

On the deterioration and restoration of mire invertebrate communities

Norbertas Noreika

Faculty of Biological and Environmental Sciences University of Helsinki 2016



On the deterioration and restoration of mire invertebrate communities

Norbertas Noreika

Faculty of Biological and Environmental Sciences
University of Helsinki
Finland

ACADEMIC DISSERTATION

To be presented for public examination with the permission of the Faculty of Biological and Environmental Sciences of the University of Helsinki in Auditorium 1041, Biocenter 2, Viikinkaari 5, Helsinki, on the 18th of March 2016, at 12 noon.

Supervised by: Doc. D. Johan Kotze
University of Helsinki, Finland

Thesis advisory committee: Prof. Otso Ovaskainen
University of Helsinki, Finland

Prof. Heikki Setälä
University of Helsinki, Finland

Reviewed by: Prof. Henrik G. Smith
Lund University, Sweden

Assoc. Prof. Terry A. Wheeler
McGill University, Canada

Examined by: Prof. Jonathan Sadler
University of Birmingham, UK

Custos: Prof. Veijo Kaitala
University of Helsinki, Finland

Layout and cover by: © Kristina Noreikienė

ISBN 978-951-51-1951-3 (paperback)

ISBN 978-951-51-1952-0 (PDF)

<http://ethesis.helsinki.fi>

Unigrafia, Helsinki 2016

*To my parents, Valė and Pranas,
who tolerated all the weird creatures I dragged home,
and to my wife Kristina and daughter Ūla Jorė,
who are now able to tolerate me at home.*

Contents

ABSTRACT	7
TIIVISTELMÄ.....	9
1. INTRODUCTION.....	11
1.1 Anthropogenic disturbances and biotic homogenization	11
1.2 Mires as model systems for investigating anthropogenic disturbances	12
1.3 Mire specialist and habitat generalist invertebrates.....	14
1.4 The responses of mire invertebrate species and communities to anthropogenic disturbances.....	16
1.4.1 The effects of landscape-level variables on the persistence and restoration of mire invertebrate communities	18
1.4.2 The effects of local variables on mire invertebrates.....	21
1.4.3 The effects of local vs. regional variables on mire invertebrates	25
1.4.4 Urbanization.....	25
1.4.5 The drainage of mires.....	26
1.4.6 The effects of restoration on mire invertebrates.....	27
2. AIMS OF THE THESIS	30
3. MATERIAL AND METHODS	32
3.1. Study sites	32
3.2. Study design.....	33
3.3. Invertebrate sampling	34
3.4. Environmental data collection	35
3.5. Statistical analyses.....	36
4. MAIN RESULTS AND DISCUSSION	37
4.1. Urbanization and the effects of mire size on mire invertebrates.....	37
4.2. The effects of drainage on mire invertebrates.....	39
4.3. The effects of restoration on mire invertebrates	40
4.4. Key local (site level) environmental variables for mire specialist species and communities	41
5. CONCLUSIONS AND FUTURE RESEARCH	43
ACKNOWLEDGEMENTS	46
REFERENCES.....	48

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

Chapter I: **Noreika N.**, Pajunen T., Kotze D.J., 2015. Urban mires as hotspots of epigaeic arthropod diversity. *Biodiversity and Conservation* 24:2991-3007.

Chapter II: **Noreika N.**, Kotiaho J.S., Penttinen J., Punttila P., Vuori A., Pajunen T., Autio O., Loukola O.J., Kotze D.J., 2015. Rapid recovery of invertebrate communities after ecological restoration of boreal mires. *Restoration Ecology* 23:566-579.

Chapter III: Punttila P., Autio O., Kotiaho J.S., Kotze D.J., Loukola O.J., **Noreika N.**, Vuori A., Vepsäläinen K., 2016. The effects of drainage and restoration of pine mires on habitat structure, vegetation and ants. *Silva Fennica* 50:1462.

Chapter IV: **Noreika N.**, Kotze D.J., Loukola O.J., Sormunen N., Vuori A., Päivinen J., Penttinen J., Punttila P., Kotiaho J.S., 2016. Specialist butterflies benefit most from the ecological restoration of mires. *Biological Conservation* 196:103-114.

© Springer (Chapter I)

© John Wiley and Sons (Chapter II)

© Silva Fennica (Chapter III)

© Elsevier Ltd (Chapter IV)

© Norbertas Noreika (Summary)

Contributions of authors to Chapters of this thesis:

	I	II	III	IV
Original idea	NN	JSK, OA, OJL	JSK, PP	JSK, JPv
Design	NN, DJK	JSK	JSK	JSK
Data collection, data compilation, species identification	NN, DJK, TP	JP, AV, OJL, OA, TP, PP, NN	JP, AV, OJL, OA, PP, NN	JP, AV, OJL, NS, NN
Data analyses	NN, DJK	NN, DJK	NN, DJK, PP	NN, DJK, JSK
Manuscript preparation	NN, DJK	NN, DJK, JSK, PP	PP, KV, DJK, NN	NN, DJK, JSK, PP

NN = Norbertas Noreika, DJK = D. Johan Kotze, JSK = Janne S. Kotiaho, PP = Pekka Punttila, TP = Timo Pajunen, JP = Jouni Penttinen, OJL = Olli J. Loukola, AV = Anna Vuori, OA = Olli Autio, KV = Kari Vepsäläinen, NS = Niina Sormunen, JPv = Jussi Päivinen

Chapter I: NN conceived the idea of the study and together with DJK designed the study. NN collected invertebrates together with DJK. NN identified carabid beetles and evaluated regional environmental variables by using QGIS. NN analyzed the data in dialogue with DJK. NN was in charge of writing and submitting the paper.

Chapter II: NN compiled (organized) the data, identified carabid beetles and analyzed the data in dialogue with DJK. NN was in charge of writing and submitting the paper.

Chapter III: NN compiled (organized) part of the data and performed part of the analysis (individual ant species responses to treatments). NN was in charge of writing certain parts of the paper (results concerning individual ant species responses to treatments) and took part in writing of the paper.

Chapter IV: NN compiled (organized) and analyzed the data, in dialogue with DJK and JSK. NN was in charge of writing and submitting the paper.

ABSTRACT

Negative anthropogenic disturbances (e.g., drainage and urbanization) are causing biotic homogenization through the replacement of specialist species with generalists. The identification and conservation of biodiversity hotspots within degraded (e.g., highly urbanized) landscapes, and ecological restoration (i.e., positive anthropogenic disturbance) have the potential to be important tools to counteract these negative effects. Mires are suitable targets for the investigation of these homogenization-reducing activities since they host many mire specialist species of, e.g. invertebrates.

The main aim of this PhD thesis was to investigate the effects of negative anthropogenic disturbances [urbanization (Chapter I) and drainage for forestry (Chapters II-IV)] on the invertebrate communities of boreal mires and how effective efforts are to reverse these negative effects through ecological restoration [i.e. positive anthropogenic disturbance (Chapters II-IV)]. In addition, the purpose was to determine which environmental variables are key in supporting mire specialist invertebrate species and communities. Therefore, this thesis started by reviewing current knowledge on the responses of mire invertebrate species and communities to anthropogenic disturbances. The effects of urbanization were studied on spiders and carabid beetles (Chapter I), while the effects of drainage for forestry and subsequent restoration were investigated on five solitary invertebrate groups (Chapter II) and social insects, i.e. ants (Chapter III). Finally, a powerful Before-After Control-Impact (BACI) design was used to reveal the effects of drainage and restoration on butterflies (Chapter IV).

Generally, both high levels of urbanization (Chapter I) and mire drainage for forestry (Chapters II-IV) had negative effects on mire specialist species (lower abundances) and invertebrate communities (homogenized and very different in structure from pristine mire communities). However, these detrimental effects can be reduced or even reversed through appropriate urban mire conservation and ecological restoration.

Local habitat conditions were shown to be particularly important for the survival of specialist invertebrate species in urban mires (Chapter I) and for the successful recovery of restored mire invertebrates (Chapters II-IV). Individual mire specialist species responded negatively to environmental variables associated with deteriorated (i.e. drained or highly urbanized) mire conditions [number of high (> 3m) trees for carabid beetles, crane flies, micromoths (Chapter II), ants (Chapter III) and butterflies (Chapter IV)] and positively to pristine mire-associated variables [*Sphagnum* cover for carabid beetles and spiders (Chapters I-II), crane flies (Chapter II) and suggestively for ants (Chapter III); larval food plant cover and

number of lower (1.5 - 3m) trees for butterflies (Chapter IV)]. The more specialized the mire species were, the more negatively they were affected by deteriorated-mire-associated variables and the more positively they responded to pristine-mire-associated variables.

I conclude that the restoration actions taken (removing tall trees but leaving smaller trees, and raising the water table level) are appropriate in creating suitable habitat conditions for mire invertebrates, as both individual specialist species and communities showed positive responses already 1-3 years since restoration (Chapters II-IV). Finally, the appropriate restoration actions in well-prioritized locations as well as urban mire conservation should reverse the trend of biotic homogenization.

TIIVISTELMÄ

Ihmistoiminnan ja ennallistamisen vaikutukset soiden selkärangatonlajistoon

Biologinen homogenisaatio eli samankaltaistuminen aiheuttaa usein erikoistuneiden spesialistilajien korvautumisen yleislajeilla, generalisteilla. Homogenisaatio on seurausta haitallisesta ihmistoiminnasta, kuten elinympäristöjen kuivattamisesta tai urbanisoitumisesta. Monimuotoisimpien elinympäristöjen tunnistaminen, suojeleminen ja ennallistaminen ovat keinoja torjua näitä haitallisia muutoksia. Soiden erikoistunut selkärangatonlajisto tarjoaa mahdollisuuden tutkia kuinka lajiston yksipuolistumista voitaisiin vähentää.

Tämän tutkimuksen tarkoituksena oli selvittää miten ympäristölle haitallinen ihmistoiminta kuten urbanisaatio (Artikkeli I) ja metsänojitus (Artikkelit II-IV) vaikuttavat boreaalisen vyöhykkeen soiden selkärangatonlajiston rakenteeseen ja kuinka havaittuja negatiivisia muutoksia lajistossa on onnistuttu torjumaan tai vähentämään aktiivisilla ennallistamistoimilla. Tutkimuksessa pyrittiin myös tunnistamaan, mitkä ympäristötekijät ovat soihin erikoistuneen lajiston kannalta keskeisimpiä ja miten suolajisto reagoi haitalliseen ihmistoimintaan.

Kaupungistumisen vaikutuksia selkärangatonryhmiin tutkittiin hämähäkeillä ja maakiitäjäisillä (Artikkeli I). Metsänojituksen ja ennallistamisen vaikutuksia lajiyhteisöihin tutkittiin viidellä eri selkärangatonryhmällä (Artikkeli II) ja sosiaalisilla hyönteisillä (muurahaisilla) (Artikkeli III). Artikkelissa neljä metsänojituksen ja ennallistamisen vaikutuksia perhosten lajistorakenteeseen päästiin tutkimaan ennen ennallistamistoimia ja sen jälkeen.

Sekä kaupungistuminen (Artikkeli I) että metsänojitus (Artikkelit II-IV) johtivat suoympäristöön erikoistuneiden selkärangattomien taantumiseen ja lajiston yksipuolistumiseen ja muuttumiseen hyvin erilaiseksi kuin luonnontilaisilla soilla. Näitä kielteisiä muutoksia on kuitenkin mahdollista lieventää tai jopa kokonaan välttää soiden suojeleminen ja ennallistamisella.

Paikalliselin ympäristön piirteillä on erittäin suuri merkitys erikoistuneen selkärangatonlajiston menestykseen sekä urbaaneilla alueilla olevilla soilla (Artikkeli I) että ojitetuilla ja ennallistetuilla soilla (Artikkelit II-IV). Suoympäristöön erikoistunut lajisto taantui ihmistoiminnan lisääntyessä soilla. Ympäristömuuttujista yli 3 metristen puiden runsastumisen havaittiin vähentävän maakiitäjäisten, vaaksiaisten, mikroperhosten, muurahaisten ja perhosten suolajistoa. Luonnontilaisilla soilla runsaana esiintyvän

rahkasammalen (*Sphagnum*) peittävyys puolestaan korreloi positiivisesti suolajiston runsauden kanssa, etenkin maakiitäjäisillä ja hämähäkeillä (Artikkeli I), vaaksiaisilla (Artikkeli II) ja viitteellisesti myös muurahaisilla (Artikkeli III). Matala puusto (1,5-3 m) ja toukkien ravintokasvien peittävyys olivat soiden perhoslajistolle (Artikkeli IV) keskeisimmät ympäristömuuttajat. Mitä erikoistuneempi soiden selkärangatonlajisto oli, sitä enemmän se oli riippuvainen luonnontilaisten soiden rakennepiirteistä ja sitä herkemmin ne reagoivat haitalliseen ihmistoimintaan.

Soiden ennallistamistoimet (korkeiden puiden poisto, pienten puiden jättäminen ja veden pinnan nosto) osoittautuivat toimiviksi keinoksi palauttaa ja ylläpitää soiden rakennepiirteitä ja luoda sopivaa elinympäristöä vaateliaille suolajeille. Jo 1-3 vuoden kuluttua ennallistamisesta oli alueen selkärangatonlajisto kehittynyt siten, että osa erikoistuneista ja vaateliaista suolajeista oli runsastunut ja lajistorakenne oli kehittymässä kohti luonnontilaisten soiden lajiston rakennetta. Soiden ennallistaminen osoittautui toimivaksi keinoksi hillitä selkärangatonlajiston homogenisaatiota. Ennallistamisen kohdentaminen arvokkaisiin suoluontokohteisiin on hyödyllistä, mutta hyviä tuloksia voi saada aikaan myös pienialaisilla soilla kaupungeissa.

1. INTRODUCTION

1.1 Anthropogenic disturbances and biotic homogenization

The Earth's 6th mass extinction is underway and the driving force of it is human activities (Ceballos et al. 2015), which can intuitively be termed anthropogenic disturbances. In general, disturbance is a change in the structure of an object (individual, community or landscape) induced by a factor that is external to that object (Pickett et al. 1989). Thus, any anthropogenic intervention to a community or the landscape that will change its structure is termed an anthropogenic disturbance. The structure (e.g., species composition or abundance) can change towards undesirable (losses of focal specialized biota, see e.g., Turner 1996) or desirable (gains of focal specialized biota, see e.g., Bowles & Jones 2012) directions. Thus, anthropogenic disturbances can be grouped into negative and positive ones, respectively. Furthermore, anthropogenic disturbances are acting at various hierarchical levels of biological organization - from individuals to communities and ecosystems (Pickett et al. 1989) and at various spatial scales - from local to landscape and regional. As such, negative disturbances acting at individual and community levels (i.e., the drainage of wetlands, peat extraction from mires, tree cutting in forests, urbanization and others) might also cause losses of focal biota at the landscape level. In addition, the effects of some disturbances can mainly be evaluated at the landscape or higher levels, e.g. the eradication (loss and fragmentation) of the area of some habitats (e.g., total mire eradication through peat mining), or land conversion to agricultural and urbanized areas.

In general, negative anthropogenic disturbances to habitats dominated by unique specialist species are causing biotic homogenization through the loss of specialist species at landscape and regional levels (Clavel et al. 2011). This biotic homogenization has three distinct forms: genetic, taxonomic and functional (Olden et al. 2004), all of which increase with increasing disturbance, such as drainage and urbanization (see Fig. 1). On the contrary, positive anthropogenic disturbances, like habitat restoration, could slow down or even reverse biotic homogenization (Bullock et al. 2011, Wortley et al. 2013) (Fig. 1).

1.2 Mires as model systems for investigating anthropogenic disturbances

Mires hosts many unique specialist species (Desrochers & Duinen 2006, Spitzer & Danks 2006). Mires are defined as active (i.e. peat-forming) peatlands (Joosten & Clarke 2002), 87% of which are found in boreal regions (Vitt 2006). Generally, mires are formed under cold and wet climate, where precipitation exceeds evapotranspiration and thus anoxic, water-logged

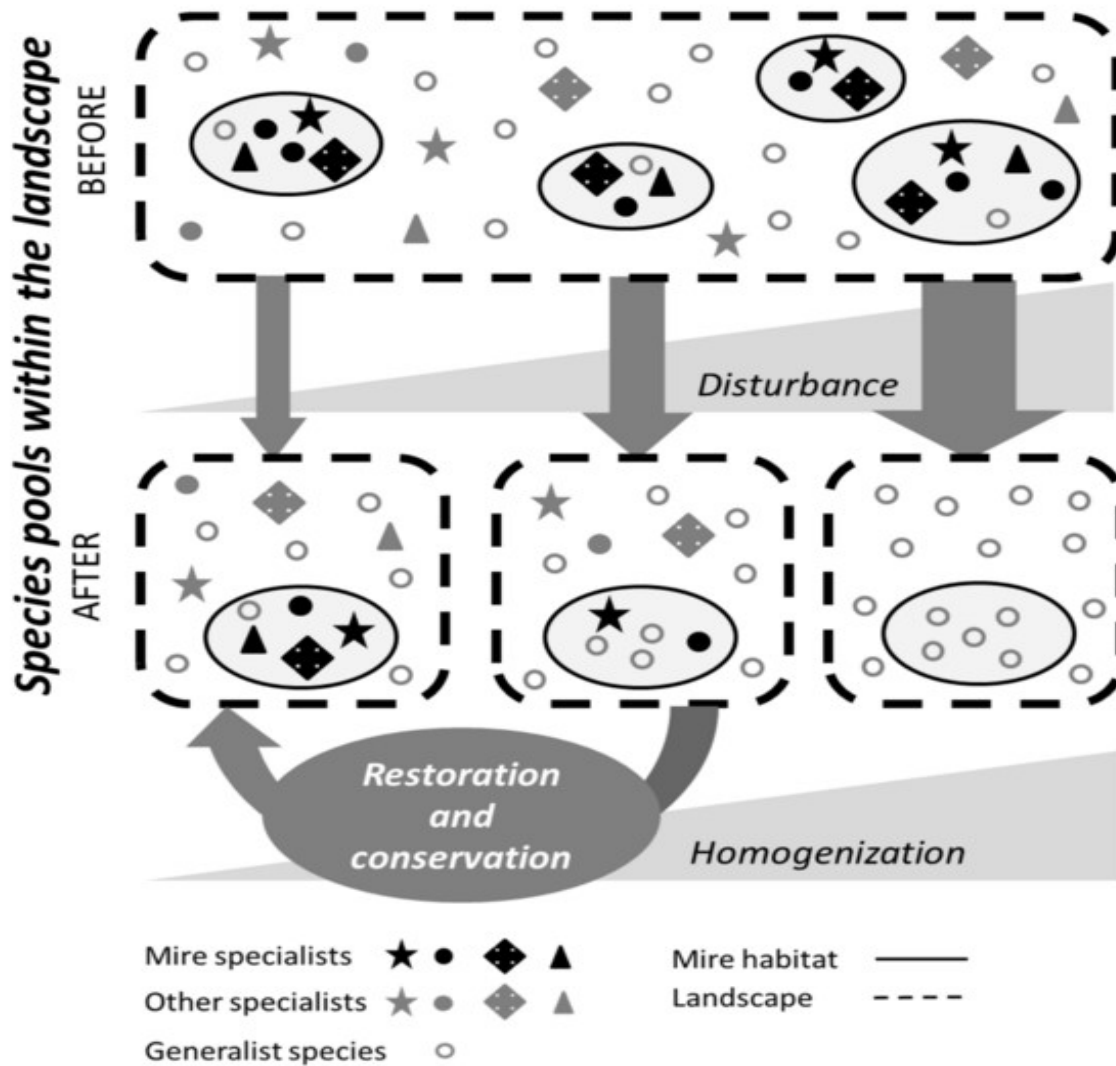


Fig. 1. Schematic representation of the relationship between a negative disturbance gradient (e.g., increasing drainage or level of urbanization) and the gradient of homogenization (taxonomic, genetic and functional) on mire invertebrate communities within the landscape. The different symbols for mire and other specialists represent different species. The concave grey arrow indicates the potentially reversed negative, or positive, disturbance effects and reduced homogenization of the landscape through restoration and conservation of the remaining mire patches (adapted from Clavel et al. 2010).

conditions inhibit the decay of organic matter, which is accumulated as peat (Rydin & Jeglum 2013). Based on the pH and availability of nutrients, mires can be grouped into (gradient from lowest pH and poorest in nutrients to highest pH and richest in nutrients): bogs, poor fens and rich fens (Rydin & Jeglum 2013). Bogs obtain all of their nutrients and water from precipitation (ombrotrophic), while fens also acquire nutrients and water from surface or ground waters (minerotrophic). Despite these differences, bogs and poor fens constitute similar environmental conditions (*Sphagnum*-dominated in the Northern hemisphere, low pH, poor in nutrients), which enables a direct comparison of ecological changes in these habitats. Wet heathlands are as well similar to bogs and poor fens, as they are also wet, nutrient-poor and acidic habitats (Thompson et al. 1995, Price 2003) and there are a number of plant and invertebrate species that these habitats share [to name a few, e.g., in Europe: plants *Calluna vulgaris*, *Empetrum nigrum*, *Sphagnum* spp. and mosses among others (Ratcliffe 1959), carabid beetles *Agonum ericeti* and *Pterostichus rhaeticus* (Vries & Boer 1990, Holmes et al. 1993), butterflies, e.g., *Callophrys augustinus* in North America (Swengel & Swengel 2010b), and *Boloria aquilonaris* and *B.eunomia* in Europe (see e.g. Cristofoli & Mahy 2010 and Lensu et al. 2011)]. In this review, I mainly concentrated on bogs and poor fens of boreal and temperate regions in both the Northern and Southern hemispheres, and whenever relevant I mentioned findings from wet peaty heathlands.

Mires are a good model system for investigating anthropogenic disturbance effects in the context of biotic homogenization because, i) they host many unique specialist species of, e.g. plants (Rydin & Jeglum 2013) and invertebrates (Desrochers & Duinen 2006, Spitzer & Danks 2006), ii) they are naturally discrete habitats (Desrochers & Duinen 2006), iii) they are environmentally sensitive habitats, iv) they are disturbed by humans at both local (e.g. drainage for forestry, small-scale peat cutting) and landscape (total loss of habitat through peat mining, increased isolation through urbanization) levels, and v) relatively recently, ecological restoration of boreal mires were initiated, which potentially may serve as a positive anthropogenic disturbance and thus should reverse biotic homogenization.

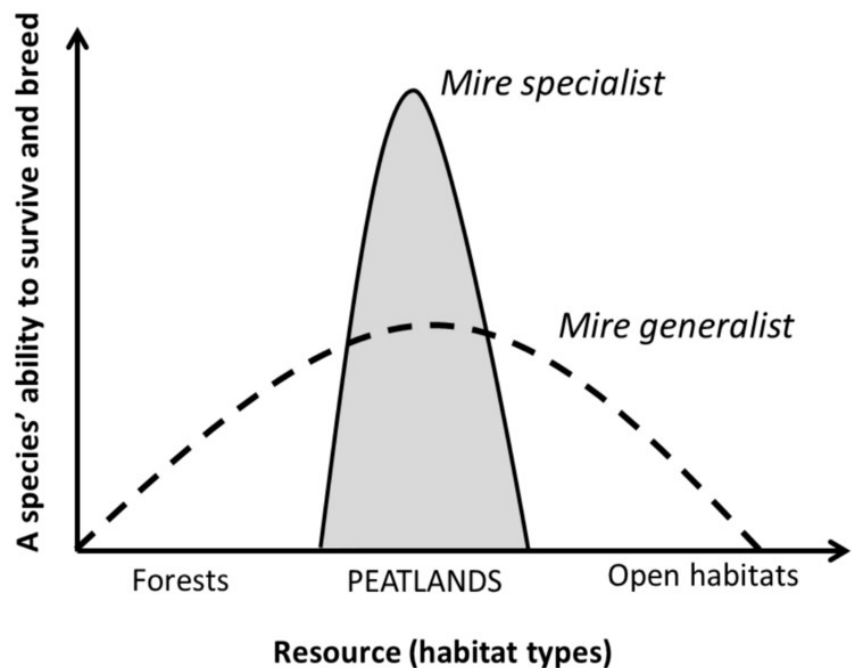
In addition, as vegetation changes in mires due to anthropogenic disturbances are well investigated (e.g., Gunnarsson et al. 2000, 2002, Haapalehto et al. 2011), the responses of specialized mire invertebrate taxa to anthropogenic disturbances seem to be a priority for investigation. Finally, since the mire surface is above the water table level due to peat accumulation, many of the invertebrates found in mires are of terrestrial origin (Batzer & Wissinger 1996). Therefore, the scope of this thesis is on how anthropogenic disturbances

(negative and positive) affect terrestrial and semi-terrestrial (where only larvae develop in the water) mire invertebrates.

1.3 Mire specialist and habitat generalist invertebrates

The population of a particular species exists within the n -dimensional hypervolume of its realized ecological niche (Hutchinson 1957). Depending on niche breadth, species might be classified as generalists (broad niche) and specialists (narrow niche) (Futuyma & Moreno 1988). However, there are two distinct classical concepts of biological specialization: Eltonian and Grinnellian (Devictor et al. 2010). Eltonian specialization defines the function that species performs in the environment, while Grinnellian specialization considers the response of a species to environmental variables (resources). From the perspective of a specific habitat type, like mires, the Grinnellian concept of specialization is more relevant as habitat type itself can be seen as a resource, which defines the level of species specialization. Mire specialists, as such, can be defined as those species that are able to survive and breed efficiently in a limited amount of habitat types, namely peatlands, available within the landscape (Fig. 2). On the contrary, habitat generalists are species that can utilize more habitat types but less efficiently, although they also may have some preferred types of habitats where they are particularly successful and thus might be named depending on the preferred habitat type, e.g. mire generalist if they prefer mires (Fig. 2).

Fig. 2. Mire specialist and generalist species definition. The specialization of a given species can be described by the variance in its ability to survive and breed (y-axis) within the range of habitats available in the landscape (x-axis). The dashed line describes the performance of a mire generalist species and the solid line of a mire specialist species (adapted from Devictor et al. 2010).



The degree of specialization might vary among different mire specialist invertebrate species, as some species are restricted to bogs (tyrphobiontic species), while others can be found in several types of mires and similar habitats (tyrphophilous species) (Spitzer & Danks 2006). For instance, some crane fly species are found in a broad range of mires, while others occur only in ombrotrophic bogs (Salmela & Ilmonen 2005, Autio et al. 2013). Alternatively, habitat generalist invertebrates (tyrphoneutral from the perspective of mire habitats; Spitzer & Danks 2006) are found within much broader ranges of habitat types available in the landscape: peatlands, forests and/or open habitats (wet and dry meadows, arable fields, etc.). Nevertheless, pristine mires are inhabited by a large number of specialist invertebrate species because these habitats are exceptional in their conditions (harsh to other species than mire specialists) compared to the surrounding landscape (poor in nutrients, acidic, wet, specific hydrological and temperature regimes; Rydin & Jeglum 2013). Furthermore, mires are very old and stable habitats as, e.g. a comparison between fossil and modern beetle populations indicated that faunal characteristics, including rare endemics, of investigated mires in England became established during the early phases of peat development, ca. 5000 years ago (Whitehouse et al. 2008). This means that local adaptations in mires should favour individuals of higher levels of specialization (Levins 1968). Indeed, local adaptations are documented for mire specialist invertebrate species, e.g. for butterflies (Turlure et al. 2013). Finally, invertebrate species associated with mires become even more restricted to mire habitats (i.e., become more specialized) with decreasing latitude in the Northern hemisphere (Desrochers & Duinen 2006, Spitzer & Danks 2006). Thus, mires serve as a refugia for an increasing number of species with a decrease in latitude and the reason of this is most likely environmental conditions provided by the mires.

However, we have limited knowledge on key environmental variables that create the niche of mire specialist invertebrate species, and thus are crucial for their persistence. Other essential questions include, i) what are the effects of local and landscape-level variables on mire specialist species and what are their relative importance for the persistence of these specialists, and ii) how would these environmental variables change due to anthropogenic disturbances and subsequently, what would be the responses of mire specialist species to these changes? Available knowledge on these questions are reviewed below.

1.4 The responses of mire invertebrate species and communities to anthropogenic disturbances

Mires hosts many unique specialist species of invertebrates and this diversity was extensively summarized by Spitzer & Danks (2006) and Desrochers & Duinen (2006). However, these reviews lack information on mire invertebrates from the Southern hemisphere, although peatlands are present there (Whinam et al. 2012, Mauquoy & Bennett 2013). Furthermore, crane flies are not mentioned, which have a number of species tightly associated with mires (Salmela & Ilmonen 2005, Autio et al. 2013). Finally, a number of anthropogenic disturbances are known to affect mire ecosystems (Turetsky & Louis 2006), but these two reviews generally lack information on the anthropogenic impacts on mire terrestrial invertebrates as Desrochers & Duinen (2006) described anthropogenic disturbance effects on vertebrates and aquatic invertebrates in mires, while Spitzer & Danks (2006) only shortly mentioned conservational issues of terrestrial mire insects. This is mainly due to the low number of published research that addressed such topics at the time. On the other hand, a number of studies addressing anthropogenic impacts on terrestrial and semi-terrestrial mire invertebrates appeared during the last decade. Thus, my aim is to fill this gap and review studies on the negative and positive effects of anthropogenic disturbances on terrestrial mire invertebrates. In general, the literature survey on mire and related habitat invertebrates revealed four main directions of mire invertebrate research:

1. *Descriptive studies on terrestrial invertebrate diversity.* These include studies that describe the diversity of terrestrial mire arthropods *per se* and their distribution patterns within mires (see Spitzer & Danks 2006), and a number of subsequent publications, e.g. on butterflies (Swengel & Swengel 2010b), crane flies (Autio et al. 2013) and spiders (Kamayev 2012). These studies also focused on the biology and ecology of mire arthropod species. The most general finding from these studies is that bog invertebrate species can be grouped into four basic ecological categories, which reflect their decreasing preference for bog habitats: i) tyrphobiontic species (live only in bogs), ii) tyrphophilous species (characteristic of bogs but not restricted to them), iii) tyrphoneutral species (live in bogs but also in other habitats), and iv) tyrphoxenous species (found in bogs, but cannot live in them). For more details, see Spitzer & Danks (2006).

2. *Studies on aquatic invertebrates.* These studies cover research on the diversity of aquatic mire invertebrates as well as the effects of mire restoration and negative anthropogenic disturbances on invertebrates living in various water bodies of mires. Water bodies investigated include both natural lakes (e.g., Baars et al. 2014, Drinan et al. 2013), ponds and pools (e.g., Hannigan & Kelly-Quinn 2012) and created via restoration (e.g., Mazerolle et al. 2006) or drainage (Whatley et al. 2014a, Whatley et al. 2014b). The diversity patterns of aquatic mire insects were reviewed by Desrochers & Duinen (2006). This review also covered various negative anthropogenic activities and restoration effects on aquatic mire invertebrates and vertebrates, and referred to some terrestrial invertebrates. One of the most critical findings from this group of studies is that a rapid water table level rise due to the building of dams on a large scale for purposes of restoration causes a loss of variation in site conditions (heterogeneity) and subsequently a decline of characteristic aquatic macroinvertebrate species (Verberk et al. 2006, Verberk et al. 2010). Such negative trends were not observed for aquatic microinvertebrates (Duinen et al. 2006). Nevertheless, by increasing the water table level gradually (by e.g. filling in the ditches), the biodiversity of peat bog aquatic invertebrates could be preserved (Verberk et al. 2010). Additionally, the importance of landscape heterogeneity for the conservation of aquatic macroinvertebrate diversity in bogs was emphasized (Verberk et al. 2006).

3. *Studies on terrestrial invertebrates in mire-like habitats (wet heathlands).* A number of studies investigated anthropogenic disturbance effects on invertebrates in wet heathlands (see below). Many of these studies can be used to draw inferences on mire habitats due to their environmental similarity and the share of similar species.

4. *Studies on terrestrial mire arthropod responses to negative (drainage, peat cutting, urbanisation, fires) and positive (restoration) anthropogenic effects.* The majority of these studies appeared only during the last decade and have not been reviewed thus far.

As descriptive studies and studies on aquatic invertebrates have extensively been reviewed earlier, it is more relevant here to pay attention to anthropogenic disturbance effects on terrestrial and semi-terrestrial invertebrates in mires. Below I review the responses of terrestrial and semi-terrestrial mire invertebrate species and communities to various negative and positive (restoration) anthropogenic disturbances, as well as the effects of various environmental variables. Wherever relevant, I also mention results from studies on wet heathlands.

1.4.1 The effects of landscape-level variables on the persistence and restoration of mire invertebrate communities

Patch size and quality, and connectivity (patch isolation and species dispersal ability) within a metapopulation are crucial for the long-term persistence of populations in the landscape as the reduction of these parameters negatively affect the size and genetic diversity of populations (Hanski 1998, Wilson & Provan 2003, Drees et al. 2011a). This is especially relevant for mires, since mire size decreases and isolation increases naturally from north to south in the Northern hemisphere (Desrochers & Duinen 2006). Thus, the fragmentation of mire habitats might have additional detrimental effects on species richness and abundance. On the other hand, since mire specialist invertebrates should be, to some degree, adapted to naturally fragmented and isolated habitat, fragmentation likely may not have a great effect and perhaps other factors (e.g., habitat quality) are more important for their persistence in the landscape. Nevertheless, landscape-level variables are fundamental in influencing invertebrate colonization of restored mires (see e.g., Watts & Didham 2006b).

Mire size

Mire size decreases due to such anthropogenic activities as drainage for forestry and peat mining. Larger mires have more microhabitats (Desrochers & Duinen 2006) and may potentially support more species than smaller ones. However, it seems that this trend is more relevant for poorly dispersing taxa, but might have no influence on better dispersing ones, as they likely can move among the smaller patches within the landscape. Indeed, the numbers of heathland specialist carabid beetles appeared to be significantly associated with area in the Netherlands (Vries et al. 1996) and larger habitat area was important for the persistence of poorly-dispersing species. On the contrary, bog size had no influence on species richness or diversity of higher Diptera (Savage et al. 2011), and some mire butterfly species were abundant in small and isolated mire habitats in Wisconsin (Swengel & Swengel 2010a).

Nevertheless, the incidence and genetic diversity of individual mire specialist invertebrate species are positively related to larger habitat area. For example, incidence increased significantly with patch area for specialist butterflies *Boloria aquilonaris* and *Clossiana selene* in wet heathlands in Belgium (Cristofoli & Mahy 2010), and with patch area and closeness for the specialist butterfly *C. tullia* in mires in England (Dennis & Eales 1997). In addition, a significant positive relationship between habitat size and allelic richness was observed for the mire specialist carabid *Agonum ericeti* (Drees et al. 2011a) and the heathland

specialist carabid *Poecilus lepidus* (Drees et al. 2011b). The latter authors suggested that heathland patches of at least 50 ha in size are necessary to conserve the genetic diversity of *P. lepidus* for a period of 100 years. Similarly, Assmann & Janssen (1999) suggested that heath fragment sizes below 40 ha are likely unsuitable for the long-term survival of populations of the carabid beetle *Carabus nitens*. Thus, it seems that mire habitats of > 50 ha in size should be prioritized for conservation if the purpose is to maintain healthy populations of mire specialist species.

Mire isolation and the dispersal abilities of species

Mires become increasingly isolated due to the loss of other mires within the landscapes and regions via drainage for forestry and agriculture, as well as peat mining. Additionally, mire specialist species may become even more isolated due to the conversion of the surrounding matrix into agricultural and urbanized areas and the increasing density of roads. Species dispersal abilities are crucial for persistence in isolated mire habitats (Vries et al. 1996) as well as for the successful colonization of restored patches (see Watts & Didham 2006b). Especially, as suggested by Drees et al. (2011a), corridors cannot be used as a surrogate for continuous habitats due to highly specific water table and nutrient conditions of peat bogs. Thus, mire isolation and species dispersal abilities are important for the successful restoration of mire invertebrate communities.

Generally, mire specialist species are poor dispersers, which may even be more pronounced in a highly fragmented landscape that reduces the genetic health of populations. For example, although reported maximum dispersal distances can be quite long for some mire specialist butterflies [e.g., 13.5 km for *B. aquilonaris* and 4.6 km for *B. eunomia* (Baguette & Schtickzelle 2006)], mire butterflies avoid dispersing out of a patch in more fragmented landscapes (Vandewoestijne & Baguette 2004, Schtickzelle et al. 2006, Swengel & Swengel 2010a). Thus, increased isolation by distance increases genetic differentiation among separated populations [for *B. eunomia* in Belgian Ardennes (Vandewoestijne & Baguette 2004), for mire moths in the Czech Republic and Austria (Šula & Spitzer 2000)] or even genetic drift [for *Carabus nitens* (Assmann & Janssen 1999), but Drees et al. (2011b) did not find evidence for isolation by distance in the genetic structure of separated *Poecilus cupreus* populations in German heathlands].

As such, in the longer term (within several decades), isolation of especially small habitat patches can cause the extinction of species within those patches. A period of 26-113 years of isolation of heathland patches appeared to be too long for heathland specialist carabid species

with low dispersal powers to persist (Vries et al. 1996), while the poor-dispersing carabid beetle *A. ericeti* went extinct in practically all small sites in the Netherlands after periods of 24-66 years of complete isolation (Vries & Boer 1990).

Finally, isolation might negatively affect not only separate populations but also whole assemblages. Indeed, the surrounding land-use at scales between 1500 and 2000 m influenced species assemblages of higher Diptera in North American mires (Savage et al. 2011). Additionally, in old heathland patches in Belgium, species richness of butterflies increased with both connectivity and area of the patch (Cristofoli & Mahy 2010).

Restoration and isolation/dispersal

Isolation and the dispersal ability of organisms are not only important for their persistence within the remaining patches, but are also fundamental in the successful colonisation of restored mires (Watts & Didham 2006b). For example, even a moderate degree of isolation (i.e. > 400 m) from an intact mire caused an almost complete collapse of insect-plant interactions in restored islands within mined mires in New Zealand [Watts & Didham (2006a), but see Watts et al. (2013), who observed an opposite trend: herbivory rates and larval density of mire specialist moth increased with isolation].

However, isolation and/or species dispersal abilities seem to be important only in the short term after restoration if the restored patches are relatively close to pristine "source" patches. For instance, although Brachycera species with high dispersal ability were able to recover quicker than dispersal-limited species in mined mires of Quebec, Canada (Taillefer & Wheeler 2012), flight ability of beetles was not the major determinant of colonization of restored peat islands in New Zealand, as fully-winged species were also slow to colonize (Watts et al. 2008). For the latter case, isolation was an important factor limiting only short-term (1-13 months) recolonization and community composition of beetles of the restored islands, but this effect diminished over longer periods of time (24-72 months) (Watts et al. 2008). In both studies above, the restored patches of mined mires were very close to pristine sites (within 1 km), which might act as a source for colonizers, and given enough time, isolation effects tend to disappear.

In addition, significant relationships were not detected between species richness of butterflies and patch structure (area, connectivity) in newly-created patches (restored 25-55 and less than 25 years ago) in wet heathlands in Belgium, but this was detected for old patches (Cristofoli & Mahy 2010). This may be considered as evidence for a colonisation credit (the number of species yet to colonise a patch) in newer habitat patches, as suggested by Cristofoli

& Mahy (2010). Thus overall, the rate and success of invertebrate community re-assembly will depend to a large extent on, i) maintaining refuges of undisturbed habitat that act as sources of potential colonists to restored habitats, and on ii) prioritizing the restoration of mire patches as close as possible to pristine sites since this would likely aid the colonisation of restored sites by specialist species (see Hanski 1998, Hanski & Ovaskainen 2003).

1.4.2 The effects of local variables on mire invertebrates

Various local (i.e., site level) variables are important in structuring mire communities. Below I summarize the known responses of mire invertebrates to changes in various local environmental variables.

Vegetation structure

Vegetation structure, as well as species composition of plant communities, have a crucial effect on the persistence of mire invertebrates. However, vegetation structure seem to be more important than plant species composition for a number of invertebrate groups of mires (see below). Even herbivores seem to be dependent on the microclimate provided by vegetation structure, although they are obviously also dependent on plant species composition (see below). Furthermore, several invertebrate groups responded mainly to changes in vegetation structure, rather than plant species composition, due to anthropogenic disturbances, both negative (e.g., drainage, peat mining) and positive (restoration, see Watts et al. 2008). Ground layer vegetation and the tree canopy are two distinct vegetation forms to which mire invertebrates respond.

Ground vegetation cover is very important both for individual species and communities of mire invertebrates. Ground vegetation cover was crucial in determining pristine (carabid beetles - Hollmen et al. 2008; dipterans - Savage et al. 2011), drained (carabid beetles - Hollmen et al. 2008; dipterans - Taillefer & Wheeler 2010), and restored (beetles - Watts et al. 2008; Taillefer & Wheeler 2012) mire invertebrate communities. Furthermore, individual mire specialist species were sensitive to changes in ground vegetation cover, and mire species preferred vegetation structure typical to mires (lower, i.e. less shaded, ground vegetation cover and tussock structures of grasses): i) the carabid beetle *C. nitens* preferred low heath sites (Assmann & Janssen 1999), ii) *A. ericeti* responded negatively to the increase of grass cover, but positively to the cover of peat and other moss species (Drees et al. 2007), iii) the observed

turnover of the most abundant mire spider species were linked to the spread of heather (*Calluna vulgaris*) (Haase & Balkenhol 2015) and similarly the proportion of photophilous spider species decreased in favour of shadiness-preferring ones most likely due to the increase of shrub cover and the nearly complete loss of *Sphagnum* mosses (Schikora 1994), and iv) grass tussock structures were linked positively to the presence of butterfly *Boloria eunomia* caterpillars and adults (Turlure et al. 2009) and the butterfly *C. tullia* (Dennis & Eales 1997). Tussocks may enable larvae to escape winter submergence, which experimentally has been shown to cause high mortality in mire butterfly caterpillars (Joy & Pullin 1997). Furthermore, host plant cover is important for herbivorous mire invertebrates, as expected (for butterflies *B. eunomia* - Turlure et al. 2009; and *C. tullia* - Weking et al. 2013), as well as nectar plants (for *B. eunomia* - Turlure et al. 2009). Structural vegetation elements were showed to be significant for the thermoregulation of bog butterfly caterpillars (*B. eunomia* and *B. aquilonaris*) (Turlure et al. 2011). Finally, vegetation structure can also have an effect on the success of breeding of some mire specialist species, as demonstrated for oviposition of the butterfly *C. tullia*, which decreased with vegetation density of the upper herb layer, but increased with host plant quantity (Weking et al. 2013).

Tree canopy cover or tree height (a proxy for radiation and temperature) are among the most influential variables in structuring mire invertebrate communities both due to drainage and restoration (e.g., for spiders - Haase & Balkenhol 2015; and beetles - Watts et al. 2008). For example, tree canopy cover or tree height had a negative effect on butterflies in mires drained for forestry in Finland (Lensu et al. 2011, Komonen et al. 2013). Furthermore, beetle community were associated with the increasing complexity of vegetation structure related to the age of restored islands (variables such as canopy density and height, total vegetation cover) in a mined peat bog in New Zealand (Watts et al. 2008). Thus, if both tree and ground layer vegetation structure are manipulated appropriately during restoration, mire invertebrates should respond positively to the restoration action.

***Sphagnum* moss and thermal conditions**

Sphagnum is a key vegetation type in the formation of mires, and is described separately here. *Sphagnum* species create favourable conditions for mire specialist invertebrate species, namely low pH and high moisture (Rydin & Jeglum 2013), and relatively stable and cool temperature (van der Molen & Wijmstra 1994). Of these variables, only the effects of moisture on mire invertebrates are extensively investigated (see below).

The conditions created by *Sphagnum* mosses have a clear positive effect on both individual mire invertebrate species and communities. Indeed, individual mire specialist species depend on *Sphagnum*, as shown for carabid beetles (Främbis 1994, Drees et al. 2007) and dipterans (Savage et al. 2011, Taillefer & Wheeler 2012). Furthermore, *Sphagnum* might even be important in creating a suitable microclimate for butterflies. For example, for the caterpillars of *B. aquilonaris* in peat bogs of Belgium, the lack of *Sphagnum* hummocks reduced larval habitat suitability (Turlure et al. 2010). These authors also experimentally showed a significant impact of temperature on their survival (higher at lower temperatures). Additionally, caterpillar density increased with the thermal buffering ability of *Sphagnum* hummocks, which suggests that these hummocks function as thermal buffers for daily temperature fluctuations, i.e. the interior parts of *Sphagnum* hummocks offered a stable environment at relatively low temperatures. Hence, *Sphagnum* hummocks represent a key resource for the survival of *B. aquilonaris*, a glacial relict species, as they function as larval thermal refuges (Turlure et al. 2010). Other larvae of mire specialist butterfly species, e.g., *B. eunomia*, also benefited from microclimates provided by *Sphagnum* hummocks (Turlure et al. 2009, Turlure et al. 2011).

Since mire specialist species respond to *Sphagnum* and the thermal conditions they provide, this also has consequences in the formation of community of mires. For instance, species assemblages of dipterans were mostly affected by the cover of *Sphagnum* mosses, bare peat, and ericaceous shrubs (Taillefer & Wheeler 2012). Similarly, the proportion of photophilous spider species decreased in favour of shadiness-preferring ones most likely due to the increase in shrub cover and nearly total loss of *Sphagnum* mosses (Schikora 1994). In addition, isopod abundance was positively correlated with soil temperature at all three studied sites in a Croatian bog (Antonović et al. 2012).

Moisture

High moisture levels is one of the main features of mire habitats, and it is expected that mire specialist species respond negatively to a decrease, and positively to an increase in moisture, e.g. due to drainage and restoration, respectively. Indeed, a number of mire specialist taxa were positively associated with moisture, in terms of their: i) abundance (crane flies in blanket bogs of England and Wales - Carroll et al. 2011; Brachycera in Canadian mires - Taillefer & Wheeler 2010), ii) diversity (Brachycera in Canadian mires - Taillefer & Wheeler 2010), iii) distribution (ground beetles in Welsh peatlands - Holmes et al. 1993), or iv) individual species responses (larvae of butterflies *Coenonympha tullia* - Dennis & Eales 1997; *B. aquilonaris* -

Turlure et al. 2010; *B. eunomia* - Turlure et al. 2009). However, *C. tullia* larvae were sensitive to prolonged submersion (Joy & Pullin 1997). Finally, mire-related taxa responded negatively to dehydration (see Haase & Balkenhol 2015), while invertebrate taxa that are not associated with mires seem to benefit from drier conditions, e.g. soil organisms in Finnish mires (Silvan et al. 2000, Laiho et al. 2001) or isopods in a Croatian mire (Antonović et al. 2012).

pH

Although low pH is one of the main features of bogs and poor fens, only very rarely have the effects of changes in pH directly been investigated for mire invertebrates. For example, in a laboratory experiment Paje & Mossakowski (1984) showed that mire carabid beetles respond to particular levels of pH and likely use pH to select suitable habitat. Indeed, among the major factors that affected ground beetles in Welsh peatlands were acidic vs. nutrient rich conditions (Holmes et al. 1993). The importance of pH has also been suggested for other mire invertebrate groups, like dragonflies and damselflies (Elo et al. 2015), although direct effects were not investigated (but see for dipterans - Taillefer & Wheeler 2012). It is likely, however, that the effects of pH, as well as moisture, are reflected through the effects of *Sphagnum* mosses (see above).

Fire (prescribed burning) and grazing

Although fire (prescribed burning) is a well-known technique in managing and restoring open habitats, like grasslands (see e.g., Bowles & Jones 2012), it is questionable whether fire (prescribed burning of the vegetation) is an appropriate management technique for mires. This is mainly because of the rareness of natural fires in mires due to their wetness. There might also be undesirable outcomes due to fire in mires, e.g. the remaining ash may increase pH and nutrient availability in mires. Nevertheless, results of Hochkirch & Adorf (2007) support prescribed burning as a management tool for Orthoptera in peat bogs in northern Germany, where fire was used to control the grass *Molinia caerulea*, yet this grass may profit from fire in the long term. These authors also suggest sheep grazing of burned sites, which may be an appropriate technique for managing bogs for mire specialist invertebrates, like the butterfly *C. tullia* in English mires (see Dennis & Eales 1997). However, burning and grazing as mire management options remain controversial as the lack of these techniques do not have an effect on mire invertebrates in the long run (e.g., 18 years without significant disturbance to mire vegetation did not cause a decline of the mire moth *Coenophila subrosea* population - Fowles et al. 2004), or the use of fire and grazing may even have a negative effect on taxa (e.g., *A.*

ericeti is negatively associated with grazing - Holmes et al. 1993). Thus, it seems that a suitable hydrological regime is sufficient to maintain mire invertebrates, and mire vegetation should not be burned or grazed.

1.4.3 The effects of local vs. regional variables on mire invertebrates

Mires are naturally discrete and become increasingly smaller and isolated with latitude from north to south in the Northern hemisphere (Desrochers & Duinen 2006), thus intuitively mire specialist invertebrates should be adapted to some level of isolation and small patch size. This leads to the question of whether local variables are overall more important for the persistence of mire invertebrates than regional ones. From a few papers, which addressed this issue, it appears to be the case, at least for some of the landscape-level variables investigated. Mire size appeared to be less important for occurrence (suggested for butterflies in bigger bogs - Swengel & Swengel 2010a, and species richness or diversity for Diptera - Savage et al. 2011), than habitat quality. Furthermore, habitat connectivity appeared to be less important both for the persistence (for the butterfly *C. tullia* - Dennis & Eales 1997) and response to restoration (for beetles - Watts et al. 2008) of invertebrates than vegetation cover (Dennis & Eales 1997, Watts et al. 2008). On the other hand, some landscape-level variables appeared to be as important for mire invertebrates as local ones, e.g. surrounding land-use at the largest scales measured (1500 and 2000 m) and vegetation cover both influenced species assemblages of Diptera (Savage et al. 2011), and resources important for the survival of *Coenonympha tullia* included both patch size and the area covered by host plants (habitat quality) (Dennis & Eales 1997). Thus, even though local conditions appear to be of primary importance to mire communities, regional variables may also play a role in conservation and restoration, if the purpose is to maintain mire invertebrates.

1.4.4 Urbanization

Desrochers & Duinen (2006) argued that mires are lost due to urban sprawl and should be conserved near populated areas. They claimed that this should be particularly relevant at the southern edges of mire ranges in the Northern hemisphere, where species richness of mire invertebrates and level of urbanization are highest. However, even if mires are present within cities, invertebrates there will be affected by various urbanization-related factors, e.g.,

increased isolation, changed hydrological regimes and temperature, pollution, changed patterns in vegetation cover and drainage (Baldwin 2011). In addition to these, edge effects and trampling are known to affect invertebrates in urban forests (Kotze et al. 2012a, Noreika & Kotze 2012). These factors might have negative effects on mire specialist species and are likely to threaten their survival within urban mires. Yet, no study that I am aware of has addressed the effects of urbanization on mire invertebrates.

1.4.5 The drainage of mires

Huge areas of non-tropical peatlands have been drained for forestry, agriculture and peat cutting, e.g. 7.2 million ha in Finland alone (Lindholm & Heikkilä 2006), and 50 million ha globally (Chapman et al. 2003). The drainage of mires not only directly degrades habitat quality for specialist invertebrates and other taxa, but also isolates pristine mire habitats (e.g., in Finland, Lindholm & Heikkilä 2006). Mire drainage for agriculture and especially peat mining differ from mire drainage for forestry as the latter is less detrimental and slower, with gradual changes in vegetation cover: graminoids and *Sphagnum* mosses decline, while trees and shrubs proliferate (Laine et al. 1995). Additionally, acidity, aeration and subsidence of the surface peat increase after drainage for forestry (Laine et al. 2006). These abiotic and biotic changes also negatively affect mire specialist invertebrates. Indeed, drainage or dehydration of mires caused a decrease in species richness of several taxa, e.g. dragonflies and damselflies (Elo et al. 2015), carabid beetles and moths (Spitzer et al. 1999), Brachycera (Taillefer & Wheeler 2010), and even the successional changes of communities, like spiders (Haase & Balkenhol 2015). Clear changes in species traits were also detected due to drainage, e.g., the proportion of shadiness-preferring species increased in comparison with photophilous species of spiders (Schikora 1994). Generally, only common and abundant species benefit from drainage of mires for forestry, as demonstrated for carabid beetles in Finland (Hollmen et al. 2008). Among probable reasons for these negative effects are the reduction of available breeding habitat, a decrease in prey, changes in pH and vegetation (see e.g. Elo et al. 2015), as well as constant water loss (Taillefer & Wheeler 2010), or an increase in shrub cover and the nearly total loss of *Sphagnum* mosses (Schikora 1994).

A reduction in moisture in mires not only changes the diversity and abundance patterns of characteristic mire taxa, but might potentially cause an invasion of taxa uncharacteristic of mires. Antonović et al. (2012) showed that isopod species richness of an isolated bog in Croatia

was surprisingly high and did not considerably differ from species richness of the edge or adjacent forest. They suggest that this was due to low water table levels, vegetation succession and the small size of the bog. Such invasions of non-mire taxa might become more pronounced due to climate change as fewer rainy days and stronger solar radiation decrease moisture in mires, and can directly promote, e.g. thermophilous spider species (Haase & Balkenhol 2015).

Furthermore, the invasion of such uncharacteristic organisms to drained mires changes ecological functions provided by invertebrates. For instance, conditions following drainage seem to be more suitable for litter-dwellers, nutrient-recyclers and decomposers (e.g., dipterans - Taillefer & Wheeler 2010; other soil invertebrates - Silvan et al. 2000; Laiho et al. 2001). Furthermore, even though Coulson et al. (1990) did not find significant differences in the rate of decomposition due to drainage in two wet heathlands in England, this likely indicates inefficient drainage in those places rather than the lack of change in ecological function (i.e. rate of decomposition) due to drainage.

Several studies have investigated the possibility of open power lines within drained mires as an alternative habitat for mire invertebrate species, but results remain questionable as openness alone cannot assure high quality habitat for mire specialists. Yet, several taxa showed positive associations with open power lines within mires drained for forestry (e.g., few carabid species - Hollmen et al. 2008; abundance and species richness of butterflies - Lensu et al. 2011). Thus, even mires drained for forestry can be managed so that they would provide suitable conditions for at least some mire-dependent invertebrates. However, management should be performed often in order to keep mires open, e.g. trees should be cleared after 2-4 growing seasons as suggested by Komonen et al. (2013).

1.4.6 The effects of restoration on mire invertebrates

In general, mires are subject to restoration after two anthropogenic disturbances: industrial mining of peat and mires drainage for forestry. These disturbances are remarkably different in their impact on mire communities, as the community is totally and rapidly destroyed in the former (the whole mire surface is removed), while changes are more gradual in the latter [several decades after drainage, mires still host a number of mire specialist plant (Laine et al. 1995) and insect (see e.g., Hollmen et al. 2008, Elo et al. 2015) species].

The restoration of mined mires

After the mining of mires, only the bare peat surface remains, which is unable to revert to natural mire communities. Naturally, such places are not recolonized by mire plant species, such as *Sphagnum* (Poulin et al. 2005), therefore mire plants are actively re-introduced (Rochefort et al. 2003). This is accomplished through several techniques, but generally results in the creation of restored habitat islands within the mined mire, with a raised water table level. The recovery of invertebrates seem to be quite rapid in such islands and likely depends on species dispersal abilities, as well as on the degree of isolation (distance from the pristine sites) of the restored islands.

Indeed, the restoration of mined mires caused a rapid (within 2-13 years) positive response of several invertebrate communities, as well as the recovery of trophic structure and insect-plant interactions. For example, beetle species composition reverted rapidly to that of undisturbed peat bogs 2 years after restoration (Watts et al. 2008), and showed a clear recovery of beetle abundance, species richness, and trophic structure 13 years after restoration commenced (Watts & Mason 2015). Furthermore, the rate of recovery of the interaction of a mire herbivore and its host plant was surprisingly rapid (i.e. between ~4 and ~6 years) (Watts & Didham 2006a). On the other hand, although Taillefer & Wheeler (2012) suggested that 7 years were sufficient for a Brachycera community to recover and to reach a level of diversity characteristic of a natural bog, this period was not long enough for recovery of the trophic composition of this group. Thus, while community structure seems to recover within several years, trophic composition might need a longer period to recover. Functional trait analysis is needed to reveal barriers to full restoration of mire invertebrate communities, as suggested by Watts & Mason (2015).

Recovery rate seems to depend on level of isolation and the dispersal abilities of species. For instance, the degree of isolation of restored islands had a major impact on the rate and patterns of recovery of invertebrate communities (Watts & Didham 2006b). These authors experimentally showed that there was a significant decrease in total species richness and abundance of invertebrates associated with potted mire plants with an increasing distance from the undisturbed habitat. Therefore, when the restoration of mined mires is performed by creating restored islands, these islands should be placed as stepping stones outwards from existing areas of intact habitat as suggested by Watts & Didham (2006b).

Species dispersal abilities seem to be crucial for the successful colonization of restored islands. For example, the most successful colonizers of the experimentally potted mire plants were aphids and lycosid spiders due to their high dispersal abilities (Watts & Didham 2006b).

In contrast, small, native, and poor-dispersing invertebrate taxa were persistently less abundant on the islands than in the undisturbed peat bog, resulting in differences in species composition, even on the oldest islands (Watts & Mason 2015). Similarly, the assemblages of small-size species of Brachycera did not recovered 7 years after restoration (Taillefer & Wheeler 2012).

Thus, for poor-dispersing invertebrates, either direct assisted migration (see e.g. Vitt et al. 2010) is needed, or alternatively, species could be inoculated along with introduced plant material during the restoration action. However, the efficiency of the latter approach seems questionable. For instance, even though the specialist mire moth *Houdinia flexilissima* did establish with viable populations from translocated host plants in mined mires in New Zealand (Watts et al. 2013), only very few Brachycera species emerged from shredded plant material in mined peatlands in Quebec (Taillefer & Wheeler 2013). Therefore, assisted migration may be required to enhance colonization by poorly dispersing invertebrate species, and even ongoing intervention to enhance their survival (Watts & Mason 2015), using individuals adapted to local conditions (Turlure et al. 2013).

The restoration of mires drained for forestry

Drainage for forestry causes mire community changes towards forest-like habitats, because lowering the water table level results in an increase in tree and shrub covers, while *Sphagnum* moss and graminoid covers decrease (Laine et al. 1995). However, a number of mire plant species are able to survive for several decades in these drained mires, and thus appropriate restoration (e.g., raising the water table level and removing high trees) will result in the return of vegetation cover characteristic of pristine mires (Haapalehto et al. 2011). This, in turn, can create suitable conditions for mire invertebrates and facilitate their recovery. Indeed, positive changes in mire invertebrates can already be observed a few years after restoration. For example, Elo et al. (2015) showed a statistically significant positive effect of the restoration of mires drained for forestry on the abundance and species richness of dragonflies and damselflies in the third year after restoration.

Not only the structure of mire invertebrate communities, but also their function (low decomposition and nutrient cycling rates) can be restored, as indicated by the number of decomposer and nutrient recycler invertebrates in restored mire sites (Silvan et al. 2000, Laiho et al. 2001). Silvan et al. (2000) also concluded that the small amount of soil invertebrates on a re-wetted site was an indication that soil conditions were unfavourable for organic matter decomposition, and thus suitable for the re-initiation of peat accumulation.

All studies on restoration discussed above (both after mining and drainage for forestry) include only the effects of restoration on solitary insects. There is a lack for knowledge on the responses of social insects to mire restoration, even though, e.g. ants are especially important ecologically, as they can influence vegetation patterns and habitat microtopography in mires (Lesica & Kanno 1998). Ant colonies also have long-lasting life cycles, thus their response to drainage and restoration may be considerably slower than solitary invertebrates.

Finally, despite the reported success of restoration, it seems that the magnitude of the benefits of drainage blocking (i.e., the building of dams on the drainage ditches) is likely to vary between locations and years, as suggested for crane flies (Carroll et al. 2011). These researchers showed that drainage blocking had a significant effect on soil moisture in both investigated years, but only increased crane fly abundance significantly in one of the years. The likely explanation for the observed difference between years is that the "insignificant for crane fly abundance" year was wetter than the "significant" year. Carroll *et al.* (2011) conclude that as summer conditions are projected to become increasingly dry, the potential importance of blocking drains to maintain crane fly populations could increase substantially under climate change. The same might be expected for other habitats and research on the effects of restoration should be done across multiple years.

2. AIMS OF THE THESIS

The main aim of this PhD thesis was to investigate the effects of negative anthropogenic disturbances (drainage for forestry and urbanization) on the invertebrate communities of boreal mires and how effective efforts are to reverse these negative effects through ecological restoration (i.e. positive anthropogenic disturbance). In addition, the purpose was to determine which environmental variables are key in supporting mire specialist invertebrate species and communities.

Chapter I investigates the effects of urbanization on epigaeic mire invertebrate (carabid beetles, Carabidae and spiders, Araneae) specialist species and communities. Here, I investigated the relative roles of regional and local variables on the diversity of mire specialist species in an urban setting. I hypothesized that (i) an increase in urbanization (percentage of impervious surfaces within a 500 m buffer around each mire) will homogenize mire invertebrate communities, (ii) local environmental variables known to affect mire species (pH, the covers of *Sphagnum* moss and other vegetation, standing wood volume) will be more

important than regional variables (level of urbanization, total mire area) to mire specialist species and communities, since mires are naturally isolated and discrete, and therefore species sorting should be a driving process in community assembly (Leibold et al. 2004), and (iii) if urban mires present environmental conditions favourable to mire specialist species, these mires may serve as hotspots of specialist species diversity within cities.

Chapter II investigated the effects of drainage for forestry and restoration on four ecologically different, solitary invertebrate groups in mires: carabid beetles (Carabidae), spiders (Araneae), crane flies (Nematocera), and macro- and micromoths (Lepidoptera). The main aim of this study was to determine whether drained mire restoration by complete ditch filling and high tree removal resulted in the recovery of these invertebrate taxa, thus supporting the Field of Dreams hypothesis, which assumes that if physical conditions of the disturbed habitat are restored, species of the original habitat will recolonize that habitat (Palmer et al. 1997). If mire specialists are present in the landscape, and the restoration practice is successful in returning the mire to pre-drainage conditions, I expected these species to respond rapidly and positively to restored environments compared to drained mires. It was also expected that key characteristics associated with pristine and drained mires (such as *Sphagnum* cover, the water table level, and the number of high trees) would be linked to the responses of species of different ecologies and to changes in mire community structure, thus providing insights into a mechanistic understanding of the responses of species to restoration.

Chapter III characterised differences in mire habitats, vegetation and social insect (ants, Formicidae) assemblages among pristine, drained for forestry (~30-40 years ago) and recently restored (~1-3 years ago) mires. I hypothesized that restoring the water table level by ditch filling and reconstructing sparse tree stands by cuttings will lead to the recovery of vegetation and the ant community. However, there might be considerable time lags in the response of ants that form long-lived perennial colonies with long colony cycles compared to solitary insects with shorter generation times.

In **Chapter IV** mire butterfly and plant responses to restoration were investigated by comparing individual species abundances and community structures 1 year prior to restoration to those thereafter (~1-3 years since restoration), using a Before-After Control-Impact design (BACI-design). The main aim of this study was to evaluate whether the restoration actions taken (raising water table and the removal of high trees) are appropriate to facilitate the successful recolonization of mire butterflies and plants. Drainage effects were also assessed, as well as butterfly responses to environmental variables associated with drained (number of tall trees) and pristine (larval food plant cover, number of low trees) mires. I hypothesized that

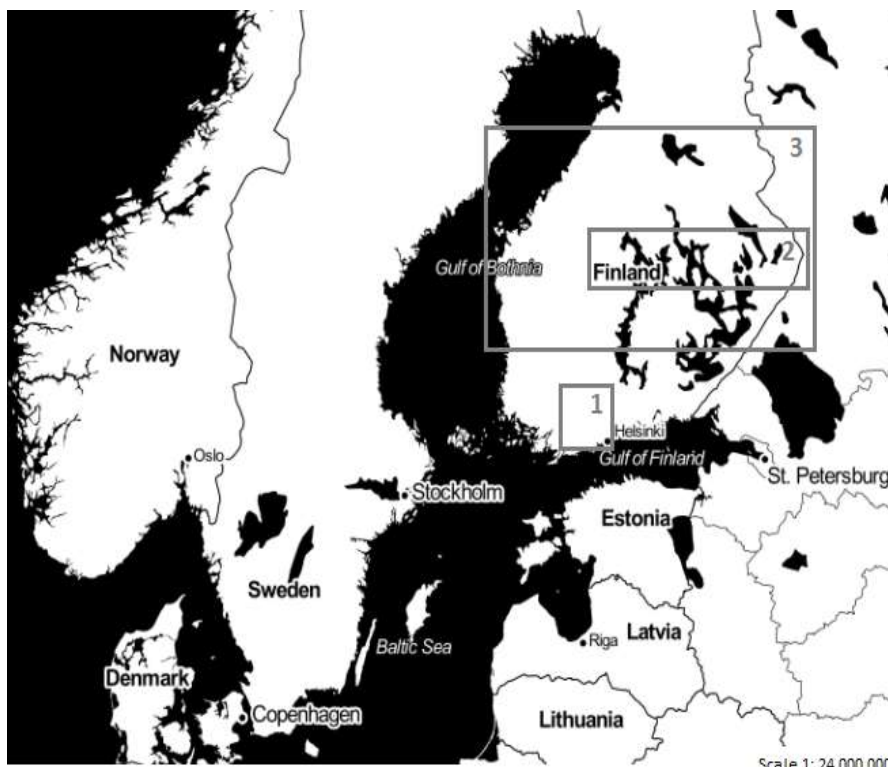
drainage will have negative effects on the abundance and richness of mire specialist species, but positive effects on generalists, while restoration will affect specialists positively and generalists negatively. Finally, I expected that mire butterflies will respond negatively to environmental variables associated with drained mires (number of tall trees) and positively to pristine mire-associated variables (larval food plant cover, number of low trees).

3. MATERIAL AND METHODS

3.1. Study sites

All studies included nutrient-poor (either poor fens or ombrotrophic bogs) pine mires, located in Finland (Fig. 3), under cold and wet climate [average annual temperatures 4-5 °C (Chapter I) or 2-4 °C (Chapters II-VI), precipitation 600-700 mm, The Finnish Meteorological Institute: <http://en.ilmatieteenlaitos.fi/normal-period-1981-2010>]. In Chapter I, twenty pine mires were selected in southern Finland, 18 of which were in the Greater Helsinki metropolitan area, and two large pristine mires (Torransuo and Luutasuo) respectively ~100 and ~70 km northwest of Helsinki. The range in size was 0.8 to 153 ha for mires in the Greater Helsinki area, while the two pristine sites (Torransuo and Luutasuo) were considerably larger (~2970 ha and 309 ha, respectively). These mires were located in the southern boreal vegetation and plateau or

Fig. 3. Locations of the study regions within Finland. Numbered grey rectangles mark approximate locations of the study sites within Finland for different chapters of this thesis: 1 - Chapter I, 2 - Chapters II and III, 3 - Chapter IV. Stamen Toner/OSM layer (map tiles by Stamen Design (stamen.com), under CC BY 3.0 (<http://creativecommons.org/licenses/by/3.0/>), data by OpenStreetMap (<http://www.openstreetmap.org/>), under ODbL (<http://opendatacommons.org/licenses/odbl/>)) was used as a background for creating the map in QGIS 2.0.1(QGIS Development Team 2013).



concentric raised bog zones (Hallanaro & Pylvanainen 2002). The studies of Chapter II and Chapter III were conducted at nine pine mires located in two regions in Finland: Central Finland and Northern Karelia. The average size of the non-drained open parts of these mires (i.e. treeless or sparsely forested) was ~390 ha (range ~20–1850 ha). Chapter IV explored 19 boreal mire complexes distributed throughout central Finland, which also included the nine mires investigated in Chapters II and III. Central Finland covers southern and middle boreal vegetation zones, including three mire zones (concentric and eccentric raised bogs, and aapa mires with low strings; Hallanaro & Pylvanainen 2002).

The drained mires were ditched for forestry ~30-40 years ago (Chapters II-IV). Restoration action in parts of the studied mires were performed by filling in the ditches with peat and by constructing dams of logs and peat at the ends of the ditches. Thus, the water table level was raised and its fluctuation amplitude reduced. Finally, a varying proportion of tall trees were cut in order to mimic the natural tree stand structure of mires. During harvesting, timber and pulpwood were removed, but all tree stumps and varying amounts of logging residues (branches and tree tops) were left behind. In Chapters II and III, mires were investigated only in 2007 (i.e. ~1-3 years after restoration), while in Chapter IV all mires were sampled one year before restoration (in 2003 and 2010), and ~1-3 years after the restoration action (in 2007 and 2014 respectively).

3.2. Study design

In Chapter I, half of the pitfall traps were placed in the treeless part and the other half in the tree-covered part of each mire. Although smaller mires contained less traps (6-14 traps) than larger ones (24-32 traps), the largest mires were underrepresented in terms of number of traps per unit area due to their very large size. Pitfall traps were placed at least 10 m apart. In total, 218 traps were installed.

In Chapters II-IV, a complete block design was used to standardize the effects of landscape features on restoration outcomes. Thus, each mire contained a drained, restored, and pristine treatment. Two 250-m-long transects, on average ca 80 m apart, were established per treatment per mire, resulting in six transects per mire. The two 250 m transects of the three treatments per mire were located ca. 600 m apart. One pitfall trap was installed in a representative location within each of three 100 m² tree-sampling plots per transect (see above), resulting in six traps per treatment per mire (i.e. 18 traps per mire, 162 traps in total)

for collecting epigaeic arthropods in Chapters II and III. In Chapter II, macromoth data were collected only from five mires located in Northern Karelia.

In Chapters II and III, nine mires were sampled only in 2007, while in Chapter IV a replicated before-after, control-impact (BACI) experimental design was established in 19 mires: nine mires were sampled in 2003 (before restoration) and 2007 (after restoration) and ten different mires were sampled in 2010 (before restoration) and 2014 (after restoration).

3.3. Invertebrate sampling

In Chapter I, pitfall traps (mouth diameter = 65 mm, depth = 95 mm) covered with plastic lids (raised 2.5 cm above ground level) were used to sample carabid beetles and spiders. The traps were half-filled with a 50 % propylene glycol–water solution to preserve the sampled arthropods. Trapping was performed in the same localities in 2011 (26 May–14 October 14) and 2012 (1 May–25 September). The traps were emptied every third to fourth week, which resulted in four visits in 2011 and five visits in 2012.

Carabid beetles and spiders (Chapter II) and ants (Chapter III) were sampled using pitfall traps (70 mm deep, 56 mm top diameter). Each trap was half-filled with a 10% NaCl solution, and a small amount of detergent was added. Beetles, spiders and ants were collected and the traps were refilled at 2-week intervals over a 6-week period from mid-May until early July in 2007.

Additionally in Chapter II, micromoths and crane flies were sampled by standardized sweep netting. The sweep net had a diameter of 28 cm and a mesh size of 0.5 mm. One sweep was performed per 2.5 m, resulting in 100 sweeps per transect (each transect was 250 m long). Sweep-net sampling was performed weekly from mid-May until mid-August in 2007 when the weather allowed sampling, and sampling occurred between 10 am and 6 pm.

Finally, macromoths in Chapter II and butterflies in Chapter IV were counted by walking along the transects at a slow, steady pace, counting all individuals observed within a fixed distance of 2.5 m on both sides of the transect line and 5 m ahead (i.e. within a moving 5 × 5 m² observation window). Stops were made to resolve identification issues (butterflies and moths were caught with a net, identified in hand and released), recording being resumed from the point where the walk was interrupted. Transect counts were carried out at temperatures between 13 and 17°C on sunny days (min. ~60 % of the sky was without clouds) or when temperatures were above 17°C on sunny or cloudy days, but without rain. Monitoring was not

carried out on windy days (a 6 on the Beaufort-scale, Saucier 1955). Counts were made mainly between 11 am - 4 pm. The number of visits varied due to weather conditions, and variation was taken into account in the statistical analyses (see below). Sampling was carried out weekly, depending on weather conditions, and the number of visits per site varied from 7 to 15. Butterfly monitoring started when the Freija fritillary (*Boloria freija*) emerged from the pupa and started to fly after hibernation, usually in the middle of May. Macromoth sampling was performed from mid-May to the end of July in 2007. Butterflies were sampled in 2003 and 2010 (before restoration) and in 2007 and 2014 (after restoration).

3.4. Environmental data collection

In Chapter I, both regional-level and site-level environmental variables were collected. QGIS 2.0.1 (QGIS Development Team 2013) was used to calculate regional variables: (i) total mire area in ha, (ii) level of urbanization around each mire (within a 500 m buffer zone) - this was used as a measure of isolation of the focal mire and included all impervious areas: buildings, pavements, roads and other asphalt- and concrete-covered surfaces, and (iii) percentage peatland cover around each mire (within a 1 km buffer zone) - a measure of potential patch connectivity (this variable was, however, not used in the analyses due to a high correlation with total mire area, $r = 0.75$). Site-level environmental variables were measured at the trap locations in the summer of 2013. Water samples were taken in mid-May by squeezing water from the peat. $\text{pH}_{\text{H}_2\text{O}}$ was measured in the laboratory the next day using a WTW inoLab pH/Cond 720 meter. Vegetation squares (1 x 1 m) were used to measure the percentage covers of litter and different vegetation types. Total standing wood volume (m^3 100 m^{-2}) of all tree species at a site was used as an indirect measure of site shadiness.

In Chapters II, III and IV, vegetation data were collected only from the nine mires in the Eastern part of Finland. In Chapters II and III vegetation were investigated only in 2007, i.e., after restoration, while in Chapter IV plant data were collected both in 2003 and 2007, i.e., before and after restoration. Three circular 100 m^2 (radius of 5.64 m) tree-sampling plots were established along each transect, 62.5 m apart. Tree data, that is the counts of stems of different tree species classified into size classes, were collected from these plots. In addition, one sampling square (5 × 5 m = 25 m^2) was established within each circular plot. Within these sampling squares, the percentage covers of mire surface topography types, i.e., microsite types (hummock, lawn, and flark) were estimated with 10% precision. To measure the water table

level, two boreholes were installed at opposite corners of each 25 m² sampling square. The boreholes were constructed using PVC pipes (2 cm diameter, 88 cm length). One vegetation square (1 × 1m) was established at each corner of each 25 m² sampling square.

3.5. Statistical analyses

Statistical analyses were performed at both individual and community levels by employing generalised linear mixed models (GLMM) and non-metric multidimensional scaling (NMDS), respectively. In addition, some other techniques were used. For GLMMs, a number of functions and packages were used in R (R Development Core Team 2013): the `glmmADMB` 0.8.0 function and package (Skaug et al. 2014) in Chapter I; the `glmer` function in the `lme4` package (Bates et al. 2013, R Development Core Team 2013) in Chapters II-IV. The response (number of individuals) was modeled following a negative binomial distribution in Chapter I, and a Poisson error distribution (O’Hara & Kotze 2010), with an individual-level random effect included to deal with possible overdispersion (Harrison 2014) in Chapters II and IV. Ant occurrence (presence/absence data) was modeled following a binomial error distribution (Chapter III). Trapping days (for carabid beetles and spiders in Chapters I-II) or the number of research visits (for butterflies in Chapter IV) was included as a logged offset term to account for differences in sampling intensity (Kotze et al. 2012b). For the NMDS analyses, we used the `vegan` 2.0-10 package (`vegan` 2.0-8 in Chapter III) in R (Oksanen et al. 2013). Carabid beetle and spider abundance data were standardized to 100 trapping days (Chapters I-II), while butterfly abundance data were standardized to 10 visits (Chapter IV). The Bray-Curtis (Chapters I, II, IV) or Raup (Chapter III) coefficient was chosen as a dissimilarity measure, and permutation tests were employed in the vector fitting procedure. More details on statistical analyses are provided in each Chapter.

4. MAIN RESULTS AND DISCUSSION

Generally, both high levels of urbanization (Chapter I) and mire drainage for forestry (Chapters II-IV) had negative effects on mire specialist species (lower activity-density) and invertebrate communities (more homogeneous), thus acting as negative anthropogenic disturbances. However, these detrimental effects can be reduced or even reversed through appropriate urban mire conservation and ecological restoration. Indeed, I showed that mire restoration by ditch infilling and partial tree removal (removing tall trees but leaving smaller ones) had a rapid and positive effect on many mire specialist invertebrate species [both increased abundance of solitary (Chapters II and IV) and increased presence of social (Chapter III) invertebrates] and on their communities, which became more similar to the pristine ones. Local habitat conditions were particularly important for the survival of invertebrate specialist species in urban mires (Chapter I) and for the successful recovery of restored mire invertebrates (Chapters II-IV). Individual mire specialist species responded negatively to environmental variables associated with deteriorated (i.e. drained or highly urbanized) mire conditions [number of tall (> 3 m) trees for carabid beetles, crane flies, micromoths (Chapter II), ants (Chapter III) and butterflies (Chapter IV)] and positively to pristine mire-associated variables [*Sphagnum* cover for carabid beetles and spiders (Chapters I-II), crane flies (Chapter II) and suggestively for ants (Chapter III); and larval food plant cover and number of lower (1.5 - 3m) trees for butterflies (Chapter IV)]. The more specialized the mire species, the more negatively they were affected by deteriorated-mire-associated variables and the more positively they responded to pristine-mire-associated variables. Thus, mires should be kept in as natural a state as possible via ecological restoration and/or urban mire conservation to ensure the establishment and survival of mire specialist species, which in turn reverse the trends of biotic homogenization.

4.1. Urbanization and the effects of mire size on mire invertebrates

In general, urbanization had a negative effect on mire specialist species abundances and community structure (more homogeneous), although a number of mire and forest specialist species were still present in urban mires (Chapter I). For instance, number of mire specialist species responded negatively to high levels of urbanization (the carabid beetle *A. ericeti*, spiders *P. sphagnicola* and *H. rubrofasciata*), yet these species and a few other mire specialists (the carabid beetle *P. rhaeticus*, the spider *A. elegans*) were present in urban mires within

Greater Helsinki (Chapter I). The presence of these species decreases homogenization at the city level, since mire specialists are usually not found in other habitats (Desrochers & Duinen 2006, Spitzer & Danks 2006). Apart from mire specialists, tree-covered parts of urban mires also harboured forest specialist species, such as the carabids *C. glabratus* and *C. violaceus*, which are scarce in fragmented forests of southern Finland (Halme & Niemela 1993), thus further contributing to overall biodiversity within cities. Nevertheless, high levels of urbanization result in the homogenization of arthropod communities of mires.

At the community level, the tree-covered parts of mires were similar in structure among all urbanization and mire size categories, while the open mire parts clearly differed among urbanization level and size categories. In particular, the open parts of large mires at low levels of urbanization are exceptional habitats, differing substantially from other mire types. Invertebrate communities of these open parts seem to be more sensitive to higher levels of urbanization and smaller mire size. This has negative consequences for biodiversity as most mire specialist species are associated with open parts of mires (Spitzer & Danks 2006) and is likely the result of differences in local environmental conditions, rather than landscape factors. For instance, in Chapter I I showed that only two specialist and four generalist species responded statistically significantly and variably to high and/or intermediate levels of urbanization, and only one specialist and two generalists showed statistically significant responses to total mire size. Regional factors (e.g., habitat isolation and area) are likely to be more important in structuring communities of actively dispersing species, while local factors (e.g., habitat quality) are possibly more influential in structuring communities of passively dispersing species (Faeth et al. 2012). This is in line with the response of spiders in Chapter I, as they are mainly dispersing passively via ballooning (Richter 1970). However, only actively-dispersing carabid beetles showed similar responses to those of spiders to regional variables. To some degree, mire carabid species are potentially more resilient to increased isolation and decreased mire size than, e.g. forest species, since mires are naturally discrete and isolated habitats (Desrochers & Duinen 2006). On the other hand, it was previously demonstrated that the mire specialist *A. ericeti* is unable to survive in isolated habitat patches smaller than ~5 ha in size for more than ~44 years (Vries & Boer 1990, Drees et al. 2011a). Only five of the studied mires in Chapter I were smaller than 5 ha in size and the majority of urban mires reached their current level of isolation 5–6 decades ago. Therefore, it might be that urban mires are either large enough to support viable mire carabid populations, or that there is a lag in their extinction after isolation (extinction debt, Hanski & Ovaskainen 2002).

4.2. The effects of drainage on mire invertebrates

In general, drainage for forestry affected mire specialist species and communities negatively of all investigated invertebrate taxa [carabid beetles, spiders, crane flies, micro- and macromoths (Chapter II), ants (Chapter III) and butterflies (Chapter IV)], while generalist species were either not associated with drainage or the association was positive. The difference between specialist and generalist species in their association to drainage was significant for all taxa and provides evidence that specialist species are more sensitive to disturbance than generalist species. This difference caused the divergence in community structure between drained and pristine sites and lead to biotic homogenization at the landscape level (McKinney & Lockwood 1999, Olden et al. 2004, Clavel et al. 2011). Similar results have also been found, e.g. for mire dipterans (Taillefer & Wheeler 2010) and dragonflies and damselflies (Elo et al. 2015). Furthermore, in grasslands, increasing disturbance facilitated generalist butterflies (Polus et al. 2007, Börschig et al. 2013) and disturbed habitats in general appeared to be more associated with generalist butterfly species (Kocher & Williams 2000).

Reasons for the decline of specialized species appear to be related to changes in the environment after drainage. The abundance (Chapters II and IV) or presence (Chapter III) of specialist species was generally negatively associated with an increasing number of tall (> 3 m) trees and a decrease in pristine-mire-related environmental conditions [e.g., *Sphagnum* cover for epigaeic invertebrates and crane flies (Chapters II and III), larval food plant cover and number of lower (1.5 – 3 m) trees for butterflies (Chapter IV)]. Similar observations on the role of increased tree growth have been reported for butterflies (Komonen et al. 2013). The main purpose of drainage is to increase tree growth and timber value for forestry and results presented here illustrate that the increased economic value comes at a cost to mire-specialized invertebrates.

However, some specialist species showed unexpected responses to drainage and restoration. The abundances of spiders *Pardosa hyperborea*, *Pirata insularis* and *Notioscopus sarcinatus*, micromoths *Catoptria margaritella* and *Crambus alienellus*, and the macromoth *Arichanna melanaria* were highest in drained sites, even though they were classified as mire specialist species (Chapter II). Furthermore, some generalists showed abundance patterns similar to those found for mire specialists [spiders *Alopecosa pulverulenta* and *Pardosa pullata*, the crane fly *Tricyphona immaculata* (Chapter II), and the butterfly *Plebeius argus/idas* (Chapter IV)]. This suggests that habitat affinities of these species might be different from what was previously thought. Alternatively, it is possible that drained sites

retained some crucial habitat characteristics (e.g. dwarf shrub cover) that are still suitable for these specialists as, e.g. mire dwarf shrubs are known to remain in mires drained for forestry for several decades (Laine et al. 1995). It is also possible that these species are, in fact, associated with drier mire types or mires with a more closed tree canopy and thus benefit temporarily from the drainage of mires.

4.3. The effects of restoration on mire invertebrates

Generally, mire restoration by ditch infilling and partial tree removal had a rapid and positive effect on all invertebrate communities investigated (Chapters II-IV) and on many individual mire specialist species. Indeed, the structure of all invertebrate and plant communities in the restored sites became more similar to the pristine sites already 1-3 years after restoration. In addition, most of the mire specialist species identified in Chapter II were abundantly collected from the restored sites. While restoration had a significantly positive effect on the abundances of only two mire specialist butterfly species (*B. aquilonaris* and *C. palaeno*) and tended to have a positive effect on a third (*P. optilete*), restoration had a significant positive overall effect on specialist species as a group (Chapter IV). However, for individual mire-specialist ant species the results were more variable and longer-term monitoring is needed to confirm the success of restoration for these social insects (Chapter III). There may be considerable time lags in the response of ants that form long-lived perennial colonies with long colony cycles compared to solitary insects with shorter generation times.

In this thesis I tested the restoration approach that does not include the active introductions of target species. Thus, the ability of a species to colonize a restored site will depend on the appropriate habitat being present, distance between restored habitats and potential source populations, a species' dispersal capabilities (Bond & Lake 2003) and landscape quality (Fahrig 2001). Furthermore, landscape context and peatland size are among the most important factors shaping species diversity in peatlands (Desrochers & Duinen 2006). Most likely, landscape features such as the commonness of pristine mires in the landscape, short distances between patches, large mire size, and habitat quality cause species selection that mold community structure and thus facilitate positive and seemingly rapid mire specialist species responses to restoration. This directly relates to the mechanistic basis of changes in community assembly (Elo et al., in press), especially if dispersal capabilities of organisms are considered. However, mire specialist invertebrates seem to be able to colonize

restored sites rapidly, likely due to short distances between mires rather than dispersal ability differences because these restored sites hosted not only good dispersers (mire specialist species of crane flies, micro- and macromoths and butterflies), but also a number of poor (mire specialist carabids) and intermediate (mire specialist spiders) dispersers. A more plausible driver for the positive response to restoration is habitat quality, in particular the recovery of *Sphagnum* moss cover and the removal of large trees (see below).

Conversely, for some mire specialists such as the spiders *Arctosa alpigena* and *Agyneta olivacea* and the crane fly *Phylidorea squalens*, environmental and biological conditions were apparently not yet suitable, as these species had their lowest numbers in restored sites (Chapter II). These species are likely to be more sensitive to environmental conditions in mires, and 1–3 years since restoration may not be enough time to re-establish their populations. Similarly, mire ant species showed variable responses to restoration most likely due to their long lasting life cycles. Therefore, longer-term monitoring is needed to evaluate the success of restoration efforts for these mire specialists.

Finally, I showed that already before restoration the mean abundances of mire specialist butterfly species were significantly higher in drained sites destined to-be-restored than in drained sites remaining in forestry use (Chapter IV). This observation was *post-hoc* after a non-planned comparison, but suggests that the to-be-restored sites were initially better for mire specialist species. This observation is interesting because the to-be-restored sites are inside Natura 2000 areas while the not-to-be restored sites are not. Therefore, the selection and demarcation of the Natura 2000 areas were successful in that it focused on areas, which despite disturbances due to drainage, have remained in better condition for specialist species. Thus, despite difficulties in implementing the Habitat Directive in general (Evans 2006, 2012), at least in this case it appears that the initial selection of Natura 2000 sites based on the criteria in Annex III (Habitat Directive, EC 1992) was appropriate, and may serve as an example of a successful conservation effort through the Habitat Directive.

4.4. Key local (site level) environmental variables for mire specialist species and communities

Local habitat conditions were particularly important for the survival of invertebrate specialist species in urban mires (Chapter I) and for the successful recovery of restored mire invertebrates (Chapters II-IV). Individual mire specialist species responded negatively to environmental variables associated with deteriorated (i.e. drained or highly urbanized) mire

conditions [number of tall (> 3m) trees for carabid beetles, crane flies, micromoths (Chapter II), ants (Chapter III) and butterflies (Chapter IV)] and positively to pristine mire-associated variables [*Sphagnum* cover for carabid beetles, spiders (Chapters I-II), crane flies (Chapter II) and suggestively for ants (Chapter III); larval food plant cover and number of lower (1.5 – 3 m) trees for butterflies (Chapter IV)]. The more specialized the mire species, the more negatively they were affected by deteriorated-mire-associated variables and the more positively they reacted to the pristine-mire-associated variables.

Results were particularly clear with regard to the response of species to two environmental characteristics directly related to restoration and pristine mire conditions, that is *Sphagnum* moss cover and the number of tall trees (> 3 m). As *Sphagnum* is the key genus for mire formation and restoration (Rocheft 2000, Rydin et al. 2006), its significant role in the persistence of mire specialist invertebrates is expected. *Sphagnum* mosses concentrate humidity and acidifies the environment (Rydin et al. 2006), and mire species likely prefer such conditions. At least, the negative response of one mire specialist spider (*Hygrolycosa rubrofasciata*) and the positive response of several generalists (carabid beetles *Oxypselaphus obscurus* and *Pterostichus diligens*, spider *Walckenaeria alticeps*) to an increase in pH indicates the respective preferences of habitat pH (Chapter I), which was also demonstrated for carabids under laboratory conditions (Paje & Mossakowski 1984). Incidentally, carabid beetles have well-developed pH receptors that may be used in habitat selection (Merivee et al. 2005). *Sphagnum* apparently does not provide suitable conditions and resources for non-specialists, such as forest generalists, possibly due to unfavorable pH values, as ombrotrophic (i.e. deriving nutrients only from precipitation) bogs are highly acidic (pH 3.5–4.2, Rydin & Jeglum 2013). Moreover, various *Sphagnum*-related local variables provide optimal conditions for mire invertebrates, like pH (Paje & Mossakowski 1984), *Sphagnum* species of hummocks (Drees et al. 2007), microtopography for carabids (Främb 1994), and soil humidity for spiders (Haase & Balkenhol 2015). Apart from unsuitable pH values, some forest generalists may not tolerate the openness or types of vegetation in mires.

Apart from *Sphagnum* cover, wet microsite-type cover (lawn and/or flark) and openness appeared to be key environmental conditions in hosting pristine mire invertebrate communities and creating suitable niches for mire specialist invertebrates (Chapter II). Similarly, *Sphagnum* mosses strongly affected open mire communities of carabid beetles and spiders, while deteriorated-mire-related variables (litter, standing wood volume, other mosses) were associated with tree-covered mire communities in urban mires (Chapter I). Interestingly, open parts of small (< 5.5 ha) mires resembled tree-covered mire communities of carabid

beetles and spiders, which is likely because of the shadiness of small mires. Indeed, the number of tall trees (Chapters II-IV) had a negative effect on individual specialist species and together with the covers of the dry microsite type (i.e. hummock) and non-*Sphagnum* mosses, and the average water table depth (Chapters II-III), these seemed to be key environmental variables in structuring drained mire invertebrate communities. Since tree biomass increases after the drainage of peatlands for forestry (Laine et al. 2006), it is no surprise that communities of drained mires contained mostly forest and generalist species.

5. CONCLUSIONS AND FUTURE RESEARCH

Generally, both mire drainage for forestry and high levels of urbanization resulted in biotic homogenization at local (site) and, subsequently, landscape levels through the loss of mire specialist species. However, these detrimental effects can be reduced or even reversed through ecological restoration and appropriate urban mire conservation. Indeed, mires support high biodiversity within urban and rural landscapes as they are inhabited by a number of mire and forest specialist species. The presence of these species decreases homogenization at the landscape level, since mire specialists are usually not found in other habitats (Desrochers & Duinen 2006, Spitzer & Danks 2006).

The challenge for ecological restoration is to reverse community homogenization and slow down or halt the loss of species. Despite the relatively short period of time since restoration, my results indicated that the abundance of most mire specialist species increased after restoration (Chapters II and IV). This rapid recovery may have been enhanced by a lack of dispersal barriers, as the restored mires form part of larger mires with varying proportions of unditched areas. These pristine or close-to-pristine patches likely provide refugia for mire species in close proximity of the drained and restored mires, and thus also serve as potential areas for recolonization of restored mires. My results, together with previous studies (e.g., Watts et al. 2008, Carroll et al. 2011, Elo et al. 2015) suggest that appropriate restoration actions in well-prioritized locations are likely to reverse the trend of biotic homogenization by facilitating specialist species. These results also lend some support to the idea that ecological restoration is a useful tool in reversing the extinction debt caused by degradation (Tilman et al. 1994, Hanski 2000) but also in creating species credit, i.e. in restoring the habitat to such an extent that species already locally extinct can recolonize the site (Hanski 2000, see also Cristofoli & Mahy 2010).

On the other hand, Chapter I suggests that naturally discrete communities of epigaeic arthropods are mainly driven by species sorting processes, which emphasizes the importance of local habitat conditions, while regional variables (and thus dispersal based mechanisms) are less important in the persistence of urban mire species and communities (Leibold et al. 2004). Thus, it seems that if local conditions are kept optimal, mire specialists are potentially able to survive in urban mires, to some extent irrespective of the level of urbanization (i.e. isolation) in the surrounding landscape. As local factors related to wetness and openness largely determine the survival of mire species (Chapters I-IV), conservational efforts should focus on promoting the quality of local habitat conditions (in particular natural hydrological regimes and openness) in both urban and rural mires. It is important to maintain the natural hydrological regime of mires since stable moisture availability is critical for *Sphagnum* growth (see McNeil & Waddington 2003), and *Sphagnum* cover in turn is important for the persistence of mire specialist arthropod species. Furthermore, mire openness should be maintained in urban and restored mires by removing taller trees, as this was demonstrated to have a positive effect on mire specialist species (Chapters II-III). However, this should be done with caution and mainly in sites where tree growth is enhanced by ditching in urban mires, since tree-cover is important for rare forest specialist species in these habitats. Generally, urban mires should be kept in as natural a state as possible, since only then can mire specialist species survive there and reduce biotic homogenization within cities.

Finally, appropriate prioritization of degraded sites for ecological restoration must be carefully considered, since resources for conservation and restoration are limited. In practice it appears that prioritization for restoration is seldom performed in a systematic manner. One reason might be a lack of appropriate landscape level data. Another reason is perhaps more unintentional: prioritization is difficult and even painful because once we start prioritizing we realize that in a world of competing interests and limited resources, every sensible thing we do is another sensible thing we do not (Gilbert 2011, Game et al. 2013). It is a simple fact that in a world of limited resources, the problem that we cannot help all species or restore all habitats, also called the conservation triage, is unavoidable (Hobbs & Kristjanson 2003, Bottrill et al. 2008, 2009, Kotiaho & Halme 2014). As a result, we must acknowledge that only a limited proportion of degraded areas can be restored. For example, the Convention on Biological Diversity has agreed that at least 15% of degraded ecosystems must be restored by 2020. However, the schedule and perhaps also the magnitude of this target is unrealistic (Kotiaho 2015). Whatever the fraction of the landscape we are going to restore, we should focus on areas where restoration will bring the greatest benefit for the investment. Issues that need to be

considered are the ecological quality of the site, the restorability of the site and the spatial location of the site. In well-connected areas, the quality of restoration sites can possibly be less than in areas that are not so well connected. The tendency of prioritizing habitats that are already very rare in the landscape will result in a network of not well connected sites. Such a network may have poor probabilities of being colonized by species and thus also experience high risks of extinction for those species that have been able to colonize the site. A better option would be to try to restore sites close to core areas of good condition habitats. Such chosen for restoration sites perhaps can even be poorer in habitat quality or represent more common habitat type. In our case, it appears that the sites chosen to be restored were already initially better for mire specialist species, thus indicating that the prioritization of restoration sites had been successful (Chapter IV). This conclusion is further supported by the observation that mire specialist species were able to recolonize the restored sites fairly rapidly after restoration.

In conclusion, results from this thesis are encouraging and suggest that ecological restoration may live up to the expectations placed on it. The time span of studies is still short, and continuous monitoring of the invertebrates is needed to fully understand the potential of ecological restoration of mires. As such, in order to enhance successful colonization and the establishment of viable mire specialist populations and communities after the restoration of drained mires, the following themes warrant attention in future research: (1) maximum allowable distance to repopulate restored mires from pristine(source) mires, (2) minimum size of restored mires, (3) landscape context (e.g. the amount of pristine mires in the landscape), (4) the effects of local adaptations on the success of re-establishment of mire specialist invertebrates (see e.g. Turlure et al. 2013), (5) the time scale for achieving desired conditions (Van Andel & Grootjans 2006), (6) the effects of climate change on mire invertebrates as there are predictions for dramatic vulnerability of mire ecosystems due to climate change (Essl et al. 2011), and (7) the role of adaptive management on mire invertebrates within restoration, especially during years of drought (see e.g., Carroll et al. 2011).

ACKNOWLEDGEMENTS

Above all I would like to express my sincere thanks to my supervisor Doc. D. Johan Kotze, without whom this thesis would not have come to light. Thank you for all your advice, support and help whenever I needed it. Thank you also for encouraging me to ask challenging scientific questions and to find solutions to scientific problems independently. As well, thank you for raising complicated questions on statistical issues - I have learned a lot from this! Finally, thank you, Johan, for our unforgettable trips to "those big bogs" - for our interesting discussions and good times in the field.

Also, I am thankful to my numerous collaborators, especially Prof. Janne S. Kotiaho and Pekka Punttila, who benevolently let me join the mire restoration project, helped me to unravel complicated mire restoration data, and kindly discussed statistical and paper preparation issues, as well as transferred my thinking into a broader perspective. It was indeed a great adventure to work with you!

Furthermore, I am grateful to Jouni Penttinen for his initial suggestion to join the mire restoration project and for his guidance, and to all the field workers and invertebrate identifiers: Anna Vuori, Olli J. Loukola, Olli Autio, Teemu Juselius and Timo Pajunen. Because of you it was possible to include so many taxa in this thesis. In addition, my special thanks goes to Doc. Leena Hamberg for introducing me to vegetation cover measurements and Doc. Pekka Pakarinen for kindly helping me in selecting suitable study sites for the first chapter of this thesis.

I warmly thank Prof. Jari Niemelä for creating a friendly and stimulating research environment at the Urban Ecology Research Group (UERG), as well as for providing valuable comments on the thesis summary and Chapter I. I would also like to thank all past and current UERG members for their support during all these years. Particularly, I would like to express my sincere thanks to Jarmo Saarikivi, whose call to somebody on a sunny day in 2012 linked me to Jouni Penttinen and changed the course of my thesis. And thank you, Jarmo, for translating the abstract of this thesis into Finnish. I would also like to thank Doc. Susanna Lehvävirta for her support and constructive criticism on my research. As well, I wish to thank Anna Ojala for her friendship and support, especially during those early days of my stay in Finland.

I am grateful to my advisory committee members, Prof. Otso Ovaskainen and Prof. Heikki Setälä for their valuable advice and comments during my PhD studies. I am greatly honored to have had Prof. Henrik G. Smith and Assoc. Prof. Terry A. Wheeler as pre-reviewers

of this thesis. I would like to thank both of them for their insightful thoughts, suggestions and questions. I highly appreciate it that Prof. Jonathan P. Sadler accepted the invitation to act as my opponent. I also thank Prof. Veijo Kaitala for serving as Custos in the public defense of my thesis.

I thank the funders which contributed to the completion of this thesis: The Otto A. Malm Foundation and the University of Helsinki. Also to the LUOVA doctoral programme, which provided travel funding.

Paskutinėmis šios padėkos eilutėmis siunčiu nuoširdų AČIŪ savo tėvams, Valei ir Pranui, už suteiktą galimybę eiti gamtininko keliu nuo pačių mažiausių dienų iki studentavimo, kad ir kokios sunkios sąlygos būtų buvusios. Taip pat esu labai dėkingas savo dviems mylimosioms - žmonai Kristinai ir dukrelei Ūlai Jorei, už jų neišsenkantį palaikymą, supratingumą, kantrybę ir dovanojamas šviesias dienas. Jums abiems labai AČIŪ!

REFERENCES

- Andel J Van, Grootjans A (2006) Concepts in restoration ecology. In: van Andel J, Aranson J (eds) Restoration ecology. Blackwell Publishing, Malden, Massachusetts, p 16–28
- Antonović I, Brigić A, Sedlar Z, Bedek J, Šoštarić R (2012) Terrestrial isopod community as indicator of succession in a peat bog. *Zookeys* 176:171–188
- Assmann T, Janssen J (1999) The Effect of Habitat Changes on the Endangered Ground Beetle *Carabus Nitens* (Coleoptera: Carabidae). *Journal of Insect Conservation* 3:107–116
- Autio O, Salmela J, Suhonen J (2013) Species richness and rarity of crane flies (Diptera, Tipuloidea) in a boreal mire. *Journal of Insect Conservation* 17:1125–1136
- Baars J-R, Murray DA, Hannigan E, Kelly-Quinn M (2014) Macroinvertebrate assemblages of small upland peatland lakes in Ireland. *Biology and Environment: Proceedings of the Royal Irish Academy* 114B:233–248
- Baguette M, Schtickzelle N (2006) Negative relationship between dispersal distance and demography in butterfly metapopulations. *Ecology* 87:648–654
- Baldwin A (2011) Plant communities of urban wetlands: patterns and controlling processes. In: Niemelä J, Breuste JH, Elmqvist T, Guntenspergen G, James P, McIntyre NE (eds) *Urban Ecology - Patterns, Processes, and Applications*. Oxford University Press, New York, p 77–84
- Bates D, Maechler M, Bolker B (2013) lme4: linear mixed-effects models using Eigen and S4 classes.
- Batzer DP, Wissinger SA (1996) Ecology of insect communities in nontidal wetlands. *Annual Review of Entomology* 41:75–100
- Bond NR, Lake PS (2003) Local habitat restoration in streams: Constraints on the effectiveness of restoration for stream biota. *Ecological Management and Restoration* 4:193–198
- Börschig C, Klein A-M, Wehrden H von, Krauss J (2013) Traits of butterfly communities change from specialist to generalist characteristics with increasing land-use intensity. *Basic and Applied Ecology* 14:547–554
- Bottrill MC, Joseph LN, Carwardine J, Bode M, Cook C, Game ET, Grantham H, Kark S, Linke S, McDonald-Madden E, Pressey RL, Walker S, Wilson KA, Possingham HP (2008) Is conservation triage just smart decision making? *Trends in Ecology and Evolution* 23:649–654
- Bottrill MC, Joseph LN, Carwardine J, Bode M, Cook C, Game ET, Grantham H, Kark S, Linke S, McDonald-Madden E, Pressey RL, Walker S, Wilson KA, Possingham HP (2009) Finite conservation funds mean triage is unavoidable. *Trends in Ecology and Evolution* 24:183–184

- Bowles ML, Jones MD (2012) Repeated burning of eastern tallgrass prairie increases richness and diversity, stabilizing late successional vegetation. *Ecological Applications* 23:464–478
- Bullock JM, Aronson J, Newton AC, Pywell RF, Rey-Benayas JM (2011) Restoration of ecosystem services and biodiversity: conflicts and opportunities. *Trends in Ecology and Evolution* 26:541–549
- Carroll MJ, Dennis P, Pearce-Higgins JW, Thomas CD (2011) Maintaining northern peatland ecosystems in a changing climate: effects of soil moisture, drainage and drain blocking on craneflies. *Global Change Biology* 17:2991–3001
- Ceballos G, Ehrlich PR, Barnosky AD, García A, Pringle RM, Palmer TM (2015) Accelerated modern human-induced species losses: Entering the sixth mass extinction. *Science Advances* 1:e1400253
- Chapman S, Buttler A, Francez A-J, Laggoun-Défarge F, Vasander H, Schloter M, Combe J, Grosvernier P, Harms H, Epron D, Gilbert D, Mitchell E (2003) Exploitation of northern peatlands and biodiversity maintenance: a conflict between economy and ecology. *Frontiers in Ecology and the Environment* 1:525–532
- Clavel J, Julliard R, Devictor V (2011) Worldwide decline of specialist species: toward a global functional homogenization? *Frontiers in Ecology and the Environment* 9:222–228
- Coulson JC, Butterfield JEL, Henderson E (1990) The Effect of Open Drainage Ditches on the Plant and Invertebrate Communities of Moorland and on the Decomposition of Peat. *Journal of Applied Ecology* 27:549–561
- Cristofoli S, Mahy G (2010) Colonisation credit in recent wet heathland butterfly communities. *Insect Conservation and Diversity* 3:83–91
- Dennis RLH, Eales HT (1997) Patch occupancy in *Coenonympha tullia* (Muller, 1764) (Lepidoptera: Satyrinae): habitat quality matters as much as patch size and isolation. *Journal of Insect Conservation* 1:167–176
- Desrochers A, Duinen G-J van (2006) Peatland Fauna. In: Wieder PDRK, Vitt PDDH (eds) *Boreal Peatland Ecosystems*. Springer Berlin Heidelberg, p 67–100
- Devictor V, Clavel J, Julliard R, Lavergne S, Mouillot D, Thuiller W, Venail P, Villéger S, Mouquet N (2010) Defining and measuring ecological specialization. *Journal of Applied Ecology* 47:15–25
- D J Futuyma, Moreno G (1988) The Evolution of Ecological Specialization. *Annual Review of Ecology and Systematics* 19:207–233
- Drees C, Matern A, Vermeulen R, Assmann T (2007) The influence of habitat quality on populations: a plea for an amended approach in the conservation of *Agonum ericeti*. *Baltic Journal of Coleopterology* 7:1–8
- Drees C, Vries HD, Härdtle W, Matern A, Persigehl M, Assmann T (2011b) Genetic erosion in a stenotopic heathland ground beetle (Coleoptera: Carabidae): a matter of habitat size? *Conservation Genetics* 12:105–117

- Drees C, Zumstein P, Buck-Dobrick T, Härdtle W, Matern A, Meyer H, Oheimb G von, Assmann T (2011a) Genetic erosion in habitat specialist shows need to protect large peat bogs. *Conservation Genetics* 12:1651–1656
- Drinan TJ, Foster GN, Nelson BH, O'Halloran J, Harrison SSC (2013) Macroinvertebrate assemblages of peatland lakes: Assessment of conservation value with respect to anthropogenic land-cover change. *Biological Conservation* 158:175–187
- Duinen GA van, Zhuge Y, Verberk WCEP, Brock AMT, Kleef HH van, Leuven RSEW, Velde G van der, Esselink H (2006) Effects of Rewetting Measures in Dutch Raised Bog Remnants on Assemblages of Aquatic Rotifera and Microcrustaceans. *Hydrobiologia* 565:187–200
- EC (1992) Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. *Official Journal L* 206:7–50
- Elo M, Kareksela S, Aapala K, Haapalehto T, Vuori H, Kotiaho JS (in press) The mechanistic basis of changes in community assembly in relation to anthropogenic disturbance and productivity. *Ecosphere*
- Elo M, Penttinen J, Kotiaho JS (2015) The effect of peatland drainage and restoration on Odonata species richness and abundance. *BMC Ecology* 15:11
- Essl F, Dullinger S, Moser D, Rabitsch W, Kleinbauer I (2011) Vulnerability of mires under climate change: implications for nature conservation and climate change adaptation. *Biodiversity and Conservation* 21:655–669
- Evans D (2006) The habitats of the European Union habitats directive. *Biology and Environment: Proceedings of the Royal Irish Academy* 106B:167–173
- Evans D (2012) Building the European Union's Natura 2000 network. *Nature Conservation* 1:11–26
- Faeth SH, Saari S, Bang C (2012) *Urban Biodiversity: Patterns, Processes and Implications for Conservation*. In: eLS. John Wiley & Sons, Ltd
- Fahrig L (2001) How much habitat is enough? *Biological Conservation* 100:65–74
- Fowles AP, Bailey MP, Hale AD (2004) Trends in the recovery of a rosy marsh moth *Coenophila subrosea* (Lepidoptera, Noctuidae) population in response to fire and conservation management on a lowland raised mire. *Journal of Insect Conservation* 8:149–158
- Främbs H (1994) The importance of habitat structure and food supply for carabid beetles (Coleoptera, Carabidae) in peat bogs. *Memoirs of the Entomological Society of Canada* 126:145–159
- Game ET, Kareiva P, Possingham HP (2013) Six Common Mistakes in Conservation Priority Setting. *Conservation Biology* 27:480–485
- Gilbert D (2011) Buried by bad decisions. *Nature* 474:275–277

- Gunnarsson U, Malmer N, Rydin H (2002) Dynamics or constancy in Sphagnum dominated mire ecosystems? A 40-year study. *Ecography* 25:685–704
- Gunnarsson U, Rydin H, Sjörs H (2000) Diversity and pH Changes after 50 Years on the Boreal Mire Skattlösbergs Stormosse, Central Sweden. *Journal of Vegetation Science* 11:277–286
- Haapalehto TO, Vasander H, Jauhiainen S, Tahvanainen T, Kotiaho JS (2011) The Effects of Peatland Restoration on Water-Table Depth, Elemental Concentrations, and Vegetation: 10 Years of Changes. *Restoration Ecology* 19:587–598
- Haase H, Balkenhol B (2015) Spiders (Araneae) as subtle indicators for successional stages in peat bogs. *Wetlands Ecology and Management* 23:453–466
- Hallanaro E-L, Pylvanainen M (2002) Nature in Northern Europe: Biodiversity in a Changing Environment. Nordic Council of Ministers, Copenhagen, Denmark
- Halme E, Niemela J (1993) Carabid beetles in fragments of coniferous forest. *Annales Zoologici Fennici* 30:17–30
- Hannigan E, Kelly-Quinn M (2012) Composition and structure of macroinvertebrate communities in contrasting open-water habitats in Irish peatlands: implications for biodiversity conservation. *Hydrobiologia* 692:19–28
- Hanski I (1998) Metapopulation dynamics. *Nature* 396:41–49
- Hanski I (2000) Extinction debt and species credit in boreal forests: modelling the consequences of different approaches to biodiversity conservation. *Annales Zoologici Fennici* 37:271–280
- Hanski I, Ovaskainen O (2002) Extinction Debt at Extinction Threshold. *Conservation Biology* 16:666–673
- Hanski I, Ovaskainen O (2003) Metapopulation theory for fragmented landscapes. *Theoretical Population Biology* 64:119–127
- Harrison XA (2014) Using observation-level random effects to model overdispersion in count data in ecology and evolution. *PeerJ* 2:e616
- Hobbs RJ, Kristjanson LJ (2003) Triage: How do we prioritize health care for landscapes? *Ecological Management and Restoration* 4:S39–S45
- Hochkirch A, Adorf F (2007) Effects of prescribed burning and wildfires on Orthoptera in Central European peat bogs. *Environmental Conservation* 34:225–235
- Hollmen A, Välimäki P, Itämies J, Oksanen J (2008) The value of open power line habitat in conservation of ground beetles (Coleoptera: Carabidae) associated with mires. *Journal of Insect Conservation* 12:163–177
- Holmes PR, Boyce DC, Reed DK (1993) The ground beetle (Coleoptera: Carabidae) fauna of welsh peatland biotopes: Factors influencing the distribution of ground beetles and conservation implications. *Biological Conservation* 63:153–161

- Hutchinson GE (1957) Concluding Remarks. Cold Spring Harbor Symposia on Quantitative Biology 22:415–427
- Joosten H, Clarke D (2002) Wise use of mires and peatlands – Background and principles including a framework for decision-making. International Mire conservation Group and International Peat Society, <http://www.mirewiseuse.com>, Saarijärvi, Finland
- Joy J, Pullin AS (1997) The effects of flooding on the survival and behaviour of overwintering large heath butterfly *Coenonympha tullia* larvae. Biological Conservation 82:61–66
- Kamayev IO (2012) Spider (Aranei) assemblages in bog-forest ecotone of the northern taiga subzone (Eastern Fennoscandia). Entomological Review 92:471–485
- Kocher SD, Williams EH (2000) The diversity and abundance of North American butterflies vary with habitat disturbance and geography. Journal of Biogeography 27:785–794
- 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
- Kotiaho JS (2015) Finland: Target for ecosystem repair is impractical. Nature 519:33–33
- Kotiaho JS, Halme P (2014) Aggregating protected habitats embraces implicit habitat conservation triage. Proceedings of Peerage of Science 1:e5
- Kotze DJ, Lehvavirta S, Koivula M, O’Hara RB, Spence JR (2012a) Effects of habitat edges and trampling on the distribution of ground beetles (Coleoptera, Carabidae) in urban forests. Journal of Insect Conservation 16:883–897
- Kotze DJ, O’Hara RB, Lehvavirta S (2012b) Dealing with Varying Detection Probability, Unequal Sample Sizes and Clumped Distributions in Count Data. PLoS ONE 7:e40923
- Laiho R, Silvan N, Cárcamo H, Vasander H (2001) Effects of water level and nutrients on spatial distribution of soil mesofauna in peatlands drained for forestry in Finland. Applied Soil Ecology 16:1–9
- Laine J, Laiho R, Minkkinen K, Vasander H (2006) Forestry and Boreal Peatlands. In: Wieder PDRK, Vitt PDDH (eds) Boreal Peatland Ecosystems. Springer Berlin Heidelberg, p 331–357
- Laine J, Vasander H, Laiho R (1995) Long-Term Effects of Water Level Drawdown on the Vegetation of Drained Pine Mires in Southern Finland. Journal of Applied Ecology 32:785–802
- Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, Holt RD, Shurin JB, Law R, Tilman D, Loreau M, Gonzalez A (2004) The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7:601–613
- Lensu T, Komonen A, Hiltula O, Päivinen J, Saari V, Kotiaho JS (2011) The role of power line rights-of-way as an alternative habitat for declined mire butterflies. Journal of Environmental Management 92:2539–2546

- Lesica P, Kannowski PB (1998) Ants Create Hummocks and Alter Structure and Vegetation of a Montana Fen. *The American Midland Naturalist* 139:58–68
- Levins R (1968) *Evolution in Changing Environments: Some Theoretical Explorations*. Princeton University Press
- Lindholm T, Heikkilä R (2006) Destruction of mires in Finland. In: Lindholm T. and Heikkilä R. (eds.) *Finland - land of mires*. Finnish Environment Institute (SYKE), Helsinki, p 179–192
- Mauquoy D, Bennett KD (2013) Peatlands in Tierra del Fuego. In: Rydin H and Jeglum JK (eds.) *The Biology of Peatlands*. Oxford University Press, Oxford, p 236–240
- Mazerolle MJ, Poulin M, Lavoie C, Rochefort L, Desrochers A, Drolet B (2006) Animal and vegetation patterns in natural and man-made bog pools: implications for restoration. *Freshwater Biology* 51:333–350
- McKinney null, Lockwood null (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology and Evolution* 14:450–453
- McNeil P, Waddington JM (2003) Moisture controls on Sphagnum growth and CO₂ exchange on a cutover bog. *Journal of Applied Ecology* 40:354–367
- Merivee E, Ploomi A, Milius M, Luik A, Heidema M (2005) Electrophysiological identification of antennal pH receptors in the ground beetle *Pterostichus oblongopunctatus*. *Physiological Entomology* 30:122–133
- Molen PC van der, Wijmstra TA (1994) The Thermal Regime of Hummock-Hollow Complexes on Clara Bog, Co. Offaly. *Biology and Environment: Proceedings of the Royal Irish Academy* 94B:209–221
- Noreika N, Kotze DJ (2012) Forest edge contrasts have a predictable effect on the spatial distribution of carabid beetles in urban forests. *Journal of Insect Conservation* 16:867–881
- O’Hara RB, Kotze DJ (2010) Do not log-transform count data. *Methods in Ecology and Evolution* 1:118–122
- Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O’Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H (2013) *vegan: Community Ecology Package*.
- Olden JD, Leroy Poff N, Douglas MR, Douglas ME, Fausch KD (2004) Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology and Evolution* 19:18–24
- Paje F, Mossakowski D (1984) pH-preferences and habitat selection in carabid beetles. *Oecologia* 64:41–46
- Palmer MA, Ambrose RF, Poff NL (1997) Ecological Theory and Community Restoration Ecology. *Restoration Ecology* 5:291–300

- Pickett STA, Kolasa J, Armesto JJ, Collins SL (1989) The Ecological Concept of Disturbance and Its Expression at Various Hierarchical Levels. *Oikos* 54:129–136
- Polus E, Vandewoestijne S, Choult J, Baguette M (2007) Tracking the effects of one century of habitat loss and fragmentation on calcareous grassland butterfly communities. *Biodiversity and Conservation* 16:3423–3436
- Poulin M, Rochefort L, Quinty F, Lavoie C (2005) Spontaneous revegetation of mined peatlands in eastern Canada. *Canadian Journal of Botany* 83:539–557
- Price EAC (2003) *Lowland Grassland and Heathland Habitats*. Routledge
- QGIS Development Team (2013) QGIS Geographic Information System. Open Source Geospatial Foundation Project
- Ratcliffe DA (1959) The Vegetation of the Carneddau, North Wales: I. Grasslands, Heaths and Bogs. *Journal of Ecology* 47:371–413
- R Development Core Team (2013) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna
- Richter CJJ (1970) Aerial dispersal in relation to habitat in eight wolf spider species (*Pardosa*, Araneae, Lycosidae). *Oecologia* 5:200–214
- Rochefort L (2000) *Sphagnum: A Keystone Genus in Habitat Restoration*. *The Bryologist* 103:503–508
- Rochefort L, Quinty F, Campeau S, Johnson K, Malterer T (2003) North American approach to the restoration of *Sphagnum* dominated peatlands. *Wetlands Ecology and Management* 11:3–20
- Rydin H, Gunnarsson U, Sundberg S (2006) The Role of *Sphagnum* in Peatland Development and Persistence. In: Wieder PDRK, Vitt PDDH (eds) *Boreal Peatland Ecosystems*. Springer Berlin Heidelberg, p 47–65
- Rydin H, Jeglum JK (2013) *The Biology of Peatlands*. Oxford University Press, Oxford
- Salmela J, Ilmonen J (2005) Crane fly (Diptera: Tipuloidea) fauna of a boreal mire system in relation to mire trophic status: implications for conservation and bioassessment. *Journal of Insect Conservation* 9:85–94
- Saucier WJ (1955) *Principles of meteorological analysis*. University of Chicago Press
- Savage J, Wheeler TA, Moores AMA, Taillefer AG (2011) Effects of Habitat Size, Vegetation Cover, and Surrounding Land Use on Diptera Diversity in Temperate Nearctic Bogs. *Wetlands* 31:125–134
- Schikora H-B (1994) Changes in the terrestrial spider fauna (Arachnida: Araneae) of a North German raised bog disturbed by human influence. 1964-1965 and 1986-1987: a comparison. *Memoirs of the Entomological Society of Canada* 126:61–71

- Schtickzelle N, Mennechez G, Baguette M (2006) Dispersal depression with habitat fragmentation in the bog fritillary butterfly. *Ecology* 87:1057–1065
- Silvan N, Laiho R, Vasander H (2000) Changes in mesofauna abundance in peat soils drained for forestry. *Forest Ecology and Management* 133:127–133
- Skaug H, Fournier D, Bolker B, Magnusson A, Nielsen A (2014) Generalized linear mixed models using AD model builder.
- Spitzer K, Bezděk A, Jaroš J (1999) Ecological Succession of a Relict Central European Peat Bog and Variability of Its Insect Biodiversity. *Journal of Insect Conservation* 3:97–106
- Spitzer K, Danks HV (2006) Insect biodiversity of boreal peat bogs. *Annual Review of Entomology* 51:137–161
- Šula J, Spitzer K (2000) Allozyme polymorphism in isolated populations of the moth *Coenophila subrosea* (Lepidoptera: Noctuidae) from three Central European peat bogs. *European Journal of Entomology* 97:7–12
- Swengel AB, Swengel SR (2010a) High and dry or sunk and dunked: lessons for tallgrass prairies from quaking bogs. *Journal of Insect Conservation* 15:165–178
- Swengel AB, Swengel SR (2010b) The butterfly fauna of Wisconsin bogs: lessons for conservation. *Biodiversity and Conservation* 19:3565–3581
- Taillefer AG, Wheeler TA (2010) Effect of drainage ditches on Brachycera (Diptera) diversity in a southern Quebec peatland. *The Canadian Entomologist* 142:160–172
- Taillefer AG, Wheeler TA (2012) Community assembly of Diptera following restoration of mined boreal bogs: taxonomic and functional diversity. *Journal of Insect Conservation* 16:165–176
- Taillefer AG, Wheeler TA (2013) Animal Colonization of Restored Peatlands: Inoculation of Plant Material as a Source of Insects. *Restoration Ecology* 21:140–144
- Thompson DBA, MacDonald AJ, Marsden JH, Galbraith CA (1995) Upland heather moorland in Great Britain: A review of international importance, vegetation change and some objectives for nature conservation. *Biological Conservation* 71:163–178
- Tilman D, May RM, Lehman CL, Nowak MA (1994) Habitat destruction and the extinction debt. *Nature* 371:65–66
- Turetsky MR, Louis VLS (2006) Disturbance in Boreal Peatlands. In: Wieder PDRK, Vitt PDDH (eds) *Boreal Peatland Ecosystems*. Springer Berlin Heidelberg, p 359–379
- Turlure C, Choult J, Baguette M, Dyck H Van (2010) Microclimatic buffering and resource-based habitat in a glacial relict butterfly: significance for conservation under climate change. *Global Change Biology* 16:1883–1893
- Turlure C, Dyck H Van, Schtickzelle N, Baguette M (2009) Resource-based habitat definition, niche overlap and conservation of two sympatric glacial relict butterflies. *Oikos* 118:950–960

- Turlure C, Radchuk V, Baguette M, Dyck H Van, Schtickzelle N (2011) On the significance of structural vegetation elements for caterpillar thermoregulation in two peat bog butterflies: *Boloria eunomia* and *B. aquilonaris*. *Journal of Thermal Biology* 36:173–180
- Turlure C, Radchuk V, Baguette M, Meijrink M, Burg A den, Vries MW, Duinen G-J (2013) Plant quality and local adaptation undermine relocation in a bog specialist butterfly. *Ecology and Evolution* 3:244–254
- Turner IM (1996) Species Loss in Fragments of Tropical Rain Forest: A Review of the Evidence. *Journal of Applied Ecology* 33:200–209
- Vandewoestijne S, Baguette M (2004) Genetic population structure of the vulnerable bog fritillary butterfly. *Hereditas* 141:199–206
- Verberk WCEP, Duinen GA van, Brock AMT, Leuven RSEW, Siepel H, Verdonschot PFM, Velde G van der, Esselink H (2006) Importance of landscape heterogeneity for the conservation of aquatic macroinvertebrate diversity in bog landscapes. *Journal for Nature Conservation* 14:78–90
- Verberk WCEP, Kuper JT, Duinen GA van, Esselink J (2006) Changes in macroinvertebrate richness and diversity following large scale rewetting measures in a heterogeneous bog landscape. *Proceedings of the Section Experimental and Applied Entomology of the Netherlands Entomological Society (NEV)* 17:27–36
- Verberk WCEP, Leuven RSEW, Duinen GA van, Esselink H (2010) Loss of environmental heterogeneity and aquatic macroinvertebrate diversity following large-scale restoration management. *Basic and Applied Ecology* 11:440–449
- Vitt DH (2006) Functional Characteristics and Indicators of Boreal Peatlands. In: Wieder PDRK, Vitt PDDH (eds) *Boreal Peatland Ecosystems*. Springer Berlin Heidelberg, p 9–24
- Vitt P, Havens K, Kramer AT, Sollenberger D, Yates E (2010) Assisted migration of plants: Changes in latitudes, changes in attitudes. *Biological Conservation* 143:18–27
- Vries HHD, Boer PJD (1990) Survival of Populations of *Agonum Ericeti* Panz. (Col., Carabidae) in Relation To Fragmentation of Habitats. *Netherlands Journal of Zoology* 40:484–498
- Vries HH de, Boer PJ den, Dijk TS van (1996) Ground beetle species in heathland fragments in relation to survival, dispersal, and habitat preference. *Oecologia* 107:332–342
- Watts CH, Clarkson BR, Didham RK (2008) Rapid beetle community convergence following experimental habitat restoration in a mined peat bog. *Biological Conservation* 141:568–579
- Watts CH, Didham RK (2006a) Rapid recovery of an insect-plant interaction following habitat loss and experimental wetland restoration. *Oecologia* 148:61–69
- Watts CH, Didham RK (2006b) Influences of Habitat Isolation on Invertebrate Colonization of *Sporanthus ferrugineus* in a Mined Peat Bog. *Restoration Ecology* 14:412–419

- Watts CH, Mason NWH (2015) If we build – they mostly come: partial functional recovery but persistent compositional differences in wetland beetle community restoration. *Restoration Ecology* 23:555–565
- Watts C, Thornburrow D, Clarkson B, Dean S (2013) Distribution and abundance of a threatened stem-boring moth, *Houdinia flexilissima*, (Lepidoptera: Batrachedridae) in New Zealand peat bogs. *The Journal of Research on the Lepidoptera* 46:81–89
- Weking S, Hermann G, Fartmann T (2013) Effects of mire type, land use and climate on a strongly declining wetland butterfly. *Journal of Insect Conservation* 17:1081–1091
- Whatley MH, Loon EE van, Cerli C, Vonk JA, Geest HG van der, Admiraal W (2014a) Linkages between benthic microbial and freshwater insect communities in degraded peatland ditches. *Ecological Indicators* 46:415–424
- Whatley MH, Loon EE van, Dam H van, Vonk JA, Geest HG van der, Admiraal W (2014b) Macrophyte loss drives decadal change in benthic invertebrates in peatland drainage ditches. *Freshwater Biology* 59:114–126
- Whinam J, Hope G, Clarkson B (2012) Mires Down Under – the Peatlands of Australasia. In: Tapio Lindholm and Raimo Heikkilä (eds.) *Mires from pole to pole*. Finnish Environment Institute (SYKE), Helsinki, p 401–417
- Whitehouse NJ, Langdon PG, Bustin R, Galsworthy S (2008) Fossil insects and ecosystem dynamics in wetlands: implications for biodiversity and conservation. *Biodiversity and Conservation* 17:2055–2078
- Wilson PJ, Provan J (2003) Effect of habitat fragmentation on levels and patterns of genetic diversity in natural populations of the peat moss *Polytrichum commune*. *Proceedings of the Royal Society of London B: Biological Sciences* 270:881–886
- Wortley L, Hero J-M, Howes M (2013) Evaluating Ecological Restoration Success: A Review of the Literature. *Restoration Ecology* 21:537–543

“The thesis is a piece of good ecological work contributing to our general understanding of disturbance ecology, but also have a large applied value when it comes to informing habitat restoration of mires.”

-Henrik G. Smith

“This dissertation addresses some key gaps in our knowledge of such systems in a northern European context.”

-Terry A. Wheeler

“Many thanks for this interesting and worthwhile study. <...> Urban mires are indeed a fascinating topic and a well suited ecosystem to test effects of urbanisation on biodiversity.”

-Biodiversity and Conservation

“Good paper discussing the potential for mire restoration in encouraging repopulation by mire specialists and other invertebrates.”

-Restoration Ecology

“It could serve as a textbook example of how to conduct landscape-scale experiments, and it offers a fresh exception to case-studies conducted at a single site only.”

-Peerage of Science

“In conservation terms, this study offers many benefits for policy makers...”

-Peerage of Science

ISBN 978-951-51-1951-3 (paperback)

ISBN 978-951-51-1952-0 (PDF)

<http://ethesis.helsinki.fi>

UNIGRAFIA

HELSINKI 2016