landscape seemed to affect the occurrence of birds and butterflies in clear-cuts as well. However, it is unclear how important direct connectivity is or whether habitat amount is more important.

Farmland birds in forest clear-cuts

Since forest clear-cuts clearly have potential as habitat for farmland birds, we investigated the use of clear-cuts by birds, particularly farmland birds, in Sweden (*Paper III*). We included 298 clear-cuts throughout Sweden covering a wide range of latitudes, enabling us to look at large scale patterns and detect regional differences. We analyzed bird communities in clear-cuts in combination with local characteristics (clear-cut size, age and vegetation height) and landscape characteristics (proportion farmland and proportion recently cut clear-cuts in the surroundings).

In total, 1170 individuals of 66 different species (more than a quarter of all species breeding in Sweden, Ottosson et al. 2012) were recorded on clear-cuts. The most common species were Willow Warbler *Phylloscopus trochilus*, Tree Pipit *Anthus trivialis*, Chaffinch *Fringilla coelebs* and Yellowhammer *Emberiza citrinella*. The observations included 10 of the 15 species that are classified as farmland indicator species in the Swedish Farmland Bird Indicator confirming that clear-cuts are indeed potential habitat for farmland birds (Söderström 2009, Żmihorski et al. 2016). We do not know to what extent these species use the clear-cuts (for foraging, nesting etc.) but given that Söderström (2009) found 59 species breeding on 54 clear-cuts cuts in a region in eastern Sweden, we suspect several of the observed species do in fact breed on clear-cuts as well.

Important to note are also the farmland bird indicator species that were *not* detected in the clear-cut surveys: Lapwing *Vanellus vanellus*, Skylark *Alauda arvensis*, Barn Swallow *Hirundo rustica*, Rook *Corvus frugilegus* and Tree sparrow *Passer montanus*. Possible reasons these species might avoid clear-cuts will likely differ between species but might include an avoidance of forest edges (e.g., Skylark, Piha et al. 2003) and dependence on human settlements for nesting (e.g., Barn swallow and Tree sparrow, Svensson et al. 1999). Food availability for adults and young might also be poorer in clear-cuts for certain species (e.g., Lapwings feeding on earthworms, Owen & Galbraith 1989, Duriez et al. 2005, Malmström et al. 2009 and starlings feeding their young with soil-living invertebrates, Bruun & Smith 2003).

By calculating the regional relative frequencies of species occurrences (summed count of individuals of species observed/summed count of all birds observed) on the clear-cuts and the Swedish Bird Survey Fixed routes we could compare if species occurred proportionally more on clear-cuts than they occurred in the region in general. Several Species that occurred proportionally more often on clear-cuts included Yellowhammer, Whinchat *Saxicola rubetra*, Red-backed shrike *Lanius collurio* and Tree pipit. Other species occurred less often (or not at all) on clear-cuts than on Fixed routes (e.g., Skylark) while some species had similar relative frequencies (e.g., Blackcap *Sylvia atricapilla*, Fig. 12).

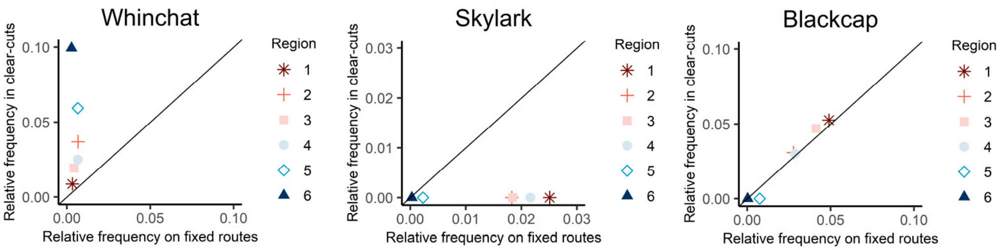

Figure 12. Relative frequencies of Whinchat (left), Skylark (middle) and Blackcap (right) on clear-cuts compared to their relative frequencies on the Swedish Bird Survey Fixed routes. Dots indicate regions and solid lines show the 1:1 relation. Values above the 1:1 line indicate that in a given region proportionally more birds were seen on clear-cuts than on Fixed routes, and vice versa. Details and other species plots in Paper III.

Distance-based redundancy analysis with subsequent permutational ANOVA suggested that bird communities varied significantly with vegetation height, clear-cut size, age, proportion of farmland in the direct surroundings (200 m buffer) and region. Clear-cuts with higher vegetation were preferred by Willow warblers and Garden warblers *Sylvia borin* and avoided by Whinchats. Surprisingly, the other farmland species as well as farmland species in total were seemingly not affected by vegetation height. A possible explanation for this is that Yellowhammers, the most abundant farmland species, is known to also use older clear-cuts and Christmas tree plantations (Gailly et al. 2017, Bakx et al. 2020). Clear-cut size positively affected Willow warbler, Whinchat and Yellowhammer abundance, as well as farmland and red-listed species as a group. Larger clear-cuts might simply be easier to reach and can hold more territories but may also contain more preferred micro-habitats. Larger clear-cuts might also be preferred since nearby forest edges or trees can lead to increased predation risk (Piha et al 2003, Żmihorski et al. 2018).

We also found the surrounding landscape to be of importance to birds occurring in clear-cuts. In particular, the proportion of farmland in nearest surroundings (200 m) explained differences in bird communities and positively affected farmland bird abundance. A higher proportion of farmland in the landscape is likely to increase chances of colonization of clear-cuts and higher abundance and diversity of farmland birds has been found in Poland as well (Żmihorski et al. 2016). In contrast to the study in Poland, Whinchats were not affected by the proportion of farmland in the surroundings. As Whinchat was negatively affected by higher vegetation heights in clear-cuts but not affected by open habitat in the surroundings, this might indicate that clear-cuts may have become a primary habitat for this species (Fig. 13). The high occurrence of Greater whitethroat *Sylvia communis* and Yellowhammer in farmland (Stjernman et al. 2013), in combination with our high numbers in clear-cuts and a positive effect of nearby farmland suggests that Greater whitethroat and Yellowhammer use clear-cuts as complementary habitat, while still depending on farmland.

Figure 13. Clear-cut in northern Sweden with a Whinchat perched on a dead tree (top left corner). (Photo: Åke Lindström)

Farmland and grassland butterflies in forest clear-cuts

In *Paper IV*, we investigated the use of clear-cuts by butterflies in two counties with contrasting landscapes: Dalarna in central Sweden, which is predominantly forest and Skåne in southernmost Sweden, which has a forest-farmland mosaic landscape. In total 120 clear-cuts were surveyed in 3 years, of which 49 in Dalarna and 71 in Skåne. We analyzed butterfly communities in clear-cuts in combination with local characteristics (clear-cut size, age and county) and landscape characteristics (proportion farmland, proportion recently cut clear-cuts and proportion broadleaf forest in the surroundings).

In total, 8359 individuals were observed (4087 in Dalarna and 4272 in Scania) and 58 species of butterflies and burnet moths were identified (Fig. 14). This is about half of the species that breed in Sweden (Pettersson et al. 2022). The most common species observed in Dalarna was Silver-studded/Idas Blue *Plebejus argus/idas.* Ringlet *Aphantopus hyperantus* was the most common species observed in Skåne.

Figure 14. Small pearl-bordered fritillary *Boloria selene*, one of the 58 species observed during the surveys, on a clear-cut in Skåne. (Photo: Helena Navalpotro)

All 14 species of the Swedish farmland indicator were observed on clear-cuts as well as 9 out of the 12 Swedish grassland butterfly indicator species. The indicator species that were not observed in our surveys were Small Blue *Cupido minimus*, Large Blue *Phengaris arion* and Marsh Fritillary *Euphydryas aurinia* and are all three diet specialist in Sweden (Eliasson et al. 2005). The other two of the five diet specialist grassland species included in the Grassland indicator were found in the clear-cut surveys, as well as the seven diet generalists. Generalist, mobile species might be better adapted to survive in intensively used landscapes such as intensive agriculture or production forest (Ekroos et al. 2010, Börschig et al. 2013, Kőrösi et al. 2022, but see Thomas 2000).

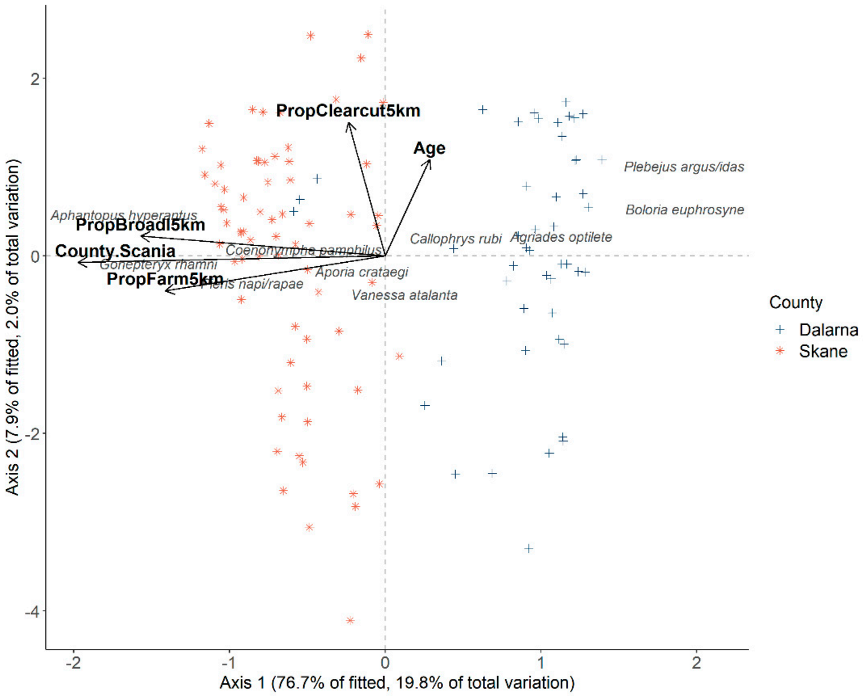

Figure 14. Distance-based redundancy analysis results visualizing the butterfly communities on clear-cuts in Dalarna and Skåne. Details In Paper IV.

The butterfly communities differed clearly between the two counties and distance-based redundancy analysis with subsequent permutational ANOVA suggested that besides county, all landscape variables at 5 km (but not 200 m) as well as clear-cut age significantly explained variation in the communities (Fig. 14). While the two counties belong to different biogeographic zones (Cervellini et al. 2020), a considerable portion of the species pool is shared.

The abundance of farmland and grassland species as well as several other species in the clear-cut center was negatively affected by clear-cut size. This negative effect was not there, or even positive in some cases, when looking at the abundance in edges of the clear-cut, suggesting that butterflies either have a preference for the edges of the clear-cuts or use these lines in the landscape for orientation. Farmland and grassland butterflies also responded to clear-cut age (as a quadratic term) suggesting that abundance increase with clear-cut age before decreasing again. Clear-cuts might be not suitable directly after clear-cutting, but as the herb layer recovers and shrubs grow in, it resembles more shrubby grasslands and thus becomes more suitable for many butterflies, before turning into forest again (Warren & Key 1991, Ibbe et al. 2011).

Both the community analysis as well as the species level analyses showed a higher importance of landscape composition at a 5 km scale than the 200 m scale. In Skåne the proportion of farmland was more important for grassland and farmland species while in Dalarna the proportion clear-cut forest had a stronger effect. This is likely due to the fact that the proportion farmland in Dalarna is small and butterflies would thus depend on other open habitat in the landscape.

Conclusions and future perspective

Biodiversity loss continues to be a global crisis, despite multiple international agreements with the goal of reversing this trend (Ceballos et al. 2015, Diaz et al. 2019). To improve biodiversity conservation we need to be able to track components of biodiversity and understand how they respond to environmental changes. *On a large scale*, biodiversity indicators are very helpful in tracking such changes and the way they are calculated have improved in recent decades (Dennis et al. 2016, Fraixedas et al. 2020). However, trends and responses of indicators differ between taxa as well as between countries and regions, and heavily depend on the species included. Therefore, *on a small scale,* we need to look at communities and species, and how they utilize habitats and how they respond to environmental changes.

Farmland and grassland birds and butterflies have been declining, a trend that has been found in several countries as well as on a European scale (Donald et al. 2001, Warren et al. 2021). The comparison of indicators on different scales in *Paper I* shows how national trends can mask regional patterns. Additionally, habitat-based indicators representing the same habitat, but based on different taxa, can give different signals. Indicators of different taxa may therefore be better used complementarily than as surrogates for other taxa or extrapolated as indicators of ecosystem health.

An important explanation to regional differences in trends and distributions of species are differences in the landscape and its configuration. In an intensely used landscape, with low amounts of natural and semi-natural habitats, some species may turn to use anthropogenic habitats such as power-line corridors, road verges and forest clear-cuts. While these habitats might not categorize as grassland or farmland in our eyes, in some cases they seem to provide similar resources to farmland and grassland species. A review of the literature (*Paper II*) showed that many farmland and grassland bird and butterfly species do use forest clear-cuts, but that variables driving their occurrence often vary or are unclear.

Our large-scale survey of birds on forest clear-cuts (*Paper III*) showed that many species occur on forest clear-cuts, including 10 of the farmland indicator species. They responded differently to environmental variables suggesting some might use clear-cuts as primary habitat in some regions (e.g., Whinchats in the north of the country) and some might use clear-cuts more as complementary habitat while still depending on farmland in the surroundings (e.g., Greater Whitethroat and

Yellowhammer). Clear-cuts are, however, not suitable for all farmland birds, such as Lapwing, Skylark, Rook, Barn Swallow and Tree Sparrow, most likely for reasons related to nesting sites, food, and predation risk.

Butterflies, including grassland and farmland indicator species, also utilize forest clear-cuts. The comparison of butterfly occurrence on forest clear-cuts in two contrasting counties (*Paper IV*) showed that butterfly communities differ between the counties and that occurrence of farmland and grassland species is affected by the amount of open habitat in the surroundings. While birds mostly responded to open habitat within a 200 m buffer of the clear-cuts, the butterflies more strongly responded to the larger scale 5 km landscape variables. While one would expect birds, as they are more mobile, to respond to the landscape at a larger scale, it suggests that many butterflies are capable of locating patches of habitat even when surrounded by forest. The contrasting influence of the nearer (200 m) proportion of open habitat on farmland bird occurrence could indicate that birds more often use clear-cuts as complementary habitat and therefore move more regularly between different habitats, while butterflies may use these habitat patches more exclusively to both feed and breed, but will cross larger distances when dispersing.

Whereas birds as well as butterflies make use of clear-cuts, these animals respond differently to environmental drivers. Considering how their ecology differs (reproductive rates, scale of movement, endo- versus ectothermy and food source specialization) this is not surprising, and also reiterates the fact that biodiversity indicators based on a single taxa are unlikely to be representative of other taxa when it comes to responses to environmental changes.

While this thesis mostly looks at larger scale occurrence patterns, to truly know if species are thriving in these man-made habitats, or if it is a potential ecological trap (Hollander et al. 2011) more detailed studies are needed on fitness output of species using clear-cuts (but see Söderström & Karlsson 2011, Gailly et al. 2020). Comparing resource availability (Hollander et al. 2015), such as butterfly host plant abundance would help to assess differences in habitat quality. Plant communities, including host plant abundance, are affected by historical land use (Lindborg & Eriksson 2004, Dahlström et al. 2006, Gustavsson et al. 2007). Consequently, whether clear-cuts were previously meadows or forest has an effect on the butterfly community found there (Ibbe et al. 2011). While we did not include land-use history in our analysis, it would be interesting to see if there is an effect on birds as well. Land-use history is therefore something that should be taken into account when considering forest clear-cuts in conservation planning.

Another factor that can influence trends and occurrence patterns is climate change, which was not addressed specifically here. Climate change has been shown to cause species to expand or shift their home ranges (Chen et al. 2011) which could in turn affect how species use the landscape as well as the indicator trends. Since butterflies seem to track climate warming faster than birds (Devictor et al. 2012) this could potentially explain the more positive trends in butterflies in shown in *Paper I*. However, for forest birds for example, climate change is likely not the main driver of trends, but rather the amount and quality of forest (Ram et al. 2017). While climate change has received a lot of attention in conservation research, and definitely affects patterns of biodiversity, habitat loss is still the largest and most imminent threat to biodiversity (Caro et al. 2022).

As semi-natural habitats have declined in the more intensively used modern landscape, it is good to consider alternative habitats in policy and conservation planning. While further studies are needed to expand our knowledge on how species, not least the currently declining grassland and farmland species, use these habitats to form more detailed management advice, the results in this thesis emphasize the importance of a landscape scale approach to conservation of both birds and butterflies. Clear-cuts near farmland could be managed with early successional species in mind, by for example leaving heaps of cutting remains for Red-backed Shrikes (Bakx et al. 2020) and less retention of low conservation value trees such as young Norway Spruce (Söderström 2009). Clear-cuts with a history as meadows could be particularly valuable to grassland butterflies (Ibbe et al. 2011) and could be used as stepping stones between remaining grasslands (Ohwaki et al. 2018). However, given that clear-cutting has a negative effect on forest biodiversity and even-aged forestry contributes to a homogenized forest, I am no advocate of clear-cutting in general. Nevertheless, while clear-cutting remains a common approach in forestry, we should strive to manage them so they may contribute to a green infrastructure for open habitat species.

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