UNIVERSITY OF TURKU

THE CONSERVATION OF DECLINING GRASSLAND SPECIES IN NOVEL HABITATS

Jussi Lampinen

TURUN YLIOPISTON JULKAISUJA – ANNALES UNIVERSITATIS TURKUENSIS
SARJA – SER. AII OSA – TOM. 362 | BIOLOGICA – GEOGRAPHICA – GEOLOGICA | TURKU 2020

UNIVERSITY OF TURKU

THE CONSERVATION OF DECLINING GRASSLAND SPECIES IN NOVEL HABITATS

Jussi Lampinen

TURUN YLIOPISTON JULKAISUJA – ANNALES UNIVERSITATIS TURKUENSIS
SARJA - SER. A II OSA - TOM. 362 | BIOLOGICA - GEOGRAPHICA - GEOLOGICA | TURKU 2020

University of Turku

Faculty of Science and Engineering
Department of Biology
Section of Ecology
Doctoral Programme in Biology, Geography and Geology (BGG)

Supervised by

Dr., docent Kalle Ruokolainen
Department of Biology
University of Turku
Finland

Reviewed by

Dr., docent Anni Arponen
Helsinki Institute of Sustainability Science (HELSUS)
University of Helsinki
Finland

Dr. Triin Reitalu
Department of Geology
Tallinn University of Technology
Estonia

Opponent

Prof. Christopher M Raymond
Helsinki Institute of Sustainability Science (HELSUS)

Ecosystems and Environment Research Program,
Faculty of Biological and Environmental Sciences

Department of Environmental Economics and Resource Management,
Faculty of Agriculture and Forestry Sciences

University of Helsinki
Finland

The originality of this thesis has been checked in accordance with the University of Turku quality assurance system using the Turnitin OriginalityCheck service.

Cover Image: Jussi Lampinen

ISBN 978-951-29-7943-1 (PRINT)
ISBN 978-951-29-7944-8 (PDF)
ISSN 0082-6979 (Print)
ISSN 2343-3183 (Online)
Painosalama Oy, Turku, Finland 2020

Kaikille kaksi- ja nelijalkaisille ystävilleni

UNIVERSITY OF TURKU
Faculty of Science and Engineering
Department of Biology
Jussi Lampinen: The Conservation of Declining Grassland Species in Novel Habitats
Doctoral Dissertation, 176 pp.
Doctoral Programme in Biology, Geography and Geology (BGG)
January 2020

ABSTRACT

Semi-natural grasslands created by traditional animal husbandry are among the most threatened habitat types in northern Europe, and many of the species adapted to them are currently endangered. Improving the conservation status of grassland species requires increasing the area of habitats that are suitable for them. This may be achieved by restoring degraded semi-natural grasslands, or by developing the management of other early-successional habitats to better suit the needs of grassland species. This thesis concerns the conservation of grassland species in young anthropogenic habitats that may function as alternatives to semi-natural grasslands under suitable management. Collectively referred to as novel habitats, these include power line clearings, road verges and urban lawns, which are all regularly managed for specific purposes. The current quality of these habitats as alternatives to semi-natural grasslands is limited by management regimes that are suboptimal for grassland species. Modifying or altering these regimes would be especially beneficial in areas which are environmentally otherwise suitable for grassland species. The implementation of any management alteration, however, is complicated by the fact that grassland conservation is not the primary motivation for managing these habitats. Rather, the current management regimes of novel habitats are driven by societal phenomena both on the level of individual novel habitat stakeholders and on the level above them. The first include phenomena such as values assigned to novel habitats and the attitudes towards particular management methods. The latter include phenomena such as legislation, established practices and norms for the appearance and functioning of novel habitats. Understanding how these social scientific phenomena drive novel habitat management is equally important in utilizing them in grassland conservation as is understanding which environmental conditions favor the population performance and species richness of grassland species in them.

This thesis aims to combine ecological data on the environmental conditions favoring grassland species and social scientific data on the valuation of and attitudes towards novel habitats to propose guidelines for managing novel habitats for greater grassland conservation benefit. Chapters I-III concern the environmental determinants for the population performance and species richness of grassland species in novel habitats, while Chapters IV-V concern the values stakeholders assign to novel habitats, the attitudes they hold towards management practices that would favor grassland species, and the barriers that prevent the implementation of such alterations. The results show that specific environmental conditions support species rich grassland communities in novel habitats, although the determinants for species richness vary between species groups. Dry soils, southerly exposition and abundant light favor the population performance and species richness of grassland plants, while grassland butterflies are favored by mesic habitat conditions. In addition, local and regional land-use history related to semi-natural grasslands is positively related to the performance of grassland species populations and to the species richness of grassland plants, but not butterflies. The results also show that the values assigned to novel habitats and the attitudes towards managing them for greater grassland conservation benefit are diverse, interrelated and differ between stakeholder groups. Stakeholders who are positive towards management alterations favoring grassland species assign positive values of species richness, beauty and wildness to grassland vegetation, while stakeholders who are negative towards these alterations assign negative values of untidiness, lack of care and unsafety to such vegetation. Specific management alterations increasing the quality of novel habitats for grassland species, such as stakeholder education, are perceived as more feasible than others. Likewise, specific implementation barriers to these alterations, such as lack of resources, are perceived more severe than others among stakeholders.

The results of this thesis, along with previous research, indicate that especially novel habitats with dry soils, abundant light and a warm microclimate are suitable for at least grassland plants and that there is support among novel habitat stakeholders for managing these habitats to better suit the needs of grassland species. However, the multivalued nature of these habitats has to be taken into account when implementing any alterations to current management regimes. This may be achieved by ensuring that novel habitats under altered management retain a cared for, maintained appearance and that the original motivations for their management, such as traffic safety in road verges, are not compromised lest the alterations or grassland species themselves be faced with negative attitudes.

KEYWORDS: Semi-natural grassland, ecosystem novelty, nature conservation, nature management, nature valuation, attitudes

TURUN YLIOPISTO
Luonnontieteiden ja tekniikan tiedekunta
Biologian laitos
Jussi Lampinen: The Conservation of Declining Grassland Species in Novel Habitats
Väitöskirja, 176 s.
Biologian, maantieteen ja geologian tohtoriohjelma (BGG)
Tammikuu 2020

TIIVISTELMÄ

Perinteisen karjatalouden luomat niityt, kedot ja muut perinnebiotoopit kuuluvat Pohjois-Euroopan uhanalaisimpiin luontotyyppeihin. Moni niihin sopeutunut kasvi- tai hyönteislaji on arvioitu uhanalaiseksi. Niittylajiston suotuisa suojelutaso edellyttäisi, että näille lajeille soveltuvien elinympäristöjen pinta-ala kasvaisi huomattavasti nykyisestä. Tämä voidaan saada aikaiseksi joko ennallistamalla tuhoutuneita perinnebiotooppeja, tai kehittämällä muiden aikaissukkessiivisten elinympäristöjen hoitoa niittylajiston tarpeita paremmin vastaavaksi. Tämä väitöskirja koskee niittylajiston suojelua nuorissa, ihmisen luomissa elinympäristöissä, jotka oikein hoidettuina voisivat toimia vaihtoehtoina perinteisen karjatalouden luomille varsinaisille perinnebiotoopeille. Tällaisia ns. uusympäristöjä ovat esimerkiksi johtoaukeat, tienvarret ja puistonurmikot, joita kaikkia hoidetaan säännöllisesti tiettyjä tarkoitusperiä varten joko niittämällä tai muilla tavoin. Säännöllisyydestään huolimatta uusympäristöjen hoitomenetelmät ovat niittylajistolle usein epäedullisia, mikä heikentää uusympäristöjen laatua niittylajien elinympäristönä. Hoitomenetelmien muokkaus niittylajistolle soveltuvammaksi olisi hyödyllistä etenkin alueilla, jotka muilta ympäristöoloiltaan soveltuvat niittylajistolle. Muokkausta kuitenkin vaikeuttaa se, ettei niittylajiston suojelu ole uusympäristöjen hoidon pääasiallinen tarkoitus, vaan nykyiset hoitomenetelmät perustuvat pitkälti yhteiskunnallisiin ilmiöihin kunkin uusympäristön ja sen sidosryhmien ympärillä. Tällaisia ovat esimerkiksi sidosryhmien uusympäristöihin liittämät arvot, sidosryhmien asenteet uusympäristöjen erilaisia hoitomenetelmiä kohtaan, uusympäristöjen hoitomenetelmiä koskeva lainsäädäntö ja niiden ulkonäköön ja toiminnallisuuteen liittyvät normit ja vakiintuneet käytännöt. Jotta uusympäristöjä olisi mahdollista hyödyntää niittylajiston suojelussa, on aivan yhtä tärkeää ymmärtää, kuinka nämä yhteiskunnalliset ilmiöt muovaavat uusympäristöjen nykyisiä hoitomenetelmiä, kuin on ymmärtää, mitkä ekologiset tekijät suosivat niittylajipopulaatioiden elinvoimaisuutta tai niittylajiyhteisöjen runsaslajisuutta uusympäristöissä.

Tässä väitöskirjassa yhdistän ekologista aineistoa niittylajistoa suosivista ympäristöoloista yhteiskuntatieteelliseen aineistoon uusympäristöihin liittyvistä asenteista ja arvoista, ja ehdotan ohjenuoria uusympäristöjen nykyistä laajemmalle hyödyntämiselle niittylajiston suojelussa. Väitöskirjan kappaleet I-III käsittelevät niittylajipopulaatioiden elinvoimaisuuteen ja niittylajiyhteisöjen lajimäärään vaikuttavia ympäristöoloja uusympäristöissä. Kappaleet IV-V puolestaan käsittelevät eri sidosryhmien uusympäristöihin liittämiä arvoja, asenteita erilaisia niittylajistoa suosivia hoitomenetelmiä kohtaan, ja käytännön esteitä, joihin tämänkaltaisten hoitomenetelmien toimeenpano törmää. Kappaleiden I-III tulosten mukaan tietyt ympäristöolot suosivat runsaslajisten niittylajiyhteisöjen kehittymistä uusympäristöissä, joskin eri lajiryhmien lajimäärä uusympäristöissä riippuu eri ympäristöoloista. Kuiva maaperä, eteläinen ekspositio ja runsas valo suosivat niittykasvipopulaatioiden elinvoimaisuutta ja niittykasviyhteisöjen runsaslajisuutta. Tuore maaperä puolestaan suosii niittyperhosyhteisöjen runsaslajisuutta. Tämän lisäksi perinnebiotooppeihin liittyvä paikallinen ja maisemallinen maankäyttöhistoria liittyy positiivisesti niittykasvipopulaatioiden elinvoimaisuuteen ja niittykasviyhteisöjen runsaslajisuuteen. Niittyperhosten lajimäärän ja maankäyttöhistorian välillä tällaista yhteyttä ei havaittu. Kappaleiden IV-V tulosten mukaan uusympäristöihin liitetyt arvot ja asenteet niittylajistoa suosivien hoitomenetelmien toimeenpanemista kohtaan ovat monimuotoisia, toisiinsa liittyviä ja vaihtelevat eri sidosryhmien välillä. Myönteisesti niittylajistoa suosiviin hoitomenetelmiin suhtautuvat sidosryhmät liittävät uusympäristöjen niittykasvillisuuteen myönteisiä runsaslajisuuden, kauneuden ja villiyden arvoja. Kielteisesti niittylajistoa suosiviin hoitomenetelmiin suhtautuvat sidosryhmät puolestaan liittävät uusympäristöjen niittykasvillisuuteen kielteisiä epäsiisteyden, hoitamattomuuden ja turvattomuuden arvoja. Tietyt niittylajistoa suosivat menetelmät, kuten sidosryhmien koulutus, koetaan toteutuskelpoisemmiksi uusympäristöjen hoidossa kuin toiset. Samaten, tietyt käytännön esteet näiden menetelmien toimeenpanolle, kuten resurssien puute, koetaan sidosryhmien parissa vakavammiksi kuin toiset.

Väitöskirjan tulosten ja aiemman tutkimuksen perusteella erityisesti valoisat, lämpimät ja maaperältään kuivat uusympäristöt soveltuvat niittykasvien elinympäristöiksi. Asenteet uusympäristöjen hoitomenetelmien kehittämiseksi niittylajeja suosivampaan suuntaan ovat eri sidosryhmissä vaihtelevia, mutta pääosin neutraaleja tai myönteisiä. Uusympäristöjen moniarvoisuus tulee kuitenkin ottaa huomioon nykyisiä hoitomenetelmiä muokatessa. Tämä voidaan varmistaa esimerkiksi siten, että niittylajistoa suosien hoidetut uusympäristöt säilyttävät siistin, hoidetun ulkoasun. On myös tärkeää varmistaa, etteivät niittylajistoa suosivat hoitomenetelmät vaaranna kunkin uusympäristön hoidon alkuperäisiä tavoitteita, kuten liikenneturvallisuutta tienvarsilla, sillä tämä johtaisi todennäköisesti kielteisiin asenteisiin itse niittylajistoa ja sitä suosivia hoitomenetelmiä kohtaan.

ASIASANAT: Perinnebiotooppi, uusympäristö, luonnonsuojelu, luonnonhoito, arvotus, asennetutkimus

Contents

List of Original Publications

This dissertation is based on the following original publications, which are referred to in the text by their Roman numerals:

I **Lampinen J**. Disturbance, microclimate and historical habitat connectivity determine the population performance of the threatened grassland specialist *Carex caryophyllea* in remnant grasslands. *Nordic Journal of Botany*, 2019; 37: e02175.

II **Lampinen J**, Ruokolainen K, Huhta AP. Urban power line corridors as novel habitats for grassland and alien plant species in south-western Finland. *PLoS ONE*, 2015; 10: e0142236.

III **Lampinen J**, Heikkinen RK, Manninen P, Ryttäri T, Kuussaari M. Importance of local habitat conditions and past and present habitat connectivity for the species richness of grassland plants and butterflies in power line clearings. *Biodiversity and Conservation*, 2018; 27: 217–233.

IV **Lampinen J**, Tuomi M, Fischer L, Neuenkamp L, Alday JG, Cancellieri L, Casado-Arzuaga I, Čeplová N, Deák B, Eriksson O, Escriche AM, Fellowes MDE, Fernandez de Manuel B, Filibeck G, Guzmán AG, Hinojosa Centeno MB, Kowarik I, Lampei-Bucharova A, Lumbierres B, Pardo i Marín R, Pons X, Rodríguez-García E, Schröder R, Sperandii M, Cerveró L, Unterweger P, Valkó O, Vázquez VM, Klaus VH. Values of cleanliness, wildness and beauty influence the acceptance of biodiverse meadow-like lawns among city residents across Europe. *Manuscript.*

V **Lampinen J**, Anttila N. Reconciling road verge management with grassland conservation faces positive attitudes among stakeholders, but several implementation barriers related to resources and valuation.
Submitted manuscript.

1 Introduction

1.1 Semi-natural grasslands

Semi-natural grasslands are early-successional communities characterized by frequent moderate disturbance, a low-growing, often treeless field layer, abundant light, and high species richness of vascular plants, insects and other groups of species (**Fig 1**, Pykälä 2001, Dengler et al. 2014, Lehtomaa et al. 2018b). As the principal source of fodder and as areas for grazing, the history of semi-natural grasslands, wooded pastures and other traditional rural biotopes in northern Europe is closely associated with the introduction of agriculture and animal husbandry into the region (Pykälä 2001, Eriksson & Cousins 2014). The first signs of cultivation and domestic animals in northern Europe appeared roughly 5500 BCE (Eriksson & Cousins 2014), reaching Finland via the Baltic region roughly 5000 BCE (Bläuer 2015). In the following millennia, in Finland especially during the late Iron Age (Alenius et al. 2017, Vanhanen 2019), forest clearing, slash-and-burn cultivation, hay-making and cattle grazing led to a proliferation of open to semi-open landscapes on a scale not likely witnessed since the megafaunal extinctions of the late Pleistocene (Svenning 2002, Johnson 2009). This greatly increased the area of suitable open habitats for many species previously dependent on temporary clearings created by forest fires or floods, or on the more permanent, yet narrow bands of coastal meadows (Pykälä 2001, Eriksson & Cousins 2014).

As human populations and their cattle expanded to new regions, several species, termed archaeophytes, accompanied them and became established into the newly opened landscapes (Suominen & Hämet-Ahti 1993). In Finland, for example, archaeophytes comprise roughly 10-25 % of all species adapted to dry or mesic grasslands (Pykälä 2001). During their greatest extent in the mid 19th century, semi-natural grasslands covered on estimate as much as 2.65 million hectares in Finland, and roughly one third of the entire area of Estonia (Suomenmaan virallinen tilasto 1869, Talvi & Talvi 2012). The prevalence of these habitats in landscapes of the time is evident in historical maps, such as the Senate maps depicting land cover in southern Finland in the late 19th and early 20th centuries (The National Archives of Finland 2019).

Figure 1. An abandoned patch of semi-natural grassland in Mikkeli, Etelä-Savo. Herbs and grasses, such as *Agrostis capillaris*, *Knautia arvensis*, *Campanula glomerata*, *Pimpinella saxifraga* and *Leucanthemum vulgare* will dominate the field layer still for a few years before a secondary succession of willows, pines and birches takes over. Picture: JL.

However, since the late 19th century, the vast majority of semi-natural grasslands both in Finland and elsewhere in northern Europe have either been cleared into arable fields, afforested for silviculture or simply abandoned and left for natural succession to take over (Luoto et al. 2003, Kivinen 2005, Eriksson & Cousins 2014, Cousins et al. 2015). This was caused by agricultural reformations and societal and political changes that left semi-natural grasslands less essential in agriculture and animal husbandry and increased the incentives for transforming them into other land use types (Luoto et al. 2003). For example, the shift from winter fodder mown and collected from semi-natural grasslands to that cultivated in fields encouraged farmers to clear suitable grasslands into arable fields. Likewise, the shift from grazing in semi-natural grasslands to grazing in permanent, improved pastures caused many of the previously essential grasslands to become abandoned. As a consequence, the once dense patchwork of semi-natural grasslands was reduced to individual, fragmented remnants during the course of the 20th century (Vainio et al. 2001, Luoto et al. 2003, Eriksson & Cousins 2014, Cousins et al. 2015). Presently only an estimated 30 000 hectares of semi-natural grasslands with conservation value remain under favorable management (Kemppainen & Lehtomaa 2009, Lehtomaa et al. 2018a) in Finland. To demonstrate the magnitude of landscape change during the past 150 years, **Fig 2** presents a comparison of the cover of semi-natural grasslands and pastures in 1880-90 (Lampinen & Turkia 2019) and those remaining to the present day in South-Western Finland (Lounais-Suomen ympäristökeskus 2008, Finnish Environment Institute 2019a).

Because of their decline, semi-natural grasslands are now among the most threatened habitat types both in Finland (Kontula & Raunio 2018) and elsewhere in Europe (Janssen et al. 2017). As a habitat of threatened species, semi-natural grasslands and other rural and cultural habitats are second only to old-growth forests (Hyvärinen et al. 2019). For example, semi-natural grasslands and wooded pastures provide primary habitat for almost 600 near threatened, threatened or regionally extinct species of vascular plants, mosses, lichens, insects or other groups of species in Finland (Hyvärinen et al. 2019). In addition, the number of species regionally extinct in Finland per habitat type is highest in semi-natural grasslands (Hyvärinen et al. 2019). Similar patterns apply in Sweden as well: Out of all red-listed Swedish species, 33% have their primary habitat in agricultural landscapes, including semi-natural grasslands (ArtDatabanken 2015).

Besides continued deterioration due to successional overgrowth or management that is suboptimal for grassland species, or downright destruction due to housing development or silviculture, the remaining fragments of semi-natural grasslands may be threatened also by extinction debt (Helm et al. 2006, Cousins 2009). Extinction debt is a phenomenon where species inhabiting a given habitat are fated to suffer local extinction in the future due to a delayed response of the species community to past decreases in habitat area or quality (Kuussaari et al. 2009). For example, plant populations of long-lived species and those capable of vegetative reproduction may respond to deteriorating habitat conditions with substantial delays compared to populations of shorter-lived species. Due to this delay, populations of the first group of species are more prone to develop extinction debts, while populations of the latter group are prone to go extinct more quickly (Saar et al. 2012). The possible presence of extinction debts indicates that the species richness of the remaining fragments of semi-natural grasslands may continue to decline in the future despite restoration efforts (Johansson et al. 2011).

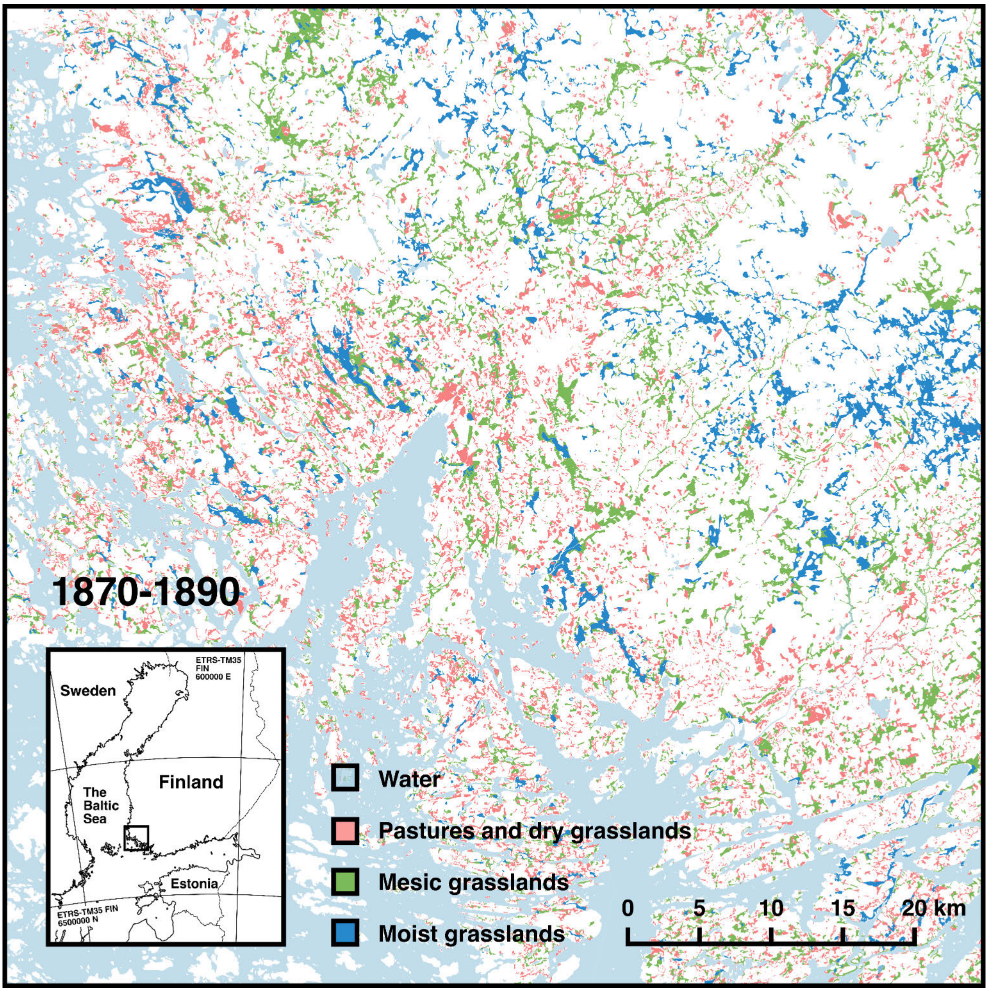


Figure 2 a). Pastures and dry grasslands (light red) and mesic (green) and moist (blue) grasslands in south-western Finland 1870-1890, based on the Senate maps, georeferenced and delineated by Lampinen & Turkia (2019).

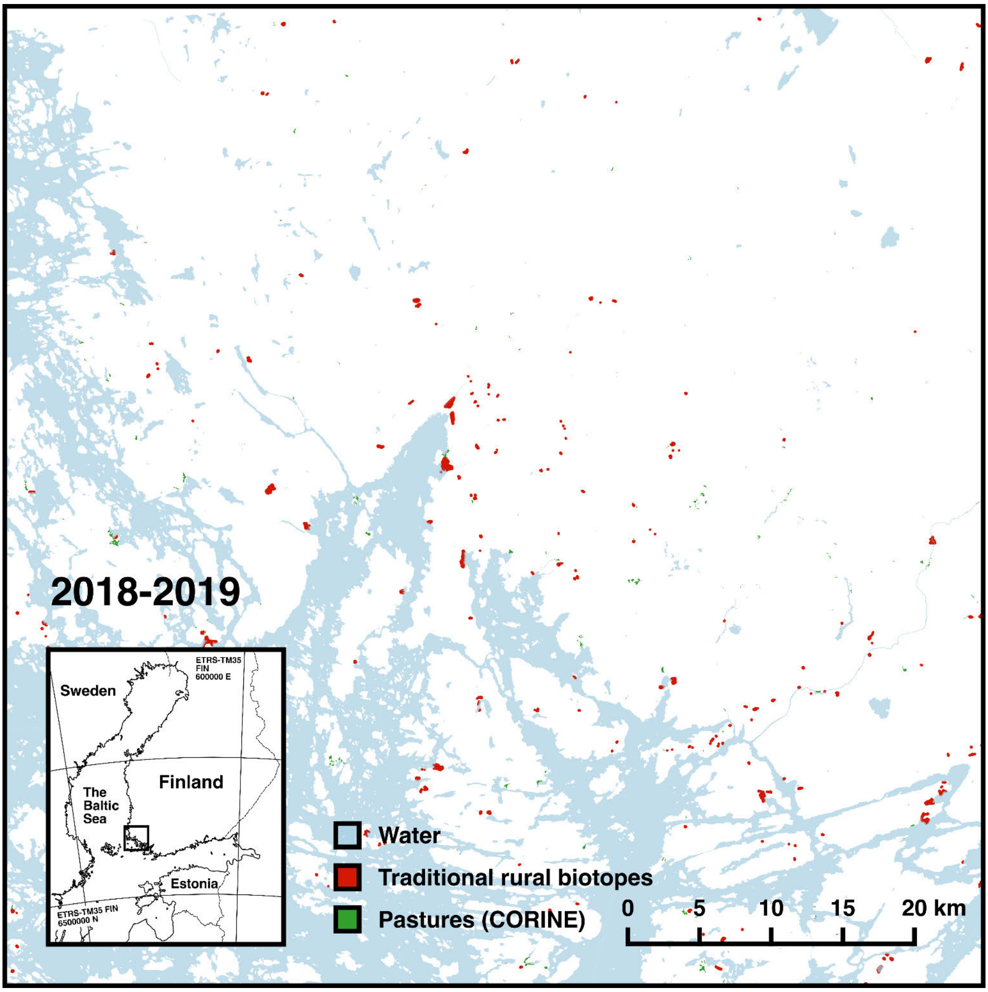


Figure 2 b). Semi-natural grasslands and other traditional rural biotopes (red) surveyed in the 1990´s (Lounais-Suomen ympäristökeskus 2008) and present pastures (green) according to CORINE 2012 land cover data (Finnish Environment Institute 2019a).

1.2 Habitats and novel habitats

Habitats are the physical settings in which individuals of a given species reside and interact with one another (Hall et al. 1997). From the species' point of view, habitats vary in quality, depending on the conditions that the species have adapted to. The quality of a particular habitat for a given species can be understood as the potential of the habitat to provide conditions that allow the species to establish populations, reproduce and persist in the habitat (Hall et al. 1997, Johnson 2007). For grassland species adapted to the abundant light and warmth typical to the early stages of succession, the most critical aspects of habitat quality include the availability of light and the intensity, frequency and continuity of disturbance such as grazing or mowing (Huhta et al. 2001, Pykälä 2005, Pykälä et al. 2005). Disturbance prevents succession from progressing towards more closed vegetation, and levels the resource competition between plant species in the field layer, thus preventing the competitive exclusion of poor competitors, e.g. small-sized species (Grime 1973). According to island biogeography and metapopulation models, also the size and connectivity to other similar habitats influence how many species may reside in a particular habitat and how well propagules and genes may flow from one habitat to another (MacArthur & Wilson 1967, Crooks & Sanjayan 2006, Hodgson et al. 2010). A grassland habitat of good quality is thus regularly disturbed, large and well-connected to other similar habitats. Conversely, a grassland habitat of poor quality is abandoned or under suboptimal management, overgrown, small and isolated from others.

Reductions in habitat quality lead to habitat degradation and ultimately habitat loss, which are considered the primary threats to the favorable conservation status of species worldwide (Baillie et al. 2004). Upon regional habitat loss, species adapted to semi-natural grasslands have three options: They may either immediately go extinct (Fischer & Stöcklin 1996), persist in the degraded remaining habitat fragments often presenting extinction debts (Cousins 2009), or resort to other, novel habitats that provide similar conditions as semi-natural grasslands (Lundholm & Richardson 2010, Auestad et al. 2011, Gardiner et al. 2018). This thesis focuses on the last of these options.

Novel habitats are environments created and managed by humans for specific purposes and characterized by partly similar structural or functional properties as natural habitats (Lundholm & Richardson 2010, Gardiner et al. 2018). Put simply, the environmental conditions in novel habitats resemble those in natural habitats to a sufficient extent for species adapted to specific natural habitats to be able to inhabit, persist and reproduce in them. Terms with similar meanings include alternative (Tikka et al. 2000; 2001), analogous (Lundholm & Richardson 2010) and surrogate habitats (Berndt et al. 2008). For example, the rooftops and ledges of urban buildings provide novel habitats for city doves (*Columba livia domestica*), a species whose ancestors inhabited rocky cliffs.

The concept of novel habitats is based on the framework of novel ecosystems (Hobbs et al. 2009; 2013; 2014). The "novelty" of a particular system in this case refers to differences in the system's qualities (such as species composition or ecosystem functioning) that are a) anthropogenic in origin, b) self-sustaining and c) beyond the historical range of variability of those qualities compared to similar natural systems of the same region (Hobbs et al. 2009; 2013; 2014, Morse et al. 2014). The degree of a system's novelty may vary, with truly novel ecosystems having shifted over a threshold to a permanently altered state that cannot be reversed without significant restoration effort (Morse et al. 2014). In comparison, less novel ecosystems ("hybrid" systems) still share similarities with natural ecosystems in e.g. species composition or ecosystem functioning but are nonetheless beyond the historical range of variability in all or some of such qualities (Hobbs et al. 2009).

The difference between novel habitats and novel ecosystems is similar to that between natural habitats and ecosystems. While habitats are physical places of species' occurrence and reproduction characterized by species-specific environmental requirements (as described above) (Hall et al. 1997), ecosystems are joint entities of species, the communities they form, and the abiotic conditions these interact with (Tansley 1935). For example, the regularly managed road verges discussed in this thesis may be perceived as a novel habitat, while the entire surrounding transport system (i.e. the constructed motorway next to the verge, the structurally rearranged, potentially polluted soils beneath it, the biotic communities of the forests and fields adjoining the road affected by the traffic, etc.) forms a novel ecosystem.

From the perspective of nature conservation, especially interesting are novel habitats and novel ecosystems that are able to provide suitable conditions for threatened species, or for those whose original (semi-)natural habitats are threatened (Lundholm & Richardson 2010, Kowarik 2011, Gardiner et al. 2018). Recent studies indicate that the declining biota of semi-natural grasslands may find suitable conditions in different types of rights-of-way (Gardiner et al. 2018), such as power line clearings (Wagner et al. 2014, Eldegard et al. 2017), road verges (Auestad et al. 2010; 2011) and railway embankments (Tikka et al 2000; 2001, Morón et al. 2014). Sites of soil and mineral extraction, such as unused gravel pits (Lenda et al. 2012) and abandoned quarries (Tropek et al. 2010), and urban greenspaces, such as green roofs (Madre et al. 2013), brownfields (Eyre et al. 2003), ruderal areas (Öckinger et al. 2009) and urban parks and lawns (Thompson et al. 2004, Fischer et al. 2013) have also been shown to sometimes provide suitable conditions for grassland species. Although all of these are anthropogenic in origin, they vary in their degree of novelty, i.e. the extent to which they resemble actual semi-natural grasslands regarding their species composition, vegetation structure and ecosystem service provision, and in the degree to which they are self-sustaining. This thesis focuses on three types of novel habitats, described in greater detail in the following.

1.2.1 Power line clearings

Power line clearings are linear, corridor-like elements clear-cut into landscapes for the purpose of transmitting electricity (**Fig 3**, Monni & Lankinen 1995, Wagner et al. 2014, Eldegard et al. 2017). Especially in forested landscapes, power line clearings are regularly either mown or otherwise managed with intervals ranging from a few to eight years (Bramble & Byrnes 1983, Luken et al. 1992, Berg et al. 2013, Fingrid 2019a, b). This is done to sustain the vegetation in the clearings in a low-growing state and thus prevent trees or shrubs from growing tall enough to short-circuit the overhead power lines (Ahmad et al. 2013). The woody debris resulting from each clear-cut is most often left on the ground (Berg et al. 2013, Fingrid 2019a, b). Due to the long interval between each management event, power line clearings often develop a dense vegetation structure characterized by bushes and tree saplings, with low-growing herbaceous vegetation being present as patches (Berg et al. 2013). In Europe, power line clearings span up to 265 000 kilometers in length (Eurelectric 2009), but the exact area under regular mowing management is difficult to assess due to variation in clearing widths and in the amount of corridor vegetation. In Finland, the area of power line clearings in regular mowing management is estimated to exceed 50 000 hectares (Kuussaari et al. 2003).

a) b)

c)

Figure 3. Power line clearings ranging from dry to mesic conditions with abundant grassland plants in **a)** Lohja, Uusimaa and **b-c)** Turku, Varsinais-Suomi. Pictures: JL.

1.2.2 Road verges

Like power line clearings, road verges are linear, narrow habitats that form a network of varying density across rural and urban landscapes (**Fig 4**) (Auffret & Cousins 2013, Gardiner et al. 2018). Lining roads on both sides, road verges are regularly mown with rotating blades or flails to prevent the verge vegetation from obstructing the visibility along the road, from attracting browsing animals, and from clogging the ditches draining the road (Parr & Way 1988, Auestad et al. 2010). Compared to power line clearings, road verges are managed with shorter intervals depending on the speed limit and amount of traffic on the road in question (Liikennevirasto 2014). In Finland, road verges have been classified into several management classes varying from the wide highway verges mown at least twice per summer to the narrow verges of rural roads mown only once per summer (Jantunen et al. 2007, Liikennevirasto 2014). The mown biomass is most often crushed or mulched and left on the ground (Schaffers et al. 1998). Upon establishment, verges are either sown with herbaceous species (Mahosenaho & Pirinen 1999, Liikennevirasto 2014) or allowed to freely become vegetated with species dispersing from the surrounding habitats (Skrindo & Pedersen 2004). Because of the intense management and the sown seed mixtures, road verges are dominated by open herbaceous vegetation. As with power line clearings, the exact area of regularly managed road verges is difficult to assess due to the varying widths of the mown part of the verge. Still, the total length of all road verges in Europe is estimated to reach as much as 4,8 million kilometers (European union road federation 2017). In Finland, the area of state-managed road verges is estimated to exceed 100 000 hectares (Jantunen et al. 2004).


a)


b)

Figure 4. Rural road verges dominated by grassland plants in **a)** Mikkeli, Etelä-Savo, with abundant *Knautia arvensis* and in **b)** Espoo, Uusimaa, with abundant *Centaurea jacea*, *Hieracium umbellatum* and *Angelica sylvestris*. Pictures: JL.

1.2.3 Urban lawns and grasslands

Lawns and grasslands established and managed for both recreational and aesthetic purposes are an essential part of urban greenspaces (**Fig 5**, Hedblom et al. 2017, Ignatieva et al. 2017). Covering vast areas in public parks, yards and private gardens, lawns and so-called amenity grasslands are sown upon establishment with seed mixtures of competitive grasses and forbs that form a uniform, dense field layer resistant to trampling (Alumai et al. 2009, Wheeler et al. 2017). This field layer is then mown with varying intervals ranging from several times per month to only once per summer, depending on the intensity of use and visual demands the lawns are subjected to. For example, in Turku, Helsinki and other large cities in Finland, lawns and amenity grasslands are classified into management classes varying from the intensively managed lawns surrounding historical public buildings in the city center to the less-intensively managed, taller grasslands surrounding recreational areas in the city outskirts (Nuotio 2007). The mown biomass is either mulched and left on the ground or removed from the lawns, again depending on the use and demands subjected to the lawn. In addition to mowing, lawns may be fertilized, irrigated and occasionally re-seeded (Thompson et al. 2004). The extent of regularly managed lawns and grasslands is difficult to assess on a large scale due to the small size and scattered distribution of lawns in urban areas (Hedblom et al. 2017). In the United States, however, estimates of the cover of turf grass lawns over the entire continent reach as much as 163 800 square kilometers (Milesi 2005).

a)

b)

Figure 5. Urban lawns mown only once or twice per season may develop a vegetation structure similar to semi-natural grasslands, although the species present are often more generalistic in nature. **a)** Turku, Finland, **b)** Münster, Germany. Pictures: JL (a) and Valentin Klaus (b).

1.3 Novel habitats and the social sciences

Because of their anthropogenic origin and regular management, all of the novel habitats described above are prime examples of social-ecological systems, i.e. systems that are shaped by both ecological and social phenomena and the interactions and feedbacks between them (Berkes et al. 2000, Liu et al. 2007, Cook et al. 2011). For example, the species composition of a given power line clearing is influenced on one hand by the ecological and biophysical preconditions of the surrounding landscape and on the other by the decision-making processes of the people perceiving and managing the clearing (Nassauer 1995, Berkes et al. 2000, Cook et al. 2011). Similar to ecological phenomena that operate on various spatial scales, the social phenomena influencing how and why a given novel habitat is managed operate on multiple scales ranging from individuals to institutions and regions (Cook et al. 2011). On the level of individuals, such phenomena include personal values and attitudes (Nassauer 1995, Nassauer et al. 2009), and on the level of institutions and regions, they include municipal regulations and policies, legislation and the economy (Liu et al. 2007, Cook et al. 2011). Again, like ecological phenomena, social phenomena may affect habitats both immediately or through legacy effects, with present habitats presenting evidence of e.g. historical management decisions based on individual beliefs or regional policies (Liu et al. 2007, Cook et al. 2011). The social scientific chapters of this thesis focus both on the phenomena operating on the level of individuals, namely the values assigned to and attitudes towards novel habitats, and on the phenomena operating on institutional and regional scales, namely the policies and decision-making that affect novel habitat management.

1.3.1 The influence of values on habitat management

Values are central to human behavior, as they form the base for beliefs, attitudes, intentions and ultimately action (Ives & Kendal 2014 and references therein), they are the "foundation on which people's prioritizations are built" (Manfredo et al. 2016). In the literature concerning nature valuation, the term "value" may refer either to underlying, held values, or assigned values, which are also called valued properties (Ives & Kendal 2014). The first of these describe personal perceptions of which behaviors or end states are desirable and important in life (Schwartz & Bilsky 1987). For example, a person may perceive equality or sustainability as important underlying values guiding their life. Assigned values, or valued properties, on the other hand, describe the reasons for which something (the object of valuation) is perceived valuable, whether extrinsic or intrinsic (Ives & Kendal 2014). Terms with similar connotations as assigned values include landscape (Raymond & Brown 2007, Ives & Kendal 2014), community (Raymond et al. 2009) and social values

(Tyrväinen et al. 2007, Vesanto 2007, Ives et al. 2017). Assigned values may be monetary, but they may just as well include any other social, aesthetic or utility feature imaginable that render the object of valuation valuable to the person perceiving it. For example, a person who owns a patch of forest may value that forest for its recreation potential or scenic beauty.

The research field of nature valuation links closely to the ecosystem services framework (Carpenter et al. 2009), as both concern features in nature that humans perceive either beneficial or desirable (services) or disadvantageous or undesirable (disservices) to themselves or the humanity at large (Schaich et al. 2010). Studies describing the values assigned to natural areas have previously focused on e.g. river reserves (Bryan et al. 2010), forests (Brown & Reed 2000), urban greenspaces (Tyrväinen et al. 2007, Ives et al. 2017), residential areas (Cook et al. 2011) and, to a lesser extent, semi-natural grasslands (Lindborg et al. 2008, Raatikainen & Barron 2017). Values assigned to novel habitats have received only little attention. There are, however, indications that novel habitats are assigned just as many values as any other regularly managed habitat, especially in urban areas, where novel habitats of various types form a significant part of urban greenspaces (Hobbs et al. 2014, Weber et al. 2014).

To an ecologist, all this text concerning values may appear abstract and trivial. However, in nature conservation it is instrumental to understand what are the values that different stakeholders assign to habitats of conservation interest, as they shed light on the attitudes and motivations preceding the conservation actions (or lack thereof) regarding these habitats (Larson et al. 2010, Ives & Kendal 2014, Ives et al. 2017). Attitudes, in turn, may be defined as statements (or "summary evaluations" (Ajzen 2001)) of a person's views over a given topic and are often expressed as preferences or agreements considering that topic (Ives & Kendal 2014). Especially in social-ecological systems, habitat management designed solely in terms of ecological values is likely to lead to negative attitudes and objection from the stakeholders of that habitat in the long run (Nassauer 1995). Examples of non-ecological assigned values that may direct the attitudes towards the management of habitats of conservation interest include especially aesthetics (Gobster et al. 2007), signs of care (Nassauer 1995) and safety (Jorgensen et al. 2002). In this context, the intrinsic or ecological value of a particular habitat or environmental concern over its conservation status are simply values among many others that shape the decision-making around conservation action in that particular habitat. Conflicts between specific assigned values may arise during habitat management when non-ecological values, such as aesthetics or safety, dictate the goals of management despite evident ecological values, such as high species richness or the presence of endangered species. Similar conflicts may arise when ecological values are dismissed during habitat management due to social phenomena operating above the level of individuals, such as institutional practices, regional legislation or collective norms (Cook et al. 2011). In situations where the implementation of ecologically sensitive habitat management is clearly constrained by the aforementioned phenomena, the term implementation barrier may be used to refer to the limiting phenomena.

1.4 Grassland conservation in novel habitats: potential, limitations and unanswered questions

To summarize the previous sections, power line clearings, road verges and urban lawns are all characterized by either frequent disturbance, open low-growing vegetation with abundant light, or both. They also cover immense areas in both rural and urban landscapes (Eurelectric 2009, European union road federation 2017, Milesi 2005) and have been shown to be much more structurally connected to one another than the remaining fragments of semi-natural grasslands are (Auffret & Cousins 2013). Novel habitats thus share some of the most crucial determinants of habitat quality for grasslands species and have indeed been found to sometimes support diverse communities of species originally adapted to semi-natural grasslands (e.g. Tikka et al. 2000, Eldegard et al. 2017).

Why, then, do grassland species continue their decline towards extinction, as evident in the most recent assessment of threatened species in Finland (Hyvärinen et al. 2019)? Despite their superficial similarity with semi-natural grasslands, all three novel habitat types discussed in this thesis differ in their own ways from them. In power line clearings and road verges, the most crucial difference is the fact that the mown biomass is not removed but is left to decay on the ground (Schaffers et al. 1998, Fingrid 2019a, b). This hinders the recruitment of grassland seedlings (Loydi et al. 2013) and the depletion of nutrients from the soil, thus favoring competitive, large species or those adapted to nutrient-rich soils (Schaffers et al. 1998, Noordijk et al. 2009). In urban lawns, the obstacles to the development of species-rich grassland vegetation are the intensity of management and the artificial fertilizers and seed mixtures of competitive species used in lawn establishment (Thompson et al. 2004, Chollet et al. 2018). Thus, the quality of novel habitats for grassland species is often less than that in traditionally managed semi-natural grasslands (**Fig 6**), and alterations to the management regimes of each novel habitat type are required to maximize their potential as grassland habitat. Accordingly, altering the management of power line clearings, road verges or lawns has often been suggested in the literature, with specific suggestions concerning e.g. readjustments to mowing schedules and the removal of the mown biomass to better mimic the management of semi-natural grasslands (e.g. Jantunen et al. 2007, Komonen et al. 2013, Garbuzov et al. 2014, Chollet et al. 2018).

If we are to hope for such management alterations to be implemented on a large scale, however, important questions remain unanswered concerning both the ecology and the social scientific aspects of grassland conservation in novel habitats. First, we must understand how local and landscape-scale environmental conditions affect the performance, occurrence, abundance and composition of grassland species in novel habitats. This is important, so that any potential management alteration may be focused into novel habitats that have the greatest potential for developing species-rich grassland vegetation. Based on previous studies we already know the answer regarding road verges, as grassland species have been shown to be especially frequent on old verges with nutrient-poor, dry soils (Jantunen et al. 2006). The local determinants of grassland species richness and occurrence in other novel habitats have been seldom studied, as have the landscape scale determinants of grassland species occurrence in any novel habitat for that matter. For example, the effects of urbanization, if there are any, on grassland species performance and grassland communities have seldom been studied. Yet understanding if and how urbanization affects grassland species is important if we are to utilize novel habitats in grassland conservation, as novel habitats are equally characteristic to urban landscapes (Hobbs et a. 2014) as historical semi-natural grasslands were to rural landscapes. Likewise, the relationship between the occurrence of grassland species in novel habitats and the present and past connectivity of that habitat to semi-natural grasslands has received little attention, despite the fact that the effects of past habitat connectivity in present grassland plant communities are well documented (e.g. Lindborg & Eriksson 2004, Helm et al. 2006).

Second, to ensure the implementation of any potential management alteration, we must understand how the stakeholders of novel habitats value these habitats and their role in grassland conservation. The values stakeholders assign to novel habitats, the potential conflicts between these values, the attitudes towards altering novel habitat management or the opinions concerning different types of potential management alterations have all received only a little, if any, attention. Yet the answers to these questions are crucial in explaining why novel habitats are currently managed the way they are, and most importantly, why they are often not managed for greater grassland conservation benefit.

Figure 6. The quality of novel habitats for grassland species may be limited by **a)** invasive species, **b)** suboptimal management regimes resulting in successional overgrowth during management intervals or **(c)** management methods that suit the needs of grassland species poorly. Pictures: JL (a-b) and Wikimedia Commons/Max Holder GmbH (c).

1.5 The aims of the thesis

This thesis consists of five chapters. Chapter I concerns the environmental determinants of the population performance of a threatened grassland specialist along a gradient of urbanization, while chapters II-III concern those for the species richness of native grassland plants, non-native plants, and grassland butterflies in power line clearings. Chapters IV-V address the attitudes of novel habitat stakeholders towards utilizing novel habitats in grassland conservation, the values they associate with novel habitats, and the barriers to the implementation of novel habitat management that would favor grassland species. The overall aim of this thesis is to combine ecological and social scientific data concerning grassland conservation in novel habitats into practical management guidelines that may be used to increase the quality of novel habitats as grassland habitat while taking into account the pre-existing reasons for the management of each novel habitat type. More specifically, the aims are:

1) To describe the local and landscape-scale environmental conditions likely to favor the performance and occurrence of grassland species in novel habitats (chapters I-III)

2) To describe the values that stakeholders assign to novel habitats, and determine how these values relate to attitudes towards utilizing novel habitats in grassland conservation (chapters IV-V)

3) To identify key barriers to managing novel habitats for greater grassland conservation benefit (chapter V)

4) To propose practical solutions for managing novel habitats in ways that increase their habitat quality for grassland species, but do not compromise the pre-existing motivations and limits for their management (chapters I-V)

2 Materials and Methods

2.1 Study areas and fieldwork

The fieldwork for this thesis was conducted in five different areas of varying geographical extent. The fieldwork for chapters I-III focused on southern Finland, more specifically the regions of Varsinais-Suomi (I, II) and Uusimaa (III). The fieldwork for chapter IV was carried out in 19 European cities ranging from Málaga to Turku, and the fieldwork for chapter V in the municipalities and traffic administrative sectors of Finland. The time and the people responsible for the fieldwork varied between the chapters. The fieldwork for chapter III was conducted already in 2003, while the fieldwork for the rest of the chapters was conducted in 2012 (II), 2015-2016 (I, IV) and 2018 (V). JL was solely responsible for the fieldwork in three chapters (I-II, V) and took part in that of two others (III-IV), with collaborators in the field including the co-authors of each chapter. Sites of data collection are presented in **Fig 7**, and more detailed descriptions of the study areas and fieldwork are included in the Materials and methods –sections of individual chapters.

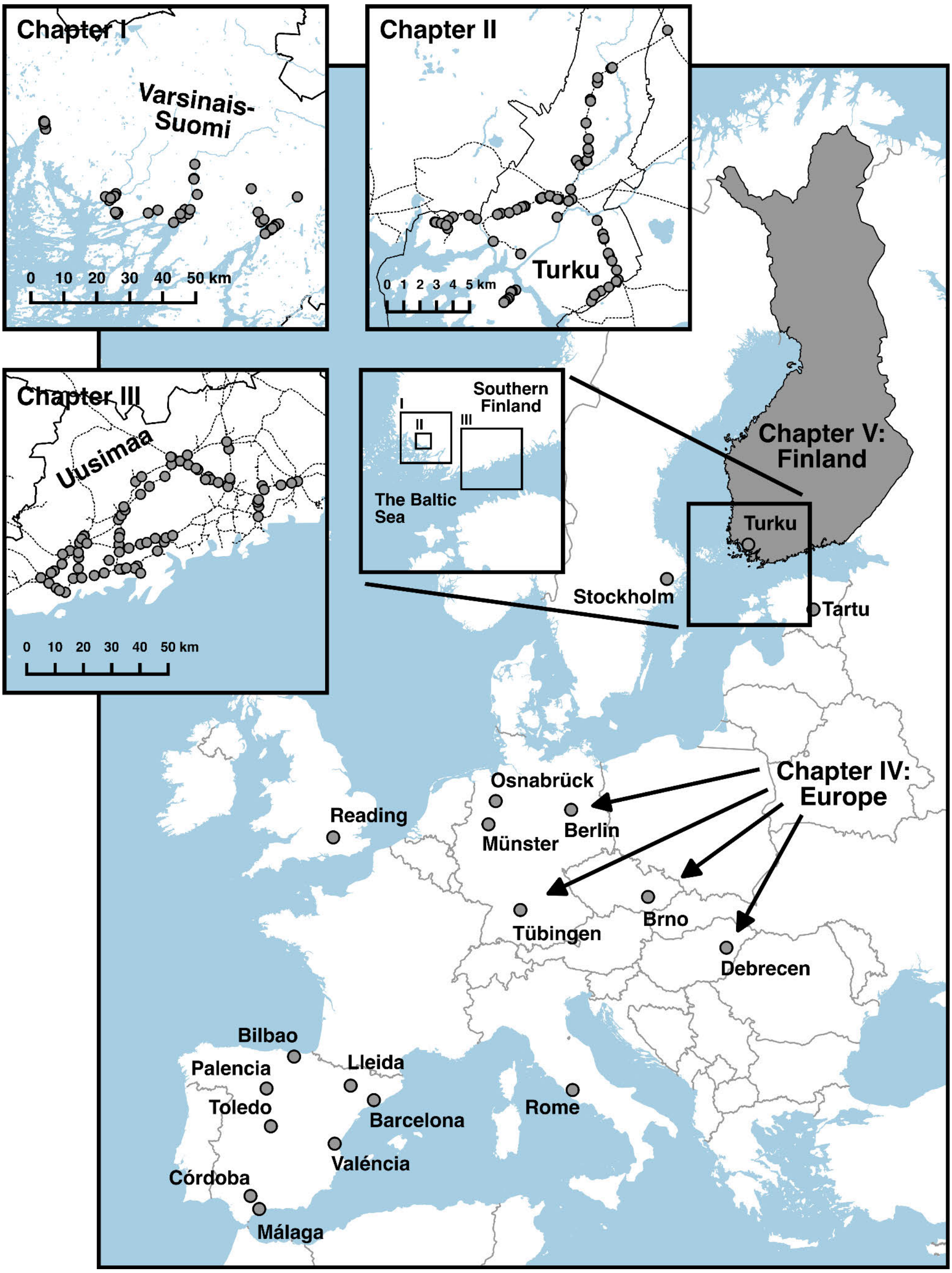


Figure 7. Locations of individual data collection sites (grey dots) in the chapters of the thesis. Dotted lines in maps depicting Chapters II and III indicate power line clearings.

2.2 Types of data

The data in this thesis comprises ecological observational data on the population and community ecology of grassland plants (I-III) and butterflies (III) inhabiting remnant grasslands (I) and novel habitats (II-III), data on the local and landscape-scale environmental conditions experienced by these species (I-III) and survey data on the attitudes and values of stakeholders of novel habitats (IV-V). In chapter I the ecological data consists of population performance metrics, such as population size estimates, of a rare specialist sedge, *Carex caryophyllea* (VU), inhabiting unmanaged remnant dry grasslands (Lampinen 2017). In chapters II-III, the ecological data consist of species richness counts of grassland plants (II-III), grassland butterflies (III) and invasive alien plants (II) inhabiting power line clearings. In chapters I-II, the ecological data were collected with quadrats of 5x5 meters (I) or 25x25 meters (II). In chapter III, the size of each quadrat was 0.25 ha, but the dimensions of each quadrat differed slightly due to differing widths of the power line clearings being sampled. The butterfly data in chapter III was collected with crisscrossing transects of 250 meters situated within each quadrat during three separate visits (Pollard & Yates 1993, Pöyry et al. 2009). The nomenclature used in the ecological data follows that of Mossberg & Stenberg (2003) (I-II) or Hämet-Ahti et al. (1998) (III) for plants and Kullberg et al. (2002) (III) for butterflies. The term "grassland species" is used in reference to species whose historical or present habitat preferences have primarily focused on dry to mesic grasslands. The classification of which species can be considered grassland species, and which not follow the definitions of Pykälä (2001) for grassland plants and Pitkänen et al. (2001) for grassland butterflies. As for alien species, the classification follows Hämet-Ahti et al. (1998) and Ministry of Agriculture and Forestry (2012).

The environmental data in chapters I-III consists of both local and landscape-scale variables collected using the same quadrats as the ecological data. Among many other variables, the local environmental data comprise Ellenberg indicator values of e.g. soil moisture, productivity and light abundance (I-II) (Ellenberg 1988, Hill et al. 1999), variables describing vegetation structure (I-III), and the topography and exposition of the site (I-III). The landscape-scale environmental data, in turn, comprise e.g. measures of connectivity of the data collection sites between one another (I) or to current or historical semi-natural grasslands (I-III). The connectivity measures were calculated following the IFM (incidence function model) measures described in Moilanen & Nieminen (2002). The landscape-scale data also comprises the cover of certain CORINE land cover types (I-II) (Finnish Environment Institute 2019a) surrounding each quadrat.

The survey data of chapters IV-V consists of attitudinal data (IV-V), value typologies (IV-V) and preference data (IV). Measured on variations of the Likert-scale (Likert 1932), the attitudinal data describe stakeholder attitudes towards utilizing novel habitats in grassland conservation (IV-V) and the perceived feasibility of individual management methods for this (V). The value typologies describe the ecological, socio-cultural and economic values (*sensu* Ives & Kendal 2014) stakeholders assign to novel habitats (IV-V). The preference data, in turn, describe stakeholder preferences of novel habitats varying in the amount of grassland vegetation they support (IV). The survey data were collected with semi-structured surveys using questionnaires with both closed and open-ended questions, either face-to-face (IV) or via email (V). The surveys were directed at stakeholders of two types of novel habitats, namely urban greenspace users (IV) and road verge managers and traffic administrators (V). The attitudinal scales were calculated as averages of several individual Likert-items, while the value typologies and preference data were based on open-ended questions and photographs of novel habitats varying in the amount of grassland vegetation they support. For more specific descriptions of the types of data collected, see the Materials and Methods –sections of individual chapters.

2.3 Sampling

The sampling methods varied between the types of data collected and the individual chapters. In chapter I, the population performance data were sampled from populations of *C. caryophyllea* that could be located during an initial field check of the populations, with the exact location of the quadrats being restricted by the location of the patches of the study species in each population. In chapters II-III, the community ecological data were sampled from power line clearings based on a set of pre-defined, subjective rules that restricted the sampling to clearings deemed at least somehow suitable for the development of grassland communities. In other words, *C. caryophyllea* populations with only imprecisely reported locations were omitted from the sampling in chapter I, and power line clearings transecting habitats unsuitable for grassland species, such as peatlands, were omitted for the most part from the sampling in chapters II-III. In total the sampled data for chapter I consists of 75 quadrats placed in 43 *C. caryophyllea* populations and the sampled data for chapters II and III of 71 and 44 quadrats placed in power line clearing communities, respectively.

The local environmental data in chapters I-III was collected with the same quadrats as the population and community ecological data, while the landscape-scale environmental data was collected after the fieldwork with GIS-software (QGIS Development Team 2019) from pre-defined buffers 100 (II), 250 (I) or 500 (III) meters in diameter surrounding each quadrat. The average distance between two sampled populations in chapter I was 1.4 km (min 121 m, max 79 km). The average distance between two sampled power line clearings in chapter II was 0.3 km (min. 45 m, max. 4 km) and in chapter III 2.9 km (min. 146 m, max. 96 km).

The survey data in chapter IV was collected as 19 samples of roughly 100 face-to-face questionnaires in 19 European cities ranging in population size and climate, amounting to a total of 2026 questionnaires. The surveys were conducted during the summer months of 2016 in at least three different locations varying in their proximity to urban greenspaces within each city. At minimum, one survey location was situated in an urban greenspace (within a park, for example), one within sight distance of an urban greenspace (close to a park, for example) and one with no visual contact to urban greenspaces (in a market square, for example). Potential respondents were approached at random at the survey locations until the required number of questionnaires (roughly 100 per study city) was achieved. The response rate in chapter IV was 44 %.

The survey data for chapter V was collected via email during the summer of 2018 as an exhaustive sample of all stakeholders responsible for the management and administration of road verges at the municipal, regional and national level in Finland, with a total of 2080 potential respondents. The email addresses of the respondents were collected from municipal and regional administrative center websites. The response rate for the survey was 17.9 %, which resulted in a total of 373 questionnaire answers. For more specific descriptions of the sampling, see the Materials and Methods –sections of individual chapters.

2.4 Quantitative and qualitative analyses

The quantitative analyses in chapters I-III concerned the relationships between population and community ecological data of grassland species and data on local and landscape-scale environmental conditions. The quantitative analyses in chapters IV-V investigated the relationships between attitudinal data and data concerning different kinds of stakeholder values assigned to novel habitats. The qualitative analyses in chapters IV-V, in turn, focused on the values associated with novel habitats and aimed at creating a typology for them with inductive qualitative content analysis (Elo & Kyngäs 2007, Cho & Lee 2014).

I began the quantitative analyses by standardizing the predictor variables measured on widely differing scales to mean of zero and unit-variance in certain chapters (II-III). I then investigated the relationships between the response and predictor variables in all chapters with regression analyses, such as generalized additive models (GAM, I) (Yee & Mitchell 1991), generalized linear models (GLM, II-III,V) (Guisan et al. 2002), linear mixed models (LMM, IV-V) (Zuur et al. 2009) and hierarchical partitioning (HP, II) (Chevan & Sutherland 1991). The relationship between the response and predictor variables was modelled as univariate models in chapter I, while the models in other chapters were multiple in nature. In these chapters, I selected the variables to be included in the final models with stepwise backward elimination based on either predictor *p*-values (IV-V) or model AIC (Akaike information criterion) (II-III). Because the likelihood of committing type I error increases with multiple comparisons (Chen et al. 2017), I controlled the final *p*-values in all models for either family-wise error rate (Holm 1979) (III) or false discovery rate (Verhoeven et al. 2005) (I-II, IV-V).

I also used multivariate methods, such as principal component analysis (PCA, IV-V) (Legendre & Legendre 1998), redundancy analysis (RDA, I) (Legendre & Legendre 1998) and distance-based redundancy analysis (dbRDA, II) (Legendre & Anderson 1999), or Pearson correlations (I-IV) (Pearson 1895) and Wilcoxon rank-sum -tests (V) (Wilcoxon 1945) in certain chapters for data exploration and interpretation. Autocorrelation issues resulting from spatially structured sampling were accounted for either by including an autocovariate of the response variable as a predictor in the regression analyses (II) (Dormann et al. 2007, Bardos et al. 2015) or by calculating and interpreting Moran's *I* (Moran 1950) (III). Detailed descriptions of the analyses are included in the Materials and methods –sections of each individual chapter.

3 Results and discussion

The main ecological result of this thesis is that novel habitats characterized by certain local- and landscape-scale environmental conditions may support species-rich grassland communities, although the specific determinants for the species richness vary between different groups of organisms. In addition, both local and regional land-use history related to semi-natural grasslands may increase the species richness of grassland plants, but not butterflies, in novel habitats. The main social scientific result of this thesis is that the values assigned to novel habitats and the attitudes towards managing them for greater grassland conservation benefit are diverse, interrelated and differ between a) novel habitat stakeholder groups and b) novel habitat types characterized by diverse grassland vegetation and those characterized by less diverse vegetation. In addition, specific management alterations that could increase the quality of novel habitats for grassland species are perceived more feasible than others, and specific implementation barriers to these alterations more severe than others, by novel habitat stakeholders. In the following, these results are discussed in detail, synthesized and developed into practical guidelines for novel habitat management that would favor grassland species while not dismissing the non-ecological values, such as utility or aesthetic values assigned to each novel habitat type.

3.1 The environmental conditions that favor grassland species in novel habitats

In Chapters I-III, I showed that variables related to disturbance, microclimate, and edaphic conditions are the primary environmental determinants for the performance of grassland plant populations in unmanaged grassland remnants (I) and for the species richness of grassland plants and butterflies in power line clearings (II-III). More precisely, I showed that bright, warm and sufficiently disturbed open habitats (**Fig 8a**) are optimal for the population performance of *Carex caryophyllea*, a dry grassland specialist, and that grassland plants are most species-rich in old power line clearings with abundant light (**Fig 8b**), southerly expositions and steep slopes. Grassland butterflies, in turn, are most species rich in recently managed power line clearings with mesic soils and low amounts of clear-cut debris. As for negative relationships, I showed that increasing shrub cover is negatively linked with the performance of *C. caryophyllea* populations (**Fig 8a**), and that the length of the time elapsed since previous clear-cut management and the amount of clear-cut debris are negatively linked with the species richness of grassland plants and butterflies in power line clearings.

First, these results show that novel habitats with suitable environmental conditions indeed support species-rich communities of grassland species, a conclusion similar to those drawn by e.g. Jantunen et al. (2006), Valtonen et al. (2007) and Eldegard et al. (2017). Second, the environmental conditions favoring the performance of grassland species populations and the species richness of grassland species in semi-natural grasslands operate in a similar fashion in novel habitats as well. The result that abundant light and a southerly exposition have a positive relationship and increasing soil moisture a negative relationship with the species richness of grassland plants in power line clearings (II) indicates that especially dry grassland specialists may find power line clearings suitable habitats. This is likely because dry clearings with bright, warm conditions are characterized by more extreme climatic conditions resulting in slower successional overgrowth between management intervals, than clearings with mesic soils. This is similar to the finding of Pykälä et al. (2005), who showed that especially sun-lit habitats with warm exposures retain high species richness of grassland species following grassland abandonment. Compared to grassland plants, I found that the species richness of grassland butterflies is positively linked with mesic habitat conditions in power line clearings (III). This could be explained by the observation by Öckinger & Smith (2006) that vegetation height in managed semi-natural grassland has a positive relationship with butterfly species richness: Mesic conditions support a more diverse, taller vegetation structure with nectar, host plants and resting sites for a wider selection of butterfly species than dry clearings with short vegetation.

The result that the species richness of both grassland plants and butterflies is negatively related to the time elapsed since previous clear-cut management and to the amount of clear-cut debris left in the clearings (III) indicates that the habitat quality of the clearings fluctuates according to the management regime of the clearings, especially in mesic soils quickly covered by shrubs. This is in line with the fact that grassland species are adapted to early-successional, open conditions and suffer from secondary succession and litter accumulation (Foster & Gross 1998, Öckinger et al. 2006, Galvánek & Lepš 2008). A simple way to increase the habitat quality of the clearings for grassland species would thus be to increase the frequency of clear-cuts and to remove the resulting debris from the clearings, as suggested by also Berg et al. (2013; 2016) and Komonen et al. (2013).

Non-native species are typical to novel habitats (Hobbs et al. 2009), and in chapter II, I showed that the highest richness of non-native plant species is found in power line clearings with productive, mesic soils close to urban land use types (**Figs 8c-d**). Two factors explain this result. First, productivity, in general, has been suggested to have a positive, though humpbacked relationship with plant species richness (Waide et al. 1999, but see Adler et al. 2011). Second, the most important prerequisites for the invasion of non-natives in a given community are the simultaneous release of resources from the use of resident species and the propagule pressure of non-native species (Davis et al. 2002). The regular management of power line clearings releases ample amounts of space, light, and nutrients from the use of resident species, while the urban surroundings rich in gardens and parks function as the source of non-native propagules. One of the vectors for these propagules to the clearings is the inappropriate disposal of garden waste. Rusterholz et al. (2012) showed, that the disposal of garden waste in forests results in an increase in the species richness of non-native plant species in those forests, and the same phenomenon was described by Lampinen (2018) in power line clearings: Clearings with mulch, compost and other material originating from nearby gardens support higher numbers of non-native plant species than clearings without such waste.

To conclude, novel habitats may support species-rich communities of both grassland plants and grassland butterflies, and the environmental conditions that favor their population performance and species richness in novel habitats appear similar to those that favor them in the remaining semi-natural grasslands. Non-native species are a prevalent part of the species community especially in urban novel habitats, but at least in power line clearings they occupy areas characterized by different environmental conditions than those occupied by grassland species.

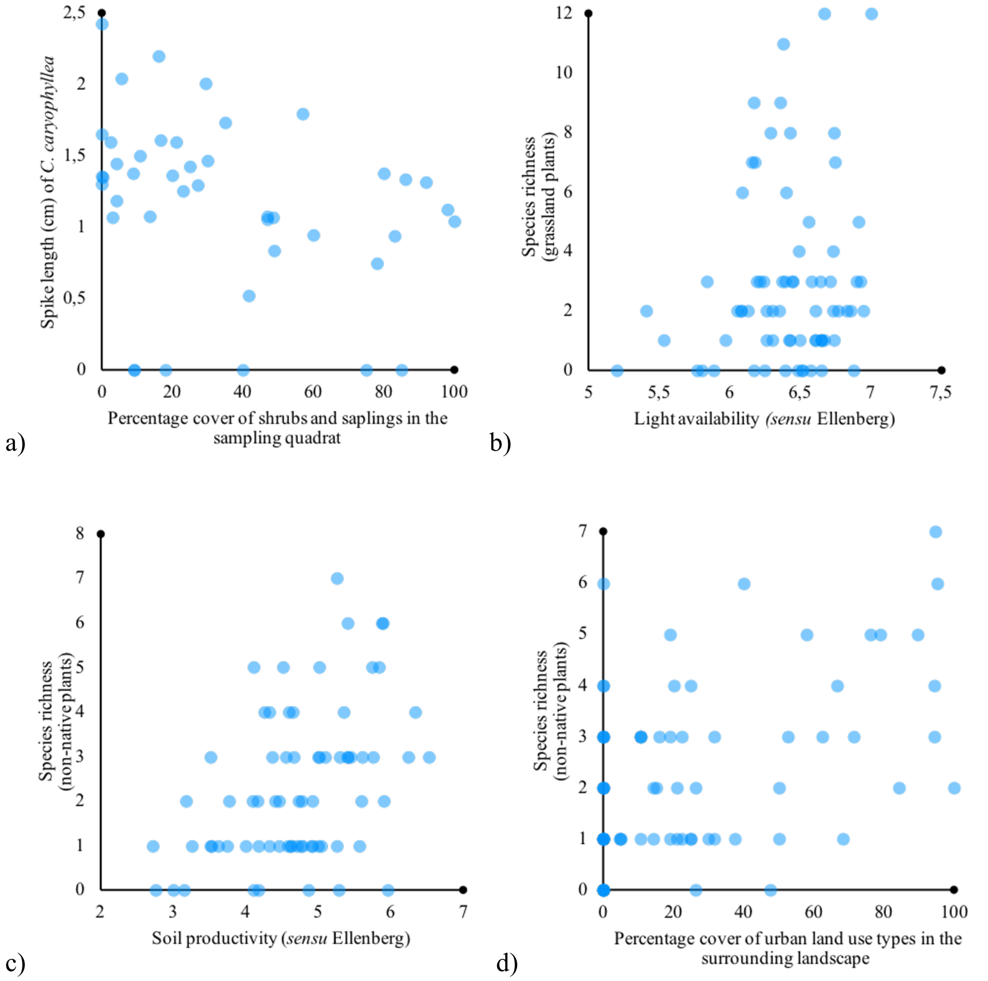


Figure 8. Relationships between **a)** the length of *Carex caryophyllea* female spikes at seed maturation (a proxy for the number of seeds produced) and the percentage cover of shrubs and saplings (I), **b)** the species richness of grassland plants and the availability of light (based on Ellenberg indicator values) (II), **c)** the species richness of invasive non-native plants and soil productivity (based on Ellenberg indicator values) (II) and **d)** the species richness of invasive non-native plants and the urbanization of the surrounding landscape (II). Figure **a** describes data collected from remnants of dry grassland, figures **b-d** data collected from power line clearings.

3.2 The relationships between present species richness of novel habitats and land-use history

In Chapters I-III, I showed that structural connectivity in the late 19th century to semi-natural grasslands has a positive relationship with the present population performance of a grassland specialist species in remnants of dry grasslands (I) and with the present species richness of grassland specialist plants in power line clearings (II-III) (**Fig 9**). I found no such relationships between past connectivity metrics and the present species richness of grassland specialist butterflies, or between present connectivity metrics and the species richness of either species group, in power line clearings (III).

These results follow those of Jonason et al. (2014), who found that the species richness of grassland plants in forest clear-cuts is higher in areas with a land-use history related to semi-natural grasslands than those that have a history of continuous forest cover. Although I found no similar relationship between grassland butterflies and past connectivity metrics, Ibbe et al. (2011) showed that also present communities of butterflies may be more species-rich in clear-cuts with a land-use history of grasslands than in those without. Together with these previous conclusions the results in this thesis highlight how historical (whether social or ecological) phenomena may result in legacy effects observable in present-day habitats (Szabó 2010).

The results in this thesis also follow the consensus that the delay with which changes in habitat area or quality result in changes in the species richness of those habitats depends on the life span, the degree of habitat specialization and the mobility of the species occupying that habitat (Kuussaari et al. 2009, Brückmann et al. 2010, Saar et al. 2012). Short-lived, mobile species such as habitat specialist butterflies either migrate elsewhere from degrading habitats or experience rapid extinctions. The latter applies also to annual specialist plants, while perennial plants may persist for long periods of time simply because of the longer age of plant individuals, especially if they are capable of clonal reproduction (Saar et al. 2012). Based on the results, power line clearings are most likely to provide habitat for two types of grassland specialist species, namely perennial grassland plants and mobile butterfly species. During the successional overgrowth of management intervals, perennial grassland plants are more likely capable of persisting in the clearings, while butterflies may migrate to other suitable habitats.

Positive relationships between past landscape patterns and present patterns of species richness indicate the presence of an extinction debt in the community (Kuussaari et al. 2009). The obvious question, however, is how to explain the presence of extinction debt in modern-day power line clearings crossing landscapes predominantly covered by forest? The most likely explanation is that the landscapes which the clearings now cross were historically utilized for forest grazing, a general custom in traditional animal husbandry shown to increase the species richness of forest field layers (Oldén et al. 2016). In forest grazing, cattle grazed in forests surrounding villages during the summer, moving rather freely from one area to another and effectively dispersing seeds of various species both within and between forests. As a consequence, small openings of grassland patches were typical to forests of the late 19th century, and grassland plant species common in the forest floor vegetation (Tonteri 2001, Vanha-Majamaa et al. 2001).

The potential extinction debt indicated by the results in Chapter III bears two important implications for novel habitat management in general. First, novel habitats may function as parts of landscape-scale networks of habitats suitable for grassland species, rather than being short-lived, isolated islands. The positive relationship between past connectivity and present species richness indicates that the area of the present-day power line clearings has functioned as grassland habitat for a sufficiently long period of time for the species richness to accumulate as a result of high connectivity between grassland patches in the surrounding landscape. Second, power line clearings may be especially important habitats for grassland species in landscapes that have experienced severe losses in the area of semi-natural grasslands. Management alterations aiming at increasing the suitability of the clearings for grassland species should thus be focused on these landscapes

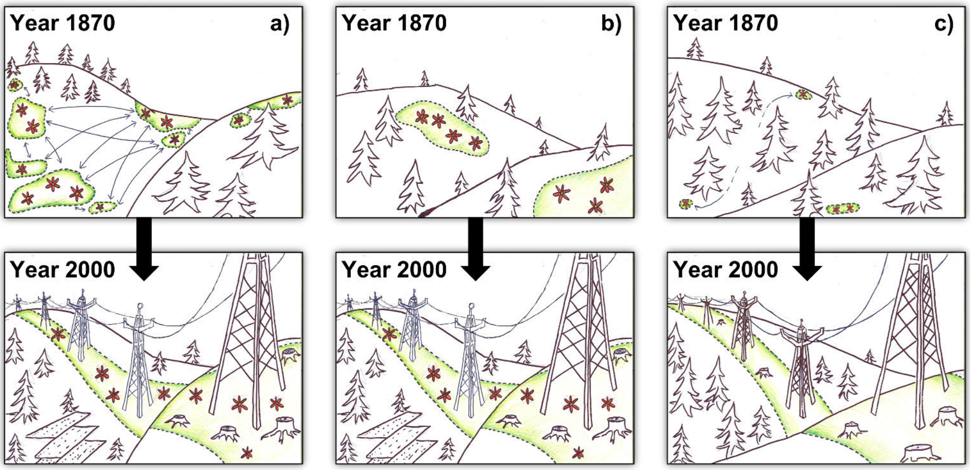


Figure 9. Conceptual relationship between landscape-scale and local land-use history related to semi-natural grasslands and the present species richness of grassland plants in power line clearings, adapted from Lampinen et al. 2017. Power line clearings situated in **a)** landscapes or **b)** localities historically rich in semi-natural grasslands may support more grassland plant species in the present day than clearings in **c)** landscapes with no history of semi-natural grasslands.

3.3 The valuation of novel habitats

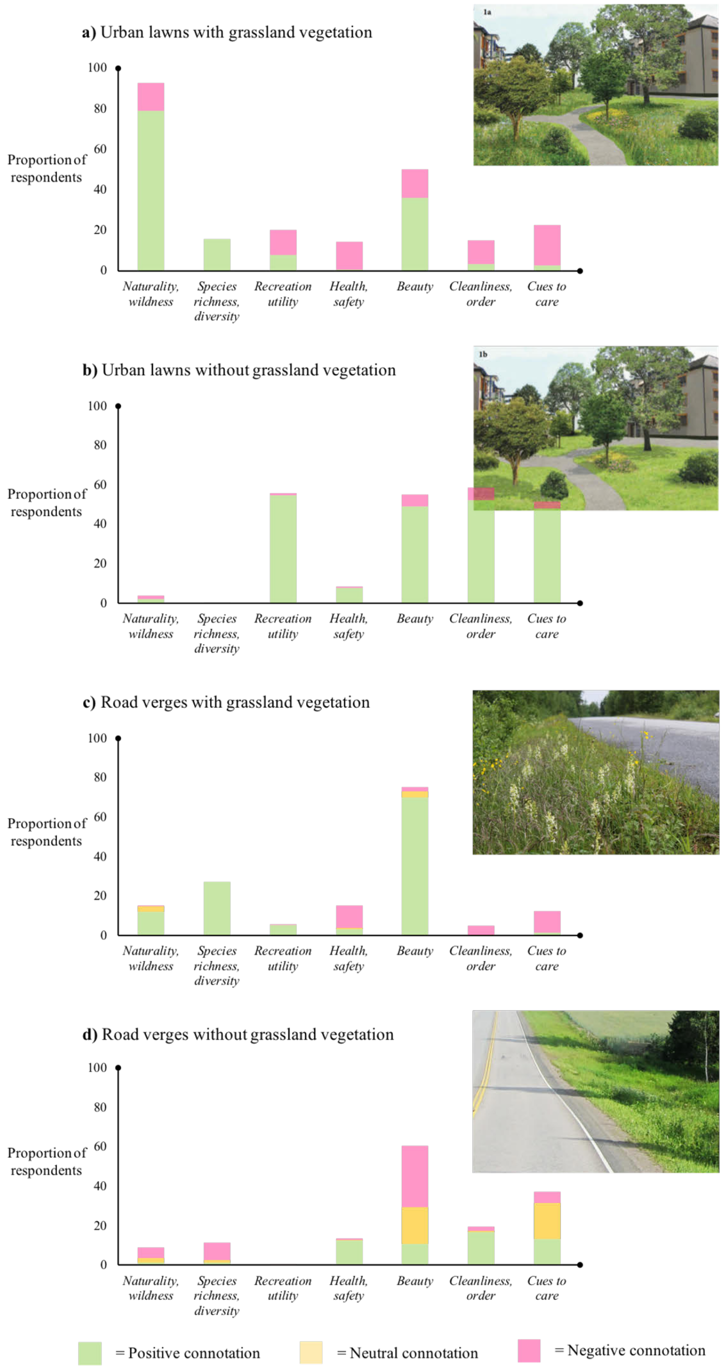
In Chapters IV-V, I showed that the stakeholders of urban lawns and road verges assign diverse ecological and socio-cultural values to these habitats and that the values differ depending on whether the novel habitat in question is currently characterized by abundant grassland vegetation or not (**Table 1**). For example, urban lawns across Europe managed as tall-growing grasslands were positively valued by urban greenspace users for their wild, natural appearance and species richness, while those managed as regular, short-cut lawns were positively valued for their recreation potential and clean, cared appearance. Negative values assigned to lawns managed as tall-growing grasslands included perceived lack of care and health-related threats (e.g. allergy, insect bites). Likewise, road verges with abundant grassland vegetation were positively valued by stakeholders for their species richness and beauty, and negatively valued for their perceived danger to traffic safety, untidiness and lack of care.

These results illustrate the multivalued nature of road verges and urban lawns and highlight how the fact that novel habitats may provide habitat for grassland species ("the grassland conservation benefit") is merely one value among many others that stakeholders of each novel habitat type may assign to them. The diversity of values of utility, aesthetics, health and safety assigned to novel habitats reflects the varying uses and purposes of these habitats. While the main historical motivation for managing semi-natural grasslands was undoubtedly economic and tangibly related to the sustenance of those managing the grasslands, the motivations for managing novel habitats are different according to each novel habitat type: While urban lawns have been established for aesthetic and recreational purposes (Hedblom et al. 2017, Ignatieva et al. 2017), road verges are managed primarily to ensure unobstructed visibility along the road environment (Parr & Way 1988, Auestad et al. 2010). In this context, it is understandable that not all stakeholders assign positive ecological values, such as species richness, to novel habitats characterized by abundant grassland vegetation or that some perceive such ecological values to conflict with the non-ecological values, such as recreation potential.

The results also follow previous, although scarce, studies investigating the valuation of novel habitats and grasslands. For example, Weber et al. (2014) identified a similar diversity of aesthetic, ecological and economic values that urban residents of Berlin assign to different types of roadside vegetation (managed vs. not managed). Similar to the results in this thesis, the study found that while unmanaged, wild-growing roadsides are especially assigned values of naturalness and wildness, those planted and managed regularly are associated with values of cleanliness and order. As for actual semi-natural grasslands, Raatikainen & Barron (2017) showed that farmers managing traditional rural biotopes assign values related to cultural heritage, biodiversity and aesthetics to these habitats and their management. Likewise, Lindborg et al. (2008) highlight the aesthetic and heritage values of the remaining semi-natural grasslands as a part of modern agricultural landscapes. In this thesis, both urban lawns and road verges characterized by grassland vegetation were indeed assigned positive values of beauty (aesthetics), identity and cultural heritage, although these were, with the exception of aesthetics, far less common than those related to the cleanliness, biodiversity and utility values mentioned above.

The strong representation of positive values of beauty and species richness assigned to novel habitats characterized by grassland vegetation likely bases on the fact that floral richness is in general perceived attractive (Lindemann-Matthies et al. 2010). This renders further leverage for introducing altered management practices in novel habitats that favor grassland species. However, the several positive values assigned to novel habitats *without* grassland vegetation and the negative values assigned to those *with* grassland vegetation imply that planning novel habitat management strictly with their grassland conservation value in mind likely results in dismissing other important motivations for their management. As we see in the next section, this may translate to negative attitudes towards utilizing novel habitats in grassland conservation.

Table 1. Examples of variation in the values assigned by stakeholders to **a-b)** urban lawns (Chapter IV, n = 2048) and **c-d)** road verges (Chapter V, n = 371) characterized by (**a**, **c**) or devoid of (**b**, **d**) grassland vegetation, extracted using photographic stimuli.



3.4 The attitudes towards managing novel habitats for greater grassland conservation benefit

In Chapters IV-V, I also showed that attitudes towards managing novel habitats for greater grassland conservation benefit vary among stakeholders from positive to neutral and negative. Among stakeholders related to road verge management, over half of both managing and administrative stakeholders supported positive attitudes towards managing road verges for greater grassland conservation benefit (**Table 2**). I also showed, that attitudes towards managing novel habitats for greater grassland conservation benefit covary with **a)** the values stakeholders assign to novel habitats (IV-V), **b)** the way stakeholders personally utilize the novel habitat in question (IV) and **c)** the stakeholders' personal backgrounds and their level of familiarity with semi-natural grasslands and their conservation value (V). Put concisely, stakeholders who are willing to manage novel habitats for greater grassland conservation benefit assign positive values of wildness, species richness and beauty to novel habitats characterized by grassland vegetation (IV-V), utilize novel habitats (in the case of urban lawns) for social and nature-related activities (IV) and are familiar with semi-natural grasslands (V). Stakeholders who are against managing novel habitats for greater grassland conservation benefit assign negative values of unsafety, untidiness, and neglect with novel habitats characterized by grassland vegetation (IV-V) and, in the case of urban lawns, utilize urban greenspaces mainly for passing through.

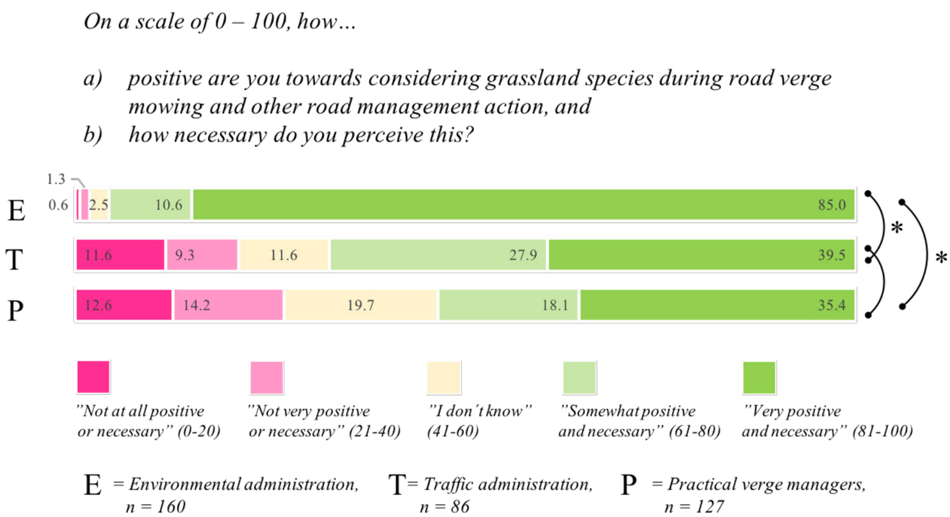
The positivity towards grassland-friendly novel habitat management found in this thesis is encouraging and relates to the results of Southon et al. (2017), who found that established meadows in urban greenspaces are preferred by greenspace users over regular, short-cut lawns. The results also echo those by Fischer et al. (2018), who found that urban greenspaces, such as streetscapes, wastelands, and forests with high plant species richness are preferred across Europe over the same urban greenspaces with lower plant species richness. However, the negative attitudes towards managing novel habitats for greater grassland conservation benefits found in this thesis are also expectable, as the potential for grassland conservation has hardly been the original intention, but rather the fortunate by-product of novel habitat management.

Understanding what determines the attitudes towards certain kind of novel habitat management helps understand why some stakeholders remain negative towards management alterations for greater grassland conservation benefit. The relationships between attitudes and values described above indicate that some road verge stakeholders are likely to always prefer the clean, cared appearance of regular road verges over the species richness of verges dominated by grassland vegetation, and some urban greenspace users to value the recreation potential of short-cut lawns over the beauty of meadow-like lawns. This is well in-line with the notion that especially values of aesthetics, cues to care, order, safety, and economics dictate whether landscapes or habitats, in this case, are perceived as desirable or particular ways of their management feasible (Nassauer 1995, Cook et al. 2011, Hoyle et al. 2017). A similar example is provided by Weber et al. (2014), who found that urban residents preferring planted, managed vegetation on roadsides justify their preference with values of aesthetics and order. Proponents of wild, unmanaged vegetation, on the other hand, justify their opinion with ecological, but also with economic values. Taken together, the results in this thesis and the research described above indicate that managing novel habitats for grassland species only would dismiss many equally important values and result in negative attitudes and objection from the stakeholders in the long run.

In Chapter V I also showed, that out of a selection of management alterations capable of increasing the quality of road verges as habitat for grassland species, stakeholder education and use of local soil and grassland species seeds in verge landscaping were considered the most feasible methods among road verge stakeholders (V). This is encouraging, as awareness concerning the ecological benefits of managing road verges as grasslands relates to positive attitudes towards actual grassland vegetation in the verges (Lucey & Barton 2011). Likewise, landscaping verges with grassland propagules has been shown to be a viable technique in establishing plant communities in the verges that bear close resemblance to those in actual semi-natural grasslands (Auestad et al. 2016). Certain management alterations, such as altering the mowing schedule of the verges to better accommodate the life cycle of grassland species, were considered less feasible by road verge stakeholders (V). This is unfortunate, as adjusting the time of mowing to late summer, so that grassland plants have the time to flower and set seed, is one of the most common and scientifically sound suggestions for improving the quality of verges for grassland species (Valtonen et al. 2006, Jantunen et al. 2007, Noordijk et al. 2009, Jakobsson et al. 2018).

Familiarity with grasslands is an understandable predictor for positive attitudes towards managing novel habitats for greater grassland conservation benefit. However, it is well known that increasing education on a problem does not alone help increase behavior that would solve that problem (Steg & Vleg 2009). Indeed, despite the fact that values readily translate to attitudes, a mismatch is often observed between attitudes towards a particular outcome and the actions that would pursue it (Schultz 2011 and references therein, Heberlein 2012). In other words, several barriers often exist between attitudes, behavioral intent and actual behavior. In the next section, the barriers facing the implementation of grassland-friendly novel habitat management are described in greater detail.

Table 2. Variation in the attitude towards managing road verges for greater grassland conservation benefit among three groups of road verge stakeholders, (E = environmental administration, T = traffic administration and P = practical verge management) calculated as the average of two Likert -items. Asterisks represent statistically significant differences in the average within group attitude between the stakeholder groups according to pairwise Wilcoxon rank-sum tests. Modified from Chapter V.



3.5 The barriers to managing novel habitats for greater grassland conservation benefit

In Chapter V, I showed that the most important perceived barriers to managing road verges for greater grassland conservation benefit are inadequate stakeholder resources, including money, employers and equipment. The perceived compromises to traffic safety that any deviation from current management regimes would result in are also considered severe barriers. In addition, the lack of information concerning semi-natural grasslands, biodiversity, or the role of novel habitats in grassland conservation, and the negative values associated with novel habitats characterized by grassland vegetation, may also be considered barriers facing the altered management of novel habitats.

These results correspond to those obtained by an interview study by Hoyle et al. (2017) concerning the perception of urban greenspace managers on the possibilities of increasing the cover of meadows in urban greenspaces at the expense of regular short-cut lawns. Especially the concern over vastly increasing management costs with the introduction of meadow management is common to the results. Also Akbar et al. (2003) mention increased costs of management as a perceived handicap of introducing road verge management that would favor grassland plants. On the other hand, the legislative and contractual constraints mentioned as barriers to grassland-friendly road verge management by O'Sullivan et al. (2017) were mentioned the least often in Chapter V. The results in Chapter V also contradict those of Southon et al. (2017), who report to have found only few barriers to accepting meadows as a part of urban greenspaces. This may be explained by the study of Southon et al. (2017) focusing on stakeholders who utilize novel habitats for recreation, while Chapter V in this thesis focused on the stakeholders responsible for the management and administration of novel habitats. In addition, the contradictory results between the two studies likely relate also to different study systems: while the study by Southon et al. (2017) concerns increasing the cover of grassland vegetation in urban greenspaces, Chapter V concerns that in road verges.

How then to overcome the barriers to implementing grassland-friendly novel habitat management? Lucey & Barton (2011) showed for road verges and Southon et al. (2017) for urban greenspaces that increased awareness of the benefits of grassland vegetation leads to more positive attitudes towards such vegetation. As mentioned above, however, positive attitudes do not necessarily lead to changes in behavior, and thus simply increasing the education of the stakeholders, despite its perceived feasibility in Chapter V, will not be enough to ensure that management is truly altered. Legislative changes resulting in laws that state how road verges should be managed could function as a top-down mechanism for ensuring that management is altered, but without substantial increases to the resources the managing stakeholders rely upon such laws would bear little consequence. As such, studies are needed to assess the realized changes to management costs and perceived traffic safety to ascertain whether the present resources simply require redistribution and whether the true problem is the negative attitudes described earlier. One solution considering both traffic safety and the need for altered management may be mosaic-like mowing. In this approach, road verges are mown as they currently are, but only the part of the verge next to the road is mown in early summer and the rest in late summer. Suggested by e.g. Noordijk et al. (2009), this alternative requires research both on the ecological consequences and the changes to costs and perceived traffic safety following its implementation.

Mosaic-like mowing could function in urban lawns as well to produce management solutions that favor the development of grassland vegetation but do not dismiss the recreation potential or aesthetic requirements urban greenspace users place on lawns. For example, in a given greenspace, spatial variation in the mowing intensity could produce areas of short-cut lawns reserved for recreation and areas of taller grass reserved for grassland species. Participatory planning among local residents, the stakeholders managing the lawns, and researchers could function in locating these areas within the greenspace so that all parties feel heard.

4 Conclusions and implications for conservation

Power line clearings, road and railway verges and various urban lawns and grasslands are among the predominant early-successional habitats of present-day Finland (**Fig 10**). Improving the current conservation status of grassland species is just as much in the hands of people managing these habitats as it is in the hands of the farmers grazing, the biologists surveying or the volunteers restoring the remaining fragments of actual semi-natural grasslands. Rather than meticulous site-specific management plans, however, a change in the entire way we manage novel habitats is required for them to be fully utilized in grassland conservation.

Based on previous research on the restoration of semi-natural grasslands and the results of chapters I-III, we now have the ecological know-how for a) identifying the conditions in novel habitats likely to result in grassland conservation potential and b) managing novel habitats in ways that maximize the benefits to grasslands species. Based on previous research in nature valuation and the results in chapters IV-V, we now understand that stakeholders assign several, sometimes conflicting values to novel habitats, and that this valuation functions as a base for attitudes towards altering the current management of novel habitats to better suit the needs of grassland species. With these results in mind, the following guidelines may be applied to the management of novel habitats for increasing their quality for grassland species irrespective of the type of novel habitat:

1. Altering the management of novel habitats to better mimic the traditional management of semi-natural grasslands is likely to increase the suitability of novel habitats for grassland species, although the responses to different management regimes may vary among different groups of species.

2. Management alterations aiming at favoring specifically grassland plants should be focused into areas characterized by dry soils, southerly slopes, and a local or regional land-use history related to semi-natural grasslands.

3. It is important to remember the multivalued nature of novel habitats when planning the implementation of any management alteration: Traffic safety in road verges, efficient electricity transportation in power line clearings, and the recreation opportunities in urban lawns are values that cannot be dismissed altogether during management planning lest the alterations be faced with negative attitudes among novel habitat stakeholders.

4. In addition to the values specific to each novel habitat type, certain values, such as order, neatness, signs of care and floral abundance are universally perceived as desirable in managed environments. Any management alteration compromising these may be perceived negatively by some novel habitat stakeholders.

5. Management alterations that favor grassland species but do not compromise the habitat-specific or universal values described above are likely to differ among novel habitat types. However, increasing stakeholder resources and awareness and including both the administrators, managers and users of novel habitats in management planning could result in solutions that all parties may conform to.

Proposals for increasing the grassland conservation value of specific novel habitat types include:

6. In power line clearings, increasing the frequency of clear-cuts and removing the resulting debris from the corridors is likely to increase the species richness of both grassland plants and butterflies inhabiting them (II-III, Berg et al. 2013; 2016).

7. In road verges, mosaic mowing targeting especially old verges with sandy, nutrient-poor soils could favor the flowering of grassland plants while not compromising traffic security or the cared appearance of the verges (V, Jantunen et al. 2006, Noordijk 2009).

8. In urban lawns, participatory planning with greenspace users could give insight into where to locate areas of tall-growing, grassland-like lawns and where to maintain regular, short-cut lawns reserved for recreation. Introducing signs of care, such as mown borders, paths and signs, into areas reserved for grassland-like lawns could increase the positive attitudes of greenspace users towards them (IV, Nassauer 1995, Southon et al. 2017).

In addition to the need for saving grassland species from further regional extinctions, conceptual leverage for implementing the above guidelines may be found in the history of grassland vegetation in Europe and the various types of habitats grassland species have occupied over the course of millennia. Grasslands of different types are estimated to have existed in Europe for at least 1,8 million years, maintained partly by the alternating periods of cold and warmer climatic conditions, partly by megafaunal grazing (Prins 1998, Pärtel et al. 2005). Following the extinction of these animals during the late Pleistocene, grassland species are thought to have retreated to remnants of open vegetation maintained by environmental conditions too harsh or too frequently disturbed for forest development (Svenning 2002). Thus, the semi-natural grasslands that spread across Europe thousands of years later as a response to the advent of agriculture and animal husbandry would have, at the time, undoubtedly appeared as novel as road verges, power line clearings and lawns appear to us today. In this context, developing the management of novel habitats to better suit the needs of grassland species simply equals helping these species take the next step in their adaptation to different kinds of early-successional, open habitats.

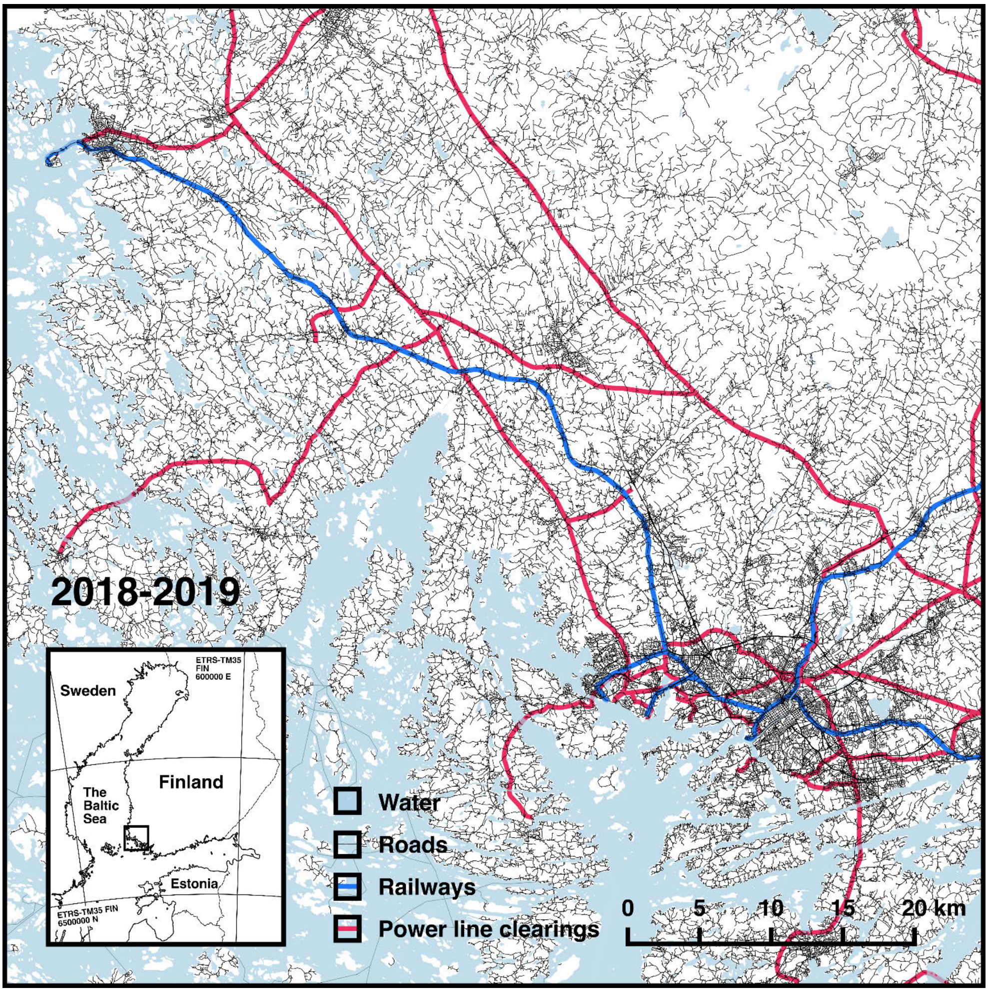


Figure 10. An example of the extent of roads (Liikennevirasto 2019), railways (Liikennevirasto 2019) and power line clearings (Finnish Environment Institute 2019b) in South-Western Finland 2019.

5 Future research needs

Even if all of the above guidelines were implemented into practice, questions would still remain unanswered concerning grassland conservation in novel habitats. The most obvious one concerns the extent, spatial configuration and exact locations of novel habitats that currently support species-rich grassland communities. While the remaining semi-natural grasslands in Finland were surveyed already in the 1990´s (Vainio et al. 2001), attempts at locating novel habitats with potential for grassland conservation have proved unsuccessful or focused into limited geographical areas. For example, Heliölä & Pöyry (2008) conclude that locating power line clearings with species-rich grassland vegetation is not possible with remote sensing data on the topography and soil of the clearings. However, by combining such data with data on the historical locations of semi-natural grasslands (Lampinen & Turkia 2019), one could locate the areas where semi-natural grasslands have historically been most abundant, and thus the novel habitats that may still be rich in grassland species. This approach could supplement field-based surveys for valuable sites, an example of which is the survey for sites of conservation value the in the road verges of Varsinais-Suomi (Myllymäki et al. 2019). Alternatively, more intricate remote sensing methods and materials, such as LIDAR (e.g. Zlinszky et al. 2014), should be piloted in locating novel habitats with grassland vegetation of conservation value.

In addition, studies are required to quantify the realized changes in the valuation of novel habitats following the implementation of management alterations that favor grassland species. Without documenting the perceived changes to the recreation possibilities of urban lawns, the traffic safety of road verges, or the management costs of power line clearings it is difficult to assess the large-scale impacts of grassland-friendly management.

Finally, assessing the long-term commitment of stakeholders to the novel management methods, and the resulting changes in species composition should also follow any implemented management alteration. Only by assuring that the management alterations are not simply interventions but rather result in a permanent change in novel habitat management may one hope for the grassland conservation value of the sites to truly increase.

Acknowledgements

This thesis would never have seen the light of day had I done everything related to it all by myself. First of all, I have to thank the Kone Foundation and the Finnish Foundation for Nature Conservation for providing me with the necessary funding to be able to take on this project. I have seldom felt as grateful as I did around Christmas 2014, having just heard of the positive funding decision from Kone.

Next, I wish to thank Triin Reitalu (TALTECH) and Anni Arponen (UH) for the effort they put into examining this thesis, and Professor Christopher Raymond (UH) for kindly acting as the opponent while I defend it. I am extremely honored for researches of such merit to participate in the final stages of this lengthy process.

I would also like to thank my supervisor Kalle Ruokolainen (UTU) for having taught me more about science than any course could. Kalle has so much patience in teaching he could probably teach my dog tell the difference between regression and correlation, something I woefully labored with for so many years. In addition to Kalle, also AP Huhta (UO) and Stephen Venn (UH) provided me with supervision in the early stages of my postgraduate studies, thanks to them as well. For supervision I wish to thank my brilliant co-authors as well, for they've taught me many lessons in how and what to write. They've also provided me with the support anyone doing a PhD-thesis without a research group surrounding them sometimes needs. Especially Mikko Kuussaari (SYKE), Risto K. Heikkinen (SYKE), Maria Tuomi (UTU), Valentin Klaus (ETH Zürich), Lena Neuenkamp (Univ. Bern), Leonie Fischer (Univ. Stuttgart) and Niina Anttila (VS-ELY) were more than pleasant to work with.

Many members of the faculty at UTU have encouraged me forward in my tight spots over the years. Hanna Tuomisto, Sanna Huttunen, Timo Vuorisalo, Kai Norrdahl and Niina Käyhkö have all provided help either with statistics, administrative issues, or the general, sometimes burdensome academic life. Tytti and Pauliina at the office, and Mia, Glenda, Tinja, Hanna, Suvi, Tuuli and others elsewhere down the corridors have made the University feel like home. And Pauliina, Aino, Tytti, Mia, Tinja and Jenni did a wonderful job at acting as the opponents in my trial defense, many thanks to all of you!

Life would truly stink without friendship, and for that I am greatly indebted to Marjaana, Anna, Bura, Essi, Iiris, Toni, Anna, Pia and Maria among many others. I´m very fond of all of you, and you've made me laugh so many times, that I will have a hard time repaying it all. Thank you, and I am sorry, for not being there on many occasions during the years, because of this thesis.

I thank my family, especially my mother, sister, aunt and cousin for the ambition and persistence I´ve inherited from them, and for the kind and firm encouragement they've so generously provided me with. And for all the long summers of my childhood spent outside at the summer cabin, no amount of gratitude would be enough for those. They have contributed to this thesis more than you perhaps guessed at the time.

Last, I would like to thank my dear dog Nakki, who so often has rested his majestic head in my lap, patiently waiting for me to finish writing, so that we could finally go for a WALK.

May you all stay forever young.

May you all live happily ever after.

And may you all cite this thesis many times while doing so.

29.12.2019

Jussi

References

Adler PB, Seabloom EW, Borer ET, Hillebrand H, Hautier Y, Hector A, Harpole WS, O'Halloran LR, Grace JB, Anderson TM, Bakker JD, Biederman LA, Brown CS, Buckley YM, Calabrese LB, Chu C, Cleland EE, Collins SL, Cottingham KL, Crawley MJ, Damschen EI, Davies KF, DeCrappeo NM, Fay PA, Firn J, Frater P, Gasarch EI, Gruner DS, Hagenah N, Lambers JHR, Humphries H, Jin VL, Kay AD, Kirkman KP, Klein JA, Knops JMH, La Pierre KJ, Lambrinos JG, Li W, MacDougall AS, McCulley RL, Melbourne BA, Mitchell CE, Moore JL, Morgan JW, Mortensen B, Orrock JL, Prober SM, Pyke DA, Risch AC, Schuetz M, Smith MD, Stevens CJ, Sullivan LL, Wang G, Wragg PD, Wright JP, Yang LH (2011) Productivity is a poor predictor of plant species richness. Science 333: 1750–1753.

Ahmad J, Malik AS, Xia L, Ashikin N (2013) Vegetation encroachment monitoring for transmission lines right-of-ways: A survey. Electric Power Systems Research 95: 339–352.

Ajzen I (2001) Nature and operation of attitudes. Annual Review of Psychology 52: 27–58.

Akbar KF, Hale WHG, Headley AD (2003) Assessment of scenic beauty of the roadside vegetation in northern England. Landscape and urban planning 63: 139–144.

Alenius T, Haggrén G, Koivisto S, Vanhanen S, Sugita S (2017) Landscape dynamics in southern Finland during the Iron Age and the Early Modern Era – Pollen-based landscape reconstruction (LRA), macrofossil and historical data from Western Uusimaa. Journal of archaeological science: Reports 12: 12–24.

Alumai A, Salminen SO, Richmond DS, Cardina J, Grewal PS (2009) Comparative evaluation of aesthetic, biological, and economic effectiveness of different lawn management programs. Urban Ecosystems 12: 127–144.

ArtDatabanken 2015. Rödlistade arter i Sverige 2015. ArtDatabanken SLU, Uppsala.

Auestad I, Rydgren K, Jongejans E, de Kroon H (2010) Pimpinella saxifraga is maintained in roadverges by mosaic management. Biological Conservation 143: 899–907.

Auestad I, Rydgren K, Austad I (2011) Road verges: potential refuges for declining grassland species despite remnant vegetation dynamics. Annales botanici fennici 48: 289–303.

Auestad I, Rydgren K, Austad I (2016) Near-natural methods promote restoration of species-rich grassland vegetation—revisiting a road verge trial after 9 years. Restoration Ecology 24: 381–389.

Auffret AG, Cousins SAO (2013) Grassland connectivity by motor vehicles and grazing livestock. Ecography 36: 1150–1157.

Baillie J, Hilton-Taylor C, Stuart SN (eds) (2004) IUCN red list of threatened species: a global species assessment. IUCN—The World Conservation Union, Gland.

Bardos DC, Guillera-Arroita G, Wintle BA (2015) Valid auto-models for spatially autocorrelated occupancy and abundance data. Methods in Ecology and Evolution 6: 1137–1149.

Berg Å, Ahrné K, Öckinger E, Svensson R, Wissman J (2013) Butterflies in semi-natural pastures and power-line corridors—effects of flower richness, management, and structural vegetation characteristics. Insect Conservation and Diversity 6: 639–657.

Berg Å, Bergman KO, Wissman J, Żmihorski M, Öckinger E (2016) Power-line corridors as source habitat for butterflies in forest landscapes. Biological Conservation 201: 320–326.

Berkes F, Folke C, Colding J (eds.) (2000) Linking social and ecological systems. Management practices and social mechanisms for building resilience. Cambridge University Press, Cambridge.
Berndt LA, Brockerhoff EG, Jactel H (2008) Relevance of exotic pine plantations as a surrogate habitat for ground beetles (Carabidae) where native forest is rare. In: Brockerhoff EG, Jactel H, Parrotta JA, Quine CP, Sayer J, Hawksworth DL (eds) Plantation Forests and Biodiversity: Oxymoron or Opportunity? Topics in Biodiversity and Conservation 9. Springer. Dordrecht
Bläuer A (2015) Voita, viljaa ja vetoeläimiä. Karjan ja karjanhoidon varhainen historia Suomessa. Karhunhammas 17: 1–224. In Finnish.
Bramble WC, Byrnes WR (1983) Thirty years of research on development of plant cover on an electric transmission right-of-way. Journal of Arboriculture 9: 67–74.
Brown H, Reed P (2000) Validation of a forest values typology for use in national forest planning. Forest Science 46: 240–247.
Brückmann SV, Krauss J, Steffan-Dewenter I (2010) Butterfly and plant specialists suffer from reduced connectivity in fragmented landscapes. Journal of Applied Ecology 47: 799–809.
Bryan BA, Raymond CM, Crossman ND, King D (2010) Comparing Spatially Explicit Ecological and Social Values for Natural Areas to Identify Effective Conservation Strategies. Conservation Biology 25: 172–181.
Carpenter SR, Mooney HA, Agard J, Capistrano D, DeFries RS, Díaz S, Dietz T, Duraiappah AK, Oteng-Yeboah A, Pereira HM, Perrings C, Reid WV, Sarukhan J, Scholes RJ, Whyte A (2009) Science for managing ecosystem services: Beyond the Millennium Ecosystem Assessment. PNAS 106: 1305–1312.
Chen S, Feng Z, Xiaolian Y (2017) A general introduction to adjustment for multiple comparisons. Journal of Thoracic Disease 9: 1725–1729.
Chevan A, Sutherland M (1991) Hierarchical partitioning. The American Statistician 45: 90–96.
Cho JY, Lee EH (2014) Reducing Confusion about Grounded Theory and Qualitative Content Analysis: Similarities and Differences. The Qualitative Report 19: 1–20.
Chollet S, Brabant C, Tessier S, Jung V (2018) From urban lawns to urban meadows: Reduction of mowing frequency increases plant taxonomic, functionals and phylogenetic diversity. Landscape and Urban Planning 180: 121–124.
Cook EM, Hall SJ, Larson KL (2011) Residential landscapes as social-ecological systems: a synthesis of multi-scalar interactions between people and their home environment. Urban Ecosystems 15: 19–52.
Cousins SAO (2009) Extinction debt in fragmented grasslands: paid or not? Journal of Vegetation Science 20: 3–7.
Cousins SAO, Auffret AG, Lindgren J, Tränk L (2015) Regional-scale land-cover change during the 20th century and its consequences for biodiversity. AMBIO 44: 17–27.
Crooks KR, Sanjayan M (eds.) (2006) Connectivity conservation. Cambridge University Press, Cambridge.
Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology 88: 528–534.
Dengler J, Janišová M, Török P, Wellstein C (2014) Biodiversity of Palearctic grasslands: a synthesis. Agriculture, Ecosystems & Environment 182: 1–14.
Dormann CF, McPherson JM, Araújo MB, Bivand R, Bolliger J, Carl G, Davies RG, Hirzel A, Jetz W, Kissling WD, Kühn I, Ohlemüller R, Peres-Neto PR, Reineking B, Schröder B, Schurr FM, Wilson R (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography 30: 609–628.
Eldegard K, Eyitayo DL, MH Lie, Moe SR (2017) Can powerline clearings be managed to promote insect-pollinated plants and species associated with semi-natural grasslands? Landscape and Urban Planning 167: 419–428.
Ellenberg H (1988) Vegetation Ecology of Central Europe. 4th edition. Cambridge University Press. Avon.

Elo S, Kyngäs H (2007) The qualitative content analysis process. Journal of Advanced Nursing 62: 107–115.
Eriksson O, Cousins SAO, Bruun HH (2002) Land-use history and fragmentation of traditionally managed grasslands in Scandinavia. Journal of Vegetation Science 13: 743–748.
Eriksson O, Cousins SAO (2014) Historical landscape perspectives on grasslands in Sweden and the Baltic region. Land 3: 300–321.
Eurelectric (2009) Power distribution in Europe – Facts and figure. A Eurelectric paper. Available: https://www3.eurelectric.org/media/113155/dso_report-web_final-2013-030-0764-01-e.pdf.
European union road federation (2017) Road statistics – Yearbook 2017. Available: http://www.erf.be/wp-content/uploads/2018/01/Road_statistics_2017.pdf
Eyre MD, Luff ML, Woodward JC (2003) Beetles (Coleoptera) on brownfield sites in England: An important conservation resource? Journal of Insect Conservation 7: 223–231.
Fingrid (2019a) Raivaajan käsikirja. In Finnish. Available: https://www.fingrid.fi/globalassets/dokumentit/fi/kantaverkko/turvallisuus/raivaajan_kasikirja_2016.pdf
Fingrid (2019b) Voimajohtoaukeiden raivaukset. In Finnish. Available: https://www.fingrid.fi/globalassets/dokumentit/fi/kantaverkko/kunnossapito/raivaus-liite-suomi.pdf
Finnish Environment Institute (2019a) CORINE land cover 2012 raster data, resolution 20 x 20 m. Database OIVA. In Finnish. Available: http://paikkatieto.ymparisto.fi/lapio/lapio_flex.html#.
Finnish Environment Institute (2019b) Database: Maastotietokanta. In Finnish. Available: http://paikkatieto.ymparisto.fi/lapio/lapio_flex.html#.
Fischer M, Stöcklin J (1996) Local extinctions of plants in remnants of extensively used calcareous grasslands 1950-1985. Conservation Biology 11: 727–737.
Fischer LK, von der Lippe M, Kowarik I (2013) Urban land use types contribute to grassland conservation: The example of Berlin. Urban Forestry & Urban Greening 12: 263–272.
Fischer LK, Honold J, Cvejić R, Delshammar T, Hilbert S, Lafortezza R, Nastran M, Nielsen AB, Pintar M, van der Jagt APN, Kowarik I (2018) Beyond green: Broad support for biodiversity in multicultural European cities. Global Environmental Change 49: 35–45.
Foster BL, Gross KL (1998) Species richness in a successional grassland: effects of nitrogen enrichment and plant litter. Ecology 79: 2593–2602.
Galvánek D, Lepš J (2008) Changes of species richness pattern in mountain grasslands: abandonment versus restoration. Biodiversity and Conservation 17: 3241–3253.
Garbuzov M, Fensome KA, Ratnieks FLW (2014) Public approval plus more wildlife: twin benefits of reduced mowing of amenity grass in a suburban public park in Saltdean, UK. Insect Conservation and Diversity 8: 107–119.
Gardiner MM, Riley CB, Bommarco R, Öckinger E (2018) Rights-of-way: a potential conservation resource. Frontiers in Ecology and the Environment 16: 149–158.
Grime JP (1973) Competitive exclusion in herbaceous vegetation. Nature 242: 344–347.
Gobster PH, Nassauer JI, Daniel TC, Fry G (2007) The shared landscape: what does aesthetics have to do with ecology? Landscape Ecology 22: 959–979.
Guisan A, Edwards TC Jr, Hastie T (2002) Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecological Modelling 157: 89–100.
Hall LS, Krausman PR, Morrison ML (1997) The habitat concept and a plea for standard terminology. Wildlife Society Bulletin 25: 173–182.
Heberlein T (2012) Navigating environmental attitudes. Conservation Biology 26: 583–585.
Hedblom M, Lindberg F, Vogel E, Wissman J, Ahrné K (2017) Estimating urban lawn cover in space and time: Case studies in three Swedish cities. Urban Ecosystems 20: 1109–1119.
Heliölä J, Pöyry J (2008) Identifying valuable grasslands on power line areas using remote sensing data. The Finnish Environment 34/2008. In Finnish.
Helm A, Hanski I, Pärtel M (2006) Slow response of plant species richness to habitat loss and fragmentation. Ecology Letters 9: 72–77.

Hill MO, Mountford JO, Roy DB, Bunce RGH (1999) Ellenberg's Indicator Values for British Plants: ECOFACT Technical Annex 2a. Institute of Terrestrial Ecology. Huntingdon.

Hobbs RJ, Higgs ES, Harris JA (2009) Novel ecosystems: implications for conservation and restoration. Trends in ecology and evolution 24: 599–605.

Hobbs RJ, Higgs ES, Hall CM (eds.) (2013) Novel ecosystems: Intervening in the new ecological world order. John-Wiley & Sons, Chichester.

Hobbs RJ, Higgs E, Hall CM, Bridgewater P, Chapin FS III, Ellis EC, Ewel JJ, Hallett LM, Harris J, Hulvey KB, Jackson ST, Kennedy PL, Kueffer C, Lach L, Lantz TC, Lugo AE, Mascaro J, Murphy SD, Nelson CR, Perring MP, Richardson DM, Seastedt TR, Standish RJ, Starzomski BM, Suding KN, Tognetti PM, Yakob L, Yung L (2014) Managing the whole landscape: historical, hybrid and novel ecosystems. Frontiers in Ecology and Environment 12: 557–564.

Hodgson JA, Moilanen A, Wintle BA, Thomas CD (2010) Habitat area, quality and connectivity: striking the balance for efficient conservation. Journal of Applied Ecology 48: 148–152.

Holm S (1979) A simple sequentially rejective multiple test procedure. Scandinavian Journal of Statistics 6: 65–70.

Hoyle H, Jorgensen A, Warren P, Dunnett N, Evans K (2017) "Not in their front yard" The opportunities and challenges of introducing perennial urban meadows: A local authority stakeholder perspective. Urban Forestry & Urban Greening 25: 139–149.

Huhta AP, Rautio P, Tuomi J, Laine K (2001) Restorative mowing on an abandoned semi-natural meadow: short-term and predicted long-term effects. Journal of Vegetation Science 12: 677–686.

Hämet-Ahti L, Suominen J, Ulvinen T, Uotila P (eds.) (1998) The Field Flora of Finland. 4th edition. Yliopistopaino. Helsinki. In Finnish.

Hyvärinen E, Juslén A, Kemppainen E, Uddström A, Liukko UM (eds.) (2019) The 2019 Red List of Finnish Species. Ministry of the Environment & Finnish Environment Institute. Helsinki.

Ibbe M, Milberg P, Tunér A, Bergman KO (2011) History matters: impact of historical land use on butterfly diversity in clear-cuts in a boreal landscape. Forest Ecology and Management 261: 1885–1891.

Ignatieva M, Eriksson F, Eriksson T, Berg P, Hedblom M (2017) The lawn as a social and cultural phenomenon in Sweden. Urban Forestry & Urban Greening 21: 213–223.

Ives CD, Kendal D (2014) The role of social values in the management of ecological systems. Journal of Environmental Management 144: 67–72.

Ives CD, Oke C, Hehir A, Gordon A, Wang Y, Bekessy SA (2017) Capturing residents' values for urban green space: Mapping, analysis and guidance for practice. Landscape and Urban Planning 161: 32–43.

Jakobsson S, Bernes C, Bullock JM, Verheyen K, Lindborg R (2018) How does roadside vegetation management affect the diversity of plants and invertebrates? A systematic review. Environmental Evidence 7: 17.

Janssen JAM, Rodwell JS, García Criado M, Gubbay S, Haynes T, Nieto A, Sanders N, Landucci F, Loidi J, Ssymank A, Tahvanainen T, Valderrabano M, Acosta A, Aronsson M, Arts G, Attorre F, Bergmeier E, Bijlsma RJ, Bioret F, Biţă-Nicolae C, Biurrun I, Calix M, Capelo J, Čarni A, Chytrý M, Dengler J, Dimopoulos P, Essl F, Gardfjell H, Gigante D, Giusso del Galdo G, Hájek M, Jansen F, Jansen J, Kapfer J, Mickolajczak A, Molina JA, Molnár Z, Paternoster D, Piernik A, Poulin B, Renaux B, Schaminée JHJ, Šumberová K, Toivonen H, Tonteri T, Tsiripidis I, Tzonev R, Valachovič M (2017) European Red List of Habitats, Part 2. Terrestrial and freshwater habitats. European Union. doi:10.2779/091371.

Jantunen J, Saarinen K, Valtonen A, Hugg T, Saarnio S (2004) Vegetation and butterfly fauna in roadside habitats. Finnish Road Administration. Finnra reports 9/2004. In Finnish.

Jantunen J, Saarinen K, Valtonen A, Saarnio S (2006) Grassland vegetation along roads differing in size and traffic density. Annales Botanici Fennici 43:107–117.

Jantunen J, Saarinen K, Valtonen A, Saarnio S (2007) Flowering and seed production success along roads with different mowing regimes. Applied Vegetation Science 10: 285–292.

Johansson VA, Cousins SAO, Eriksson O (2011) Remnant Populations and Plant Functional Traits in Abandoned Semi-Natural Grasslands. Folia Geobotanica 46: 165–179.

Johnson MD (2007) Measuring habitat quality: A review. The Condor 109: 489–504.

Johnson CN (2009) Ecological consequences of Late Quaternary extinctions of megafauna. Proceedings of the Royal Society B 276: 2509–2519.

Jonason D, Ibbe M, Milberg P, Tunér A, Westerberg L, Bergman KO (2014) Vegetation in clear-cuts depends on previous land use: a century-old grassland legacy. Ecology and Evolution 4: 4287–4295.

Jorgensen A, Hitchmough J, Calvert T (2002) Woodland spaces and edges: their impact on perception of safety and preference. Landscape and Urban Planning 60: 135–150.

Kemppainen R, Lehtomaa L (2009) Perinnebiotooppien hoidon tila ja tavoitteet. Valtakunnallinen kooste perinnebiotooppien alueellisista hoito-ohjelmista. Lounais-Suomen ympäristökeskuksen raportteja 2/2009. In Finnish.

Kivinen S (2005) Regional distribution and biodiversity perspectives of Finnish grasslands. Fennia 183: 37–56.

Komonen A, Lensu T, Kotiaho JS (2013) Optimal timing of power line rights-of-ways management for the conservation of butterflies. Insect Conservation and Diversity 6: 522–529.

Kontula T, Raunio A (eds.) (2018) Threatened habitat types in Finland 2018, Red List of habitats Part I: Results and basis for assessment. The Finnish Environment 5/2018. Suomen ympäristökeskus & Ympäristöministeriö. Helsinki. In Finnish.

Kowarik I (2011) Novel urban ecosystems, biodiversity and conservation. Environmental Pollution 159: 1974–1983.

Kullberg J, Albrecht A, Kaila L, Varis V (2002) Checklist of Finnish Lepidoptera—Suomen perhosten luettelo. Sahlbergia 6: 45–190.

Kuussaari M, Ryttäri T, Heikkinen R, Manninen P, Aitolehti M, Pöyry J, Pykälä J, Ikävalko J (2003) Significance of power line areas for grassland plants and butterflies. The Finnish Environment 638. 1–65. In Finnish.

Kuussaari M, Bommarco R, Heikkinen RK, Helm A, Krauss J, Lindborg R, Öckinger E, Pärtel M, Pino J, Rodá F, Stefanescu C, Teder T, Zobel M, Steffan-Dewenter I (2009) Extinction debt: a challenge for biodiversity conservation. Trends in Ecology and Evolution 24: 564–571

Lampinen J (2017) The present size, protection status, threats and restoration requirements of *Carex caryophyllea* -populations in continental Finland. *Memoranda Societatis pro Fauna et Flora Fennica* **93**: 106–135.

Lampinen J, Heikkinen RK, Kuussaari M (2017) The potential of power line clearings to provide habitat for grassland specialist species depends on local land-use history and past connectivity to grasslands. Conference poster. British Ecological Society Annual meeting “Ecology Across Borders 2017” Ghent, Belgium 11.-14.12.2017.

Lampinen J (2018) Non-native species richness along power-line corridors is partly related to garden-waste disposal. *Lutukka* **34**: 86–92. In Finnish.

Lampinen J, Turkia T (2019) Pastures and semi-natural grasslands in Finland Proper 1870-1890 – Georeferenced and delineated based on the Senate Maps. In preparation.

Larson KL, Cook E, Strawhacker C, Hall SJ (2010) The influence of diverse values, ecological structure and geographic context on residents multifaceted landscaping decisions. Human ecology 38: 747–761.

Legendre P, Anderson MJ (1999) Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. Ecological Monographs 69: 1–24.

Legendre P, Legendre P (1998) Numerical Ecology. 2nd edition. Elsevier. Amsterdam.

Lehtomaa L, Ahonen I, Hakamäki H, Häggblom M, Jutila H, Järvinen C, Kemppainen R, Kondelin H, Laitinen T, Lipponen M, Mussaari M, Pessa J, Raatikainen KJ, Raatikainen K, Tuominen S, Vainio M, Vieno M, Vuomajoki M (2018a) Seminatural grasslands. In: Kontula T, Raunio A (2018) Threatened habitat types in Finland 2018, Red List of habitats Part I: Results and basis for assessment. The Finnish Environment 5/2018. Finnish Environment Institute & Ministry of the Environment. Helsinki. In Finnish.

Lehtomaa L, Ahonen I, Hakamäki H, Jantunen J, Jutila H, Järvinen C, Kemppainen R, Kondelin H, Laitinen T, Lipponen M, Mussaari M, Pessa J, Raatikainen KJ, Raatikainen K, Tuominen S, Vainio M, Vieno M, Vuomajoki M (2018b) Seminatural grasslands. In: Kontula T, Raunio A (2018) Threatened habitat types in Finland 2018, Red List of habitats Part II: Descriptions of habitat types. The Finnish Environment 5/2018. Finnish Environment Institute & Ministry of the Environment. Helsinki. In Finnish.

Lenda M, Skórka P, Morón D, Rosin ZM, Tryjanowski P (2012) The importance of the gravel excavation industry for the conservation of grassland butterflies. Biological Conservation 148: 180–190.

Liikennevirasto (2014) Viherrakentaminen ja -hoito tieympäristössä. Liikenneviraston ohjeita 18/2014. ISSN 1798-6648. In Finnish.

Liikennevirasto (2019) GIS data on the transport network of Finland. Database: DIGIROAD. Available: https://vayla.fi/avoindata/digiroad/aineisto#.XX_IMS17HjA

Likert R (1932) A technique for the measurement of attitudes. Archives of Psychology 140: 1–55.

Lindborg R & Eriksson O (2004) Historical landscape connectivity affects present plant species diversity. Ecology 85: 1840–1845.

Lindborg R, Bengtsson J, Berg Å, Cousins SAO, Eriksson O, Gustafsson T, Hasund KP, Lenoir L, Pihlgren A, Sjödin E, Stenseke M (2008) A landscape perspective on conservation of semi-natural grasslands. Agriculture, Ecosystems and Environment 125: 213–222.

Lindemann-Matthies P, Junge X, Matthies D (2010) The influence of plant diversity on people's perception and aesthetic appreciation of grassland vegetation. Biological Conservation 143: 195–202.

Liu J, Dietz T, Carpenter SR, Alberti M, Folke C, Moran E, Pell AN, Deadman P, Kratz T, Lubchenko J, Ostrom E, Ouyang Z, Provencher W, Redman CL, Schneider SH, Taylor WW (2007) Complexity of coupled human and natural systems. Science 317: 1513–1516.

Lounais-Suomen ympäristökeskus (2008) Perinnemaisemat -open access dataset on the location and area of extant traditional rural biotopes surveyed in 1992-1997. In Finnish. Available: http://kartat.lounaispaikka.fi/ms6/perinnemaisemat

Loydi A, Eckstein RL, Otte A, Donath TW (2013) Effects of litter on seedling establishment in natural and semi-natural grasslands: a meta-analysis. Journal of Ecology 101: 454–464.

Lucey A, Barton S (2011) Influencing Public Perception of Sustainable Roadside Vegetation Management Strategies. Journal of Environmental Horticulture 29: 119–124.

Luken JO, Hinton AC, Baker DG (1992) Response of Woody Plant Communities in Power-Line Corridors to Frequent Anthropogenic Disturbance. Ecological Applications 2: 356–362.

Lundholm JT, Richardson PJ (2010) Habitat analogues for reconciliation ecology in urban and industrial environments. Journal of Applied Ecology 47: 966–975.

Luoto M, Rekolainen S, Aakkula J, Pykälä J (2003) Loss of plant species richness and habitat connectivity in grasslands associated with agricultural change in Finland. Ambio 32: 447–452.

MacArthur R, Wilson EO (1967) The theory of island biogeography. Princeton University Press, Princeton.

Madre F, Vergnes A, Machon N, Clergeau (2013) a comparison of 3 types of green roof as habitats for arthropods. Ecological Engineering 57: 109–117.

Mahosenho T, Pirinen T (1999) Establishing meadow vegetation on road verges. Study results and literature review. Tielaitoksen selvityksiä 12/1999. Tiehallinto, Helsinki. In Finnish.

Manfredo MJ, Bruskotter JT, Teel TL, Fulton D, Schwartz SH, Arlinghaus R, Oishi S, Uskul AK, Redford K, Kitayama S, Sullivan L (2016) Why social values cannot be changed for the sake of conservation. Conservation Biology 31: 772–780.

Milesi C, Running SW, Elvidge CD, Dietz JB, Tuttle BT, Nemani RR (2005) Mapping and modeling the biogeochemical cycling of turf grasses in the United States. Environmental Management 36: 426–438.

Ministry of Agriculture and Forestry (eds. Niemivuo-Lahti J) (2012) Finland's National Strategy on Invasive Alien Species. Juvenes Print. In Finnish.

Moilanen A, Nieminen M (2002) Simple connectivity measures in spatial ecology. Ecology 83: 1131–1145.

Monni S, Lankinen A (1995) Sähkön tuotannon ja siirron biodiversiteettivaikutusten arviointimahdollisuudet. Helsingin yliopiston kasvitieteen julkaisuja 21. Helsingin yliopiston Ekologian ja systematiikan laitos. Helsinki. In Finnish.

Moran PAP (1950) Notes on continuous stochastic phenomena. Biometrika 37: 17–23.

Morón D, Skórka P, Lenda M, Rożej-Pabijan E, Wantuch M, Kajzer-Bonk J, Celary W, Mielczarek E, Tryjanowski P (2014) Railway Embankments as New Habitat for Pollinators in an Agricultural Landscape. PLoS ONE 9(7): e101297.

Morse NB, Pellissier PA, Cianciola EN, Brereton RL, Sullivan MM, Shonka NK, Wheeler TB, McDowell WH (2014) Novel ecosystems in the Anthropocene: a revision of the novel ecosystem concept for pragmatic applications. Ecology and Society 19: 12.

Mossberg B, Stenberg L (transl. Vuokko S, Väre H) (2003) Suuri Pohjolan Kasvio. 2nd edition. Tammi. Helsinki. In Finnish.

Myllymäki T, Nupponen K, Nieminen M (2019) Roadside biodiversity pilot project in southwestern Finland. Publications of the Finnish Transport Infrastructure Agency 1/2019. In Finnish.

Nassauer JI (1995) Messy ecosystems, orderly frames. Landscape Journal 14: 161–169.

Nassauer JI, Wang Z, Dayrell E (2009) What will the neighbors think? Cultural norms and ecological design. Landscape and Urban Planning 92: 282–292.

National Archives of Finland (2019) Senaatin kartasto, Maanmittaushallituksen historiallinen kartta-arkisto. In Finnish. Available: http://digi.narc.fi/digi/dosearch.ka?sartun=137171.KA.

Nuotio AK (eds.) (2007) Viheralueiden hoitoluokitus. Viherympäristöliitto ry julkaisu 36. In Finnish.

Noordijk J, Delille K, Schaffers AP, Sýkora KV (2009) Optimizing grassland management for flower-visiting insects in roadside verges. Biological Conservation 142: 2097–2103.

Oldén A, Raatikainen KJ, Tervonen K, Halme P (2016) Grazing and soil pH are biodiversity drivers of vascular plants and bryophytes in boreal wood-pastures. Agriculture, Ecosystems & Environment 222: 171–184.

O'Sullivan OS, Holt AR, Warren PH, Evans KL (2017) Optimizing UK urban road verge contributions to biodiversity and ecosystem services with cost-effective management. Journal of environmental management 191: 162–171.

Parr TW, Way JM (1988) Management of roadside vegetation: the long-term effects of cutting. Journal of applied ecology 25: 1073–1087.

Pearson K (1895) Notes on regression and inheritance in the case of two parents. Proceedings of the Royal Society of London 58: 240–242.

Pitkänen M, Kuussaari M, Pöyry J (2001) Butterflies. In: Pitkänen M, Tiainen J (eds) Biodiversity of agricultural landscapes in Finland. BirdLife Finland Conservation Series No. 3. Yliopistopaino. Helsinki.

Pollard E, Yates T (1993) Monitoring butterflies for ecology and conservation. Chapman and Hall. London.

Prins HHT (1998) Origins and development of grassland communities in northwestern Europe. Grazing and conservation management. Springer, Dordrecht.

Pykälä J (2001) Maintaining biodiversity through traditional animal husbandry. The Finnish Environment 495: 1–205. In Finnish.

Pykälä J (2005) Cattle grazing increases plant species richness of most species trait groups in mesic semi-natural grasslands. Plant Ecology 175: 217–226.

Pykälä J, Luoto M, Heikkinen RK, Kontula T (2005) Plant species richness and persistence of rare plants in abandoned semi-natural grasslands in northern Europe. Basic and Applied Ecology 6: 25–33.

Pärtel M, Bruun HH, Sammul M (2005) Biodiversity in temperate European grasslands: origin and conservation. Grassland Science in Europe 10: 1–14.

Pöyry J, Paukkunen J, Heliölä J, Kuussaari M (2009) Relative contributions of local and regional factors to species richness and total density of butterflies and moths in semi-natural grasslands. Oecologia 160: 577–587.

QGIS Development Team (2019) QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org.

Raatikainen KJ, Barron ES (2017) Current agri-environmental policies dismiss varied perceptions and discourses on management of traditional rural biotopes. Land Use Policy 69: 564–576.

Raymond C, Brown G (2007) A method for assessing protected area allocations using a typology of landscape values. Journal of Environmental Planning and Management 49: 797–812.

Raymond C, Bryan BA, MacDonald DH, Cast A, Strathearn S, Grandgirard A, Kalivas T (2009) Mapping community values for natural capital and ecosystem services. Ecological Economics 68: 1301–1315.

Rusterholz HP, Wirz D, Baur B (2012) Garden waste deposits as a source for non-native plants in mixed deciduous forests. Applied Vegetation Science 15: 329–337.

Saar L, Takkis K, Pärtel M, Helm A (2012) Which plant traits predict species loss in calcareous grasslands with extinction debt? Diversity and Distributions 18: 808–817.

Schaich H, Bieling C, Plieninger T (2010) Linking Ecosystem Services with Cultural Landscape Research. GAIA 19: 269–277.

Schaffers AP, Vesseur MC, Sykora KV (1998) Effects of delayed hay removal on the nutrient balance of roadside plant communities. Journal of Applied Ecology 35: 349–364.

Schultz PW (2011) Conservation means behavior. Conservation Biology 25: 1080–1083.

Schwartz SH, Bilsky W (1987) Toward a universal psychological structure of human values. Journal of Personality and Social Psychology 53: 550–562.

Skrindo AB, Pedersen PA (2004) Natural revegetation of indigeneous roadside vegetation by propagules from topsoil. Urban Forestry & Urban Greening 3: 29–37.

Soini K, Pouta E, Salmiovirta M, Uusitalo M, Kivinen T (2011) Local residents' perceptions of energy landscape: the case of transmission lines. Land Use Policy 28: 294–305.

Southon GE, Jorgensen A, Dunnett N, Hoyle H, Evans KL (2017) Biodiverse perennial meadows have aesthetic value and increase residents' perception of site quality in urban green-space. Landscape and Urban Planning 158: 105–118.

Steg L, Vleg C (2009) Encouraging pro-environmental behaviour: An integrative review and research agenda. Journal of Environmental Psychology 29: 309–317.

Suomenmaan virallinen tilasto (1869) III Aineita Suomen maanviljelystilastoon. Tilastollinen virasto. Helsinki. In Finnish.

Svenning JC (2002) A review of natural vegetation openness in north-western Europe. Biological Conservation 104: 133–148.

Szabó P (2010) Why history matters in ecology: An interdisciplinary perspective. Environmental Conservation 37: 380–387.

Talvi T, Talvi T (2012) Semi-natural communities. Preservation and management. Ministry of Agriculture. Viidumäe – Tallinn.

Tansley AG (1935) The use and abuse of vegetational concepts and terms. Ecology 16: 284–307.

Thompson K, Hodgson JG, Smith RM, Warren PH, Gaston KJ (2004) Urban domestic gardens (III): Composition and diversity of lawn floras. Journal of Vegetation Science 15: 373–378.

Tikka PM, Koski PS, Kivelä RA, Kuitunen MT (2000) Can grassland plant communities be preserved on road and railway verges? Applied Vegetation Science 3: 25–32.

Tikka PM, Högmander H, Koski PS (2001) Road and railway verges serve as dispersal corridors for grassland plants. Landscape Ecology 16: 659–666.
Tonteri T (2001) Ruohot. In: Reinikainen A, Mäkipää R, Vanha-Majamaa I, Hotanen J (eds.) (2001) Kasvit muuttuvassa metsäluonnossa. Tammi. Helsinki.
Tropek R, Kadlec T, Karesova P, Spitzer L, Kocarek P, Malenovsky I, Banar P, Tuf IH, Hejda M, Konvicka M (2010) Spontaneous succession in limestone quarries as an effective restoration tool for endangered arthropods and plants. Journal of Applied Ecology 47: 139–147.
Tyrväinen L, Mäkinen K, Schipperijn J (2007) Tools for mapping social values of urban woodlands and other green areas. Landscape and Urban Planning 79: 5–19.
Yee TW, Mitchell ND (1991) Generalized additive models in plant ecology. Journal of Vegetation Science 2: 587–602.
Vainio M, Kekäläinen H, Alanen A, Pykälä J (2001) Traditional rural biotopes in Finland. Final report of the nationwide inventory. The Finnish Environment 527 1–163. In Finnish.
Valtonen A, Saarinen K, Jantunen J (2006) Effect of different mowing regimes on butterflies and diurnal moths on road verges. Animal Biodiversity and Conservation 29: 133–148.
Valtonen A, Saarinen K, Jantunen J (2007) Intersection reservations as habitats for meadow butterflies and diurnal moths: Guidelines for planning and management. Landscape and Urban Planning 79: 201–209.
Vanha-Majamaa I, Korpela L, Reinikainen A (2001) Heinäkasvit. In: Reinikainen A, Mäkipää R, Vanha-Majamaa I, Hotanen J (eds.) (2001) Kasvit muuttuvassa metsäluonnossa. Tammi. Helsinki.
Vanhanen S (2019) Pre-historic cultivation and plant gathering in Finland. An archaeobotanical study. Academic dissertation, 91 p. Department of Cultures, University of Helsinki.
Verhoeven KJF, Simonsen KL, McIntyre LM (2005) Implementing false discovery rate control: increasing your power. Oikos 108: 643–647.
Vesanto T (2007) Turun viheralueiden sosiaalisten arvojen kartoitus. Turun kaupunki, Ympäristö- ja kaavoitusvirasto. Turku. In Finnish.
Wagner DL, Metzler KJ, Leicht-Young SA, Motzkin G (2014) Vegetation composition along a New England transmission line corridor and its implications for other trophic levels. Forest Ecology and Management 327: 231–239.
Waide RB, Willig MR, Steiner CF, Mittelbach G, Gough L, Dodson SI, Juday GP, Parmenter R (1999) The relationship between productivity and species richness. Annual Review of Ecology and Systematics 30: 257–300.
Weber F, Kowarik I, Säumel I (2014) A walk on the wild side: Perceptions of roadside vegetation beyond trees. Urban Forestry & Urban Greening 13: 205–212.
Wheeler MM, Neill C, Groffman PM, Avolio M, Bettez N, Cavender-Bares J, Chowdury RR, Darling L, Grove JM, Hall SJ, Heffernan JB, Hobbie SE, Larson KL, Morse JL, Nelson KC, Ogden LA, O'Neil-Dunne J, Pataki DE, Polsky C, Steele M, Trammell TLE (2017) Continental-scale homogenization of residential lawn plant communities. Landscape and Urban Planning 165: 54–63.
Wilcoxon F (1945) Individual comparisons by ranking methods. Biometrics Bulletin 1: 80–83.
Zlinszky A, Schroiff A, Kania A, Deák B, Mücke W, Vári Á, Székely B, Pfeifer N (2014) Categorizing grassland vegetation with full-waveform airborne laser scanning: A feasibility study for detecting Natura 2000 habitat types. Remote Sensing 6: 8056–8087.
Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed Effects Models and Extensions in Ecology with R. Springer. New York.
Öckinger E, Eriksson AK, Smith HG (2006) Effects of grassland abandonment, restoration and management on butterflies and vascular plants. Biological Conservation 133: 291–300.
Öckinger E, Smith HG (2006) Landscape composition and habitat area affects butterfly species richness in semi-natural grasslands. Oecologia 149: 526–534.
Öckinger E, Dannestam Å, Smith HG (2009) The importance of fragmentation and habitat quality of urban grasslands for butterfly diversity. Landscape and Urban Planning 93: 31–37.

UNIVERSITY OF TURKU

ISBN 978-951-29-7943-1 (PRINT)
ISBN 978-951-29-7944-8 (PDF)
ISSN 0082-6979 (Print)
ISSN 2343-3183 (Online)

Painosalama Oy, Turku, Finland 2020