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University of Turku

Faculty of Science and Engineering
Department of Biology
Doctoral programme in Biology, Geography and Geology (BGG)

Supervised by

Dr. Jukka Suhonen
Department of Biology
University of Turku, Finland

Professor Kai Norrdahl
Department of Biology
University of Turku, Finland

Reviewed by

Professor Robby Stoks
Section Ecology,
Evolution and Conservation Biology,
Department of Biology
University of Ku Leuven, Belgium

Senior Research Scientist Jani Heino
Section Freshwater Centre
Finnish Environment Institute, Oulu,
Finland

Opponent

Professor Jouni Taskinen
Department of Biological and
Environment Sciences,
University of Jyväskylä, Finland

ISBN 978-951-29-7988-2 (PRINT)
ISBN 978-951-29-7989-9 (PDF)
ISSN 0082-6979 (Print)
ISSN 2343-3183 (Online)
Painosalama Oy, Turku, Finland 2020

Dedicated to my daughters Aava and Tuuli

UNIVERSITY OF TURKU
Faculty of Science and Engineering
Department of Biology
ESA KORKEAMÄKI: Local extinction risk and community structure of Odonata in Fennoscandia
Doctoral Dissertation, 89 pp.
Doctoral Programme in Biology, Geography and Geology (BGG)
March 2020

ABSTRACT

A key need in conservation biology is to identify the ecological traits of a species that make it vulnerable. This thesis focuses on population traits and extinction risk of dragonflies and damselflies (order Odonata) in Finland and Sweden. First, I examined whether species occupancy frequency distributions (SOFD) of odonates vary among the lakes and ponds of four geographical regions. Second, I determined the main habitats, species traits, and local population distributions of Odonata in Central Finland.

I found that in the southern regions, the SOFD was dominated by species that occur at few sites, while in the northern regions the distribution was bimodal. In the northern parts of the range, rare species inhabited only high-quality sites. Size of the geographical range, breeding habitat requirements, and degree of generalism/specialism largely explained the observed variation in species occupancy frequency.

Specialized species with limited distributions had a greater extinction risk than widely distributed generalist species. However, when the effect of species' geographical range sizes was controlled, I found that extinction risk was actually lower for specialist species than for generalist species, probably due to the fact that generalist species occur in both low- and high-quality habitats. In particular, an extremely high extinction rate was found for peatland-associated species and dynamic lotic headwater populations. Taken together, my results indicate that extinction risk is shaped by the relationship between species population size, distribution, specialization, and habitat quality. The results of this thesis are consistent with existing predictions of species vulnerability and source-sink theory. In conclusion, my research highlights the necessity for conservation biologists to study the quality of freshwater habitats, because this is likely to be an important factor affecting the likelihood of extinction for populations in aquatic environments.

KEYWORDS: core-satellite species hypothesis, extinction risk, habitat quality, Odonata, species occupancy frequency, source-sink dynamics

TURUN YLIOPISTO
Luonnontieteiden ja tekniikan tiedekunta
Biologian laitos
ESA KORKEAMÄKI: Sudenkorentopopulaatioiden häviämisriski ja niiden eliöyhteisöjen rakenne Fennoskandiassa
Väitöskirja, 89 s.
Biologian, maantieteen ja geologian tohtoriohjelma
Maaliskuu 2020

TIIVISTELMÄ

Luonnonsuojelubiologiassa yksi keskeinen tarve on määrittää, mitkä ekologiset ominaisuudet vaikuttavat populaatioiden häviämiseen elinympäristöistään. Väitöskirjassani tutkin sudenkorentojen (Odonata) populaatioiden ekologisia piirteitä ja Suomessa ja Ruotsissa. Aluksi selvitin, Fennoskandian sudenkorentoyhteisöjen rakennetta neljällä eri maantieteellisellä alueella. Väitöskirjan muissa osioissa keskityin Keski-Suomen sudenkorentopopulaatioiden häviämisriskiin ja sen syihin. Sukupuuttoriskin selvittämiseksi aiemmin kartoitetuilla paikoilla toistettiin sudenkorentokartoitukset.

Eteläisimmissä vesistöissä sudenkorentoyhteisö koostui harvoissa paikoissa esiintyvistä lajeista (satelliittilajit), mutta pohjoisimmissa vesistöissä sudenkorentoyhteisö painottui kaksijakoisesti joko ydin- tai satelliittilajeihin. Levinneisyysalueiden rajoilla näyttää satelliittilajeilla olevan populaatioita vain niille parhaiten soveltuvissa elinympäristöissä. Biologiset tekijät, kuten lajien levinneisyysalue, lisääntymisalueet sekä lajien erikoistuminen johonkin elinympäristötyyppiin, näyttävät selittävän sudenkorentoyhteisöissä esiintyviä eroja.

Laajalle levinneiden ja erilaissa elinympäristötyypeissä esiintyvien lajien populaatioiden riski hävitä oli pieni. Kuitenkin, kun levinneisyyden vaikutus populaatioiden häviämiseen oli kontrolloitu, havaittiin, että ns. habitaattispesialistien populaatioiden häviämisriski olikin pienempi kuin ns. generalistien. Tämä voi johtua siitä syystä, että populaatioiden elinkyky huonolaatuisissa nielualueissa on heikkoa, koska säilyminen on lähdealueilta tulevan muuton varassa. Häviämisriski oli suurin suolla elävillä populaatioilla ja pienissä, häiriöille herkissä virtavesissä. Tulokset osoittavat, että populaation koon lisäksi lajien levinneisyys, erikoistumisaste ja elinympäristön laatu vaikuttavat populaatioiden häviämisriskiin. Väitöskirjani tulokset ovat yhteensopivia lähde-nielu hypoteesin ja luonnonsuojelubiologian ennustamien häviämisherkkyyksien kanssa. Tutkimukseni korostaa tarvetta tutkia elinympäristöjen laatua, koska sillä näyttää olevan merkittävä vaikutus eliöiden sukupuuttoriskiin.

AVAINSANAT: core-satellite species hypothesis, extinction risk, habitat quality, Odonata, species occupancy frequency, source-sink dynamics

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List of Original Publications

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

I Korkeamäki, E., Elo, M., Sahlen, G., Salmela, J. & Suhonen J., 2018. Regional variations in occupancy frequency distributions patterns between odonate assemblages in Fennoscandia. *Ecosphere* 9:1-15.

II Korkeamäki, E. & Suhonen, J., 2002. Distribution and habitat specialization of species affect local extinctions in dragonfly Odonata populations. *Ecography* 25:459-465.

III Suhonen, J., Hilli-Lukkarinen, M., Korkeamäki, E., Kuitunen, M., Kullas, J., Penttinen, J. & Salmela, J., 2010. Local extinction probability of an odonate population was higher in the sink than in the source habitat patches. *Conservation Biology* 24:1148-1153.

IV Suhonen, J., Korkeamäki, E., Salmela, J. & Kuitunen, M., 2014. Risk of Local Extinction of Odonata Freshwater Habitat Generalists and habitat Specialists. *Conservation Biology* 28:783-789.

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Author contributions to the original publications:

	I	**II**	**III**	**IV**
Original idea	JS, EK	JS, EK	EK, JS	JS, EK
Field work/Data collection	EK, GS, JSa, ME	EK	EK, JSa, JP, JK, MH-L	EK, JSa, JP, JK
Data handling	EK, JS, GS, ME	EK, JS	JS, EK	JS, EK
Analysis	JS	JS, EK	JS	JS, EK
Writing	EK, JS, ME, GS	EK, JS	JS, EK, JS, MK	JS, EK, JSa, MK

EK = Esa Korkeamäki, JS = Jukka Suhonen, JSa = Jukka Salmela, GS = Göran Sahlen, MK = Markku Kuitunen, ME = Merja Elo, MH-L = Milla Hilli-Lukkarinen, JP = Jouni Penttinen, JK = Johanna Kullas

1 Introduction

1.1 Biodiversity crisis globally and locally

Species extinction and ecosystem degradation are proceeding rapidly and at an ever-accelerating pace. Studies of the fossil record have suggested that, naturally, about one to five species should be expected to go extinct each year. Instead, recent estimates place the current rate of species loss approximately 1000 times higher than this background rate (De Vos et al. 2015). The Loss of biodiversity is worldwide and consist of terrestrial, ocean and freshwater habitats (e.g. Blowes et al. 2019).

Over a quarter of all species assessed by the IUCN have been classified as threatened with extinction. Numerous aquatic species, such as damselfly and dragonfly (Odonata) species in the temperate zone, have declined in their distributions and abundance since the second half of the 20th century (Kalkman et al. 2008) as a consequence of alterations in their aquatic habitats. A recent IUCN assessment indicated that 10% of the world´s Odonata species are threatened with extinction (Sánchez-Bayo & Wyckhuys 2019). The most important aspect of biodiversity loss is the extinction of local populations. Simply put, if fewer individuals enter a population, through birth or immigration, than leave it, through death or emigration, the local population declines. Local extinctions may ultimately lead to the loss of a species if this process is not counterbalanced by colonization and range expansion.

1.2 Species distribution or range size

Temperature is likely the single most important abiotic factor limiting insect survival in temperate zones. By itself, however, temperature is a poor predictor of insect distributions due to the effects of many other abiotic factors and species interactions (Fält-Nordman 2018). At a fundamental level, the presence of suitable habitat patches, in which both the appropriate abiotic and biotic factors are present, determines a species’ occupancy and abundance. Together, habitat patches form a landscape mosaic and the presence of a given species in a patch may be a function of a patch’s size and isolation, but also of the type of neighboring habitats (Andrén 1994).

The shape of the species occupancy frequency distribution (SOFD) is one of the most studied areas in community ecology (see reviews by McGeoch & Gaston 2002; Jenkins 2011). In natural communities, most of the species occur either at a few sites (satellite species; rare species) or at many sites (core species; common species), forming a bimodal core-satellite pattern (Hanski 1999). Therefore, dynamics in local abundance and regional distribution are independent (Hanski 1982; Brown 1984).

Immigration from nearby populations may enhance the persistence of an extinction-prone population; in this way, the distribution or geographical range of a species plays an important role in its ability to colonize a potential habitat. Generally, species with a wide distribution are locally abundant, whereas the populations of a species with a narrow distribution are small (Andrewartha & Birch 1954; Hanski 1982; Hanski & Gyllenberg 1997). The probability of local population extinction increases with decreasing population size (O´Grady et al. 2004) and reduces with intraspecific immigration from nearby habitats. Therefore widely distributed species generally have a smaller extinction risk than species with a limited distribution (Hanski 1982; Collen et al. 2011).

1.3 Problems of compromised populations

A population’s survival is affected by numerous internal and external factors. Internal factors include population density and demographic structure, while external factors relate to interactions with other species and the impact of the habitat, and therefore comprise both biotic and abiotic relationships. Small populations have been proven to have a relatively high extinction risk, and hence a shorter expected lifetime, than large ones (e.g. Diamond 1984; Pimm et al. 1988; Schoener & Spiller 1992; Primack 1993). However, population size alone can be a poor predictor of extinction, because many other closely linked factors may have an opposite (Woodroffe & Ginsberg 1998) or synergistic (Davies et al. 2004) effect on local extinction risk. For example, the presence of strong competitors within the same trophic level or of predators and/or parasites would place more pressure on a local population. The risk of local extinction of a population increases with its degree of isolation and reduced immigration from nearby populations. Ultimately, however, population extinction is the product of internal factors, such as when reduced individual survival, diminished breeding success, isolation, and insufficient effective population size drive populations to extinction.

1.4 Habitat changes and loss of habitat quality

The factors that drive species and populations to extinction are almost always linked, either directly or indirectly, to alterations in the environment (Ehrlich 1988).

Worldwide, the quality of aquatic habitats has declined in recent decades due to pollution, digging, dredging, canalization, acidification, and eutrophication, which has endangered or caused the extinction of many aquatic species (Bagge & Salmela 1978; Kalkman et al. 2008). The process leading to extinction is mainly caused by habitat degradation, whose effect on biodiversity is worsened by ongoing human-induced climate change and the range expansion of other species. It has been argued that abiotic disturbances are the major causes of extinction, but changing species interactions are also an important cause of population declines and extinctions (Cahill et al. 2012; Voje et al. 2015).

In a large, suitable habitat, the expected lifetime of a population is longer than in a small habitat of low quality. Local extinction has been suggested to be more common in sink populations than in source populations because in true sink populations, the mortality rate is higher than the birth rate, and immigration from a nearby source population may reduce the extinction risk (Dias 1996; Thomas et al. 1996). Poor-quality habitats that nonetheless manage to attract new individuals have been observed in both natural and human-altered settings (Kristan 2003; Horváth et al. 2007; Hale et al. 2015). It is not easy to unequivocally identify a true sink habitat for a given species (Dias 1996). However, the identification of source habitats is an important tool for conservation management. Efforts to protect only sink habitats will probably still result in species extinction if the area or the quality of the source habitat is reduced (e.g. Dias 1996; Thomas et al. 1996).

1.5 Habitat specialization of species

The species that live in a community are often described as either habitat specialists or generalists, despite the fact that species occasionally demonstrate traits associated with both habits. A local habitat-generalist species is one that generally has a wide range of local habitats as well as a relatively wide distribution area. A habitat-specialist species is the opposite: specialists require a certain type of habitat, for example, streams or lakes, but not both. Due to restrictions on their habitat use, habitat specialists usually have a limited distribution.

Habitat specialists are less opportunistic than generalists, and must search longer for a suitable habitat site. However, the distinction between generalists and specialists is not always clear or consistent, due to the heterogeneity of water habitats and local adaptations within the species present. For example, in central Finland, populations of the damselfly (Zygoptera) species *Pyrrhosoma nymphula* are restricted to shadowing slow-flowing streams (e.g. Hiekkanen & Valle 1937), whereas the southern population of the same species inhabits a wide range of waters (Dijkstra & Lewington 2006). Another example is found in the dragonfly (Anisoptera) species *Aeshna caerulea,* which is restricted in southern and central

Finland to peatland habitats (or habitats of *Sphagnum* spp. moss in mires), whereas in northern Finland it occurs in a wider habitat niche (Karjalainen 2002). Moreover, natural and human-induced phenomena such as habitat modifications and global climate change are leading factors behind range and habitat expansion (Cahill et al. 2012). When environmental conditions change, generalists are able to adapt, but specialists tend to fall victim to extinction much more easily.

1.6 Aims of the thesis

There are many ways to do conservation research: theoretical, empirical or experimental, basic or applied. This thesis is based on extensive field work and empirical observations of populations and communities in waterbodies of different kinds. Using existing reference works, I present a comparative quantitative approach, with which I re-examined previously described populations, species, ecological traits, and habitat variables, depending on the type of waterbody. The community structure of Odonata species was assessed in Chapter **I** and the extinction risk of local populations was explored in Chapters **II-IV**. Ultimately, the aim of this thesis was to study the population structure and extinction risk of many different Odonata species. My main goal was to produce practical knowledge that could contribute to the conservation of aquatic species and ecosystems.

Specific research questions of the work:

Chapter **I**: Do the shapes of species occupancy frequency distributions (SOFDs) vary among the lakes and ponds of four geographical regions in Finland and Sweden? Chapter **I** presents data from extensive field work and investigates three basic questions: How do (i) the area of lakes and ponds, (ii) species' geographical range size, and (iii) habitat specialization affect species richness? My main hypothesis was that southern regions with a larger species pool have fewer core Odonata species than regions at higher latitudes with a more-limited species pool.

Chapter **II:** How do population distribution, habitat specialization, and habitat quality affect the local extinction risk of Odonata populations in streams of central Finland? Differences in local extinction risk were also compared between upstream and downstream populations.

Chapter **III** addresses one main question: How does habitat quality affect the local extinction risk of Odonata populations in central Finland in both lotic and lentic waterbodies? My basic hypothesis was that the risk of Odonata extinction is greater for populations occurring in low-quality than in high-quality habitats. The field work was conducted in streams, lakes, and ponds throughout central Finland.

This thesis culminates in Chapter **IV**, which asks the question: How general or complex are the effects of species distribution, habitat specialization, and habitat quality in determining extinction risk in the waterbodies of central Finland? The effects of species distribution and main habitat type on extinction risk were tested using field data collected from the streams, lakes, and ponds of central Finland.

2 Materials and Methods

Definitions:

A population was defined as a group of individuals of the same species living in a particular habitat with the ability to interbreed. Each local Odonata population included all developmental phases of a given species. The distribution or range size of a species was defined as the geographical area within which a species has been found. Local extinction was defined as the condition in which a population ceased to exist in the habitat(s) in question although it still exists elsewhere. In this thesis, the local extinction of an Odonata population means that any individuals, larvae, exuviae, or adults that had been identified in a previous study were not detected again here.

2.1 Study species

Insects in the order Odonata (dragonflies and damselflies) play an important role in aquatic ecosystems as semiaquatic predators (Corbet 1999). Each species demonstrates a characteristic association with a certain type of habitat, a link that is shaped by both the ecological requirements of adults, their association with both aquatic habitats and terrestrial landscapes, their selectivity with regard to oviposition sites and the influence of aquatic processes on the larval phase, which leads to their persistence in waterbodies. However, such specific ecological requirements also make Odonata particularly susceptible to certain types of habitat changes (Clark & Samways 1996; Sahlen & Ekestubbe 2001; Schindler et al. 2003; Foote & Rice Hornung 2005). In 1995, when the first field work included in this thesis was conducted, the well-documented Finnish Odonata fauna consisted of 52 species. In 2019, this list has increased to 62 species and their documented range has expanded northwards, possibly due to global warming. It is important to note, though, that even if some species may be increasing their distributional range, certain populations within that range may be disappearing (Askew 2004).

Odonates represent a useful study order with which to explore the aspects of population ecology that contribute to extinction risk, and possess several characteristics in particular that make them valuable for this type of research. First, the larval stage, which is spent underwater, has adapted to many types of waterbodies, including pools, canals, ponds, lakes, streams, rivers, and brackish waters (Norling & Sahlen 1997; Wildermuth 2010). Second, it is possible to survey the species present in natural waterbodies because the characteristic activities that occur at breeding sites enable the identification of different species. Third, in central and southern Finland and Sweden the species pool is of an appropriate size to facilitate the study of population survival in different types of waterbodies. Fourth, all species require water throughout their larval development, which means that populations are usually isolated during the aquatic stages, but the dispersion of and habitat selection by mobile adults may connect nearby populations. The dispersal ability varies between species and orders, and in aquatic insects it depends mainly on body size (e.g. McCauley et al. 2014; Heino 2015). The closely linked freshwater ponds, lakes, and streams in Finland and Sweden are therefore excellent natural habitats in which to study the relationship between species traits, habitat quality, and species diversity. Finally, Odonata species are conspicuous, easy to monitor, taxonomically well defined (Clark & Samways 1996; Kalkman et al. 2008; Samways & McGeoch 2010), and well-studied in the area under consideration here, with local surveys going back decades. Additionally, species traits play an important role in determining species` ability to resist environmental changes (Powney et al. 2015). Taken together, these characteristics make this study system ideal for population-level studies to examine important questions of conservation biology.

2.2 Field work

This thesis presents the results of extensive field work, without an explicit experimental design. All the work presented in Chapters **II-IV** was conducted in central Finland, whereas in Chapter **I,** parts of southern Finland and Sweden are also included. In Chapters **II-IV**, all the field work presented covered two odonate flight seasons at each habitat**.**

Chapter **I** summarizes data on Odonata populations gathered between 1995 and 2016 from Finnish and Swedish lakes and permanent ponds (Fig. 1). The chapter is based on well documented local faunistic studies from four different regions. The waterbodies were divided into four groups based on their geographical location: (i) southern Sweden (55° - 58° N, n = 94), (ii) central Sweden (58° - 61° 20’ N, n = 91), (iii) southern Finland (60° - 61° 30’ N, n = 58), and (iv) central Finland (61° 30’- 63° 30’ N, n = 49). A total of 46 odonate species were recorded in 292 waterbodies. All data were obtained through intensive field work. In all studied waterbodies, the aim was to detect the majority of the species present while missing as few rare ones as possible.

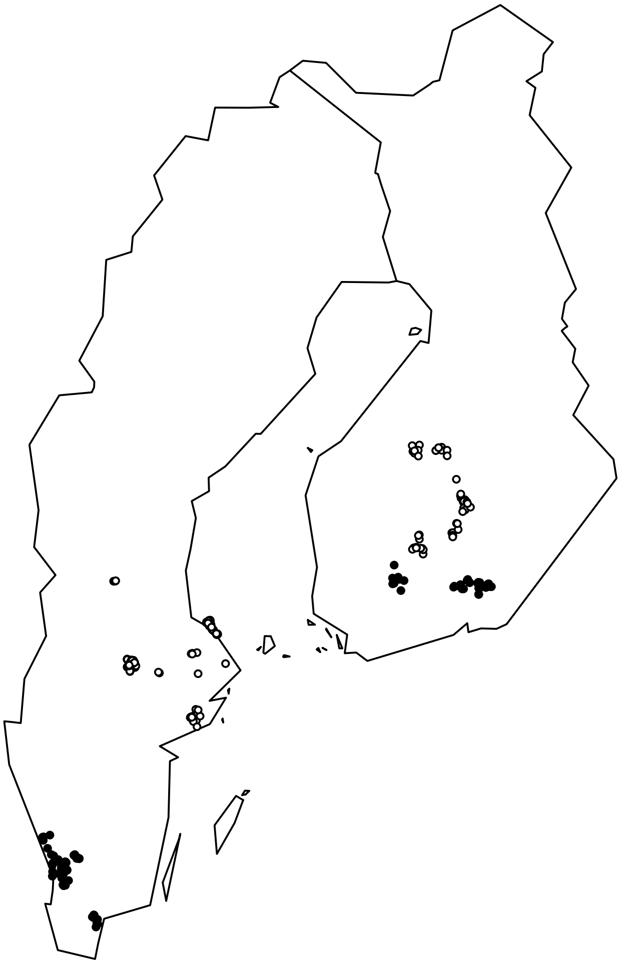

Figure 1. Location of the 292 studied waterbodies (Chapter **I**) in Southern Sweden (filled dot), in Central Sweden (open dot), in Southern Finland (filled dot) and in Central Finland (open dot). See location of the 34 streams (**II, III, IV**) and 23 lakes and ponds (**III** and **IV)** in Central Finland in original publication, Chapter **III**, Fig.1).

In Chapter **II**, I considered local surveys of Odonata populations (conducted from 1930 to 1975) in 34 streams of central Finland. I re-examined these well documented local populations using the same method as were used in the earlier studies. In Chapters **III** and **IV**, ponds and lakes were also searched; local surveys of the populations were conducted from 1995 to 2003 with the specific goal of re-examining previously documented populations. The persistence of each odonate population were determined by surveying all streams during the summers of 1995 and 1996 and the lakes and ponds during the summers of 2002 and 2003. Altogether, in Chapters **III** and **IV**, 34 streams and 23 ponds and lakes were examined, all situated in central Finland and located within 150 km of each other. In the previous studies of dragonfly populations, the presence of a species was mainly determined by confirming the presence of adults. To locate adults, each site was visited on sunny days at least 4 times during the flight period (**II-IV**). Each Odonata species was identified using binoculars in different parts of waterbodies. Those species that could not be identified while in flight were caught with a butterfly net. All odonate species that were observed and recorded within 50 m of a pond or lakes were included in the study. I assumed that all species would be present as adults; however, smaller numbers of larvae were also sampled and the exuviae were collected on the shoreline.

2.3 Lotic and lentic species

Dragonflies and damselflies are often opportunists in their choice of a breeding site. However, the habitat preferences of dragonflies are dependent on many key factors. For example, some species prefer lotic habitats because of suitable stream plant communities, stream-adapted shape of larvae and a high oxygen need. Females may lay eggs on aquatic macrophytes and mosses in lakes, ponds, pools, creeks, rivers, or streams (Corbet 1999). I categorized each species as preferring one of the three main breeding habitat types: running or still water or both. This method was based on Valle's (1952) categorization, and it is generally reliable. Specialist species are less opportunistic than generalist species, but the categorization of a given species can be flexible due to the heterogeneity of water habitats and local adaptations of the species. Moreover, natural and human-induced causes such as habitat alteration and global climate change can strongly influence range and habitat expansion. Because of the long timespan encompassed by the studies considered here, I was able to combine many sources of information and carefully check species' geographical ranges and habitat selection. However, species categorization does vary slightly among the studies of Chapter **I-IV**, due in part to differences in the question under examination.

Chapter **I** considers data from extensive field work in lentic lakes and ponds over a wide geographical range of Finland and Sweden (Korkeamäki & Suhonen 2002; Suhonen et al. 2010; Suhonen et al. 2014; Sahlén unpublished data, see original publication, Chapter **I**, Table 1). The odonate species occurring in these waterbodies were categorized into one of three groups: a) generalists (G), breeding in both standing and running water (at least in Finland or Sweden), b) specialists (S) breeding mainly in standing water, and c) tourists (R) mainly breeding in running water but sometimes encountered in standing water (see original publication, Chapter **I**, Table 2). Species occurring both in lotic and lentic environments were included in the generalist group so that the population´s adaptations to local habitats were noted within the wide geographical study area. In total, the dataset included 14 generalist species, 28 specialist species, and 5 tourist species.

In the first extinction study of central Finland, in Chapter **II**, I categorized each species as preferring one of the three main breeding habitat types: running or still water or both. Generalist species inhabit both habitat types, lentic and lotic, although they usually demonstrate a preference for one of the two. The main breeding habitat of each species was designated as being of high quality and the less-preferred breeding habitat as low quality.

In Chapters **III** and **IV**, the 15 most-abundant species were categorized as generalists, because they were found in both habitat types in the study sites (Fig. 5). In Chapter **IV**, the data set was larger (31 species) and the remaining 16 species were categorized as specialists, because they were found in only lotic (7 species) or lentic (9 species) habitats within the study sites. Data on the habitat selection of odonates in central Finland were obtained from work in streams, rivers, lakes and ponds. Species occurring in both lotic and lentic environments were included in the lentic group, so that the lotic group includes only species strictly dependent on habitats with running water. In this study, three species with low extinction rates that demonstrate more-or-less generalist habits in Finland (*Coenagrion hastulatum, Aeshna grandis*, and *Somatochlora metallica*) were categorized simply as running- or still-water species according to each species' main habitat (see Chapter **IV**, Table 1).

2.4 Species distribution

In Chapter **I** (published 2018) the geographical ranges of species are depicted as the number of occupied 50 x 50 km squares; these maps were created by Boudot & Kalkman (2015) and represent an up-to-date compilation of known records in Sweden and Finland (up to 2014).

Chapters **II** and **IV** (published 2002-2014) focus on waterbodies situated in central Finland. The distribution of each of the studied species in Finland was determined using previously published distribution maps, with those by Valtonen (1980) considered to be the most accurate since they were based upon extensive atlas work on dragonfly distributions in Finland. Species distributions are presented as frequencies, that is, the number of occupied and standardized coordinate system squares (10 km x 10 km) in the maps of Valtonen (1980). Each inhabited square was considered a separate unit and the occupied squares for each of the species were counted.

2.5 Data analyses

Detailed descriptions of the experiments and statistical analyses are given in the original articles on which Chapters **I-IV** are based. Briefly, the shape of the species occupancy frequency distribution (SOFD, article **I**) was based on new methods described by Jenkins (2011). All other published articles (**II-IV)** make use of common statistical analyses. The empirical extinction probability for each species was calculated by dividing the number of vanished populations by the number of previously reported populations in waterbodies (**II, III, IV**). The geographical range area was estimated from odonate species' distribution maps as a count of the number of occupied 50 km x 50 km squares in Sweden and Finland (**I**) and 10 x 10 km squares in Finland (**II** and **IV**). Each species was used as an independent data point in all statistical tests.

In Chapter **I**, the multi-model inference approach to the regression of empirically ranked species-occupancy curves (RSOCs) was applied (Jenkins 2011). All analyses described below are based on relative occupancy (presence/absence) data in individual waterbodies.

First, the sum of all occupied areas of waterbodies was calculated for a given species. Then, each occupancy area was divided by the total area of all waterbodies, to obtain the relative proportion of waterbody area occupied by each species (Hanski 1999). Second, species were sorted by their relative occupancy values in decreasing order, where R_i is the rank value for species i. The relative occupancy of species was plotted (O_i) as a function of $R_{i,}$ resulting in a RSOC. Third, the most common core-satellite species patterns (unimodal-satellite dominant, bimodal symmetrical, or bimodal asymmetrical) were compared to determine which gave the best fit for the assemblages (Jenkins 2011). Each of the following three SOFD patterns was fitted:

1. Unimodal-satellite mode (exponential concave): $Oi = y_0 + a*\exp(-bRi)$ with the initial parameters $y_0 = 0.01$, $a = 1.0$, and $b = 0.01$.
2. Bimodal symmetrical (sigmoidal symmetric): $Oi = a/(1 + \exp(-bRi + c)$, with the initial parameters $a = 1.0$, $b = -0.1$, and $c = -1.0$.
3. Bimodal asymmetric (sigmoidal asymmetric): $Oi = a[1 - \exp(-bRi^c)]$, with the initial parameters $a = 1.0$, $b = -1.0$, and $c = -1.0$,

where y_0, a, b, and c are estimated parameters.

The nonlinear regressions used the Levenberg–Marquardt algorithm (999 iterations) according to Jenkins (2011), and parameters were estimated by means of ordinary least squares (OLS) with the IBM SPSS statistical package. A version of the Akaike information criterion (AIC) that corrected for small sample sizes (AICc) was used to measure the fit of the models, with the lowest AICc value indicating the best fit (Jenkins 2011; Anderson et al. 2000).

In Chapter **I**, the Pearson correlation of species richness to waterbody area was calculated. As the localities varied from small ponds to relatively large lakes, the waterbody area was $\log_{10}$ transformed before analysis (**I**). Spearman rank correlation was used to test the geographical range of each species in relation to its body size, measured as the mean value of minimum and maximum hindwing length, as presented in Dijkstra and Lewington (2006) (**I**). The relationship between a species' geographical range and the number of waterbodies occupied was determined using generalized linear models with type III errors, based on a negative binomial distribution with log link (**I**). In this model, the geographical range of each species in Finland and Sweden was included as a continuous covariate. In this model, the breeding habitat type was a categorical factor, and the species' geographical range in Finland and Sweden, as well as its body size, measured as mean hindwing length (mean of minimum and maximum hindwing lengths; Dijkstra & Lewington 2006), were used as continuous covariates. Differences between breeding-habitat type within a given geographical range were tested with a Kruskal-Wallis test, as the data were not normally distributed (**I**).

Species' occupancy proportions were arcsine square root-transformed prior to statistical analysis (**II**). The effect of species distribution on extinction rate was tested with parametric correlations. A linear regression analysis was used to test whether there were differences between the extinction risks of lotic and lentic species, using the residuals between the distribution of species in Finland and the probability of extinction (arcsine root-transformed) (**II**). The differences in relative extinction risk between lotic and lentic species were tested with a t-test (**II**). One species, *Somatochlora metallica,* was omitted from this analysis, since it is common in both standing and running waters (**II**). Differences between lentic-habitat specialists and other species, as well as the differences between stream-specialist lotic species and widely distributed generalist species, were tested using a Mann-Whitney U-test (**II**). When a small stream flowed into a larger stream, either directly or through lentic water, the small stream was defined as upstream and the larger stream as downstream. If a species was identified in both upstream and downstream sections of a given river continuum, the populations were paired (upstream/downstream) and subjected to a sign test (**II**). Differences between low-quality and high-quality habitats with respect to relative extinction probability were tested with the Wilcoxon rank test (**III**).

The hypothesis that species with only a few local populations were the most prone to extinction was tested with Spearman's rank correlation test (r_s) (**III**). In Chapter **IV,** the effect of species distribution (continuous covariate) in Finland and habitat type (categorical factor: running and/or standing water) on extinction probability was tested with generalized linear models and a binomial probability distribution (0 for persisting populations and 1 for vanished populations) with type

III errors. The link function was logit. The model used the events-per-trial option, in which the number of extinct populations varied by event and the number of previously reported populations varied by trial. The interaction between these two variables was not statistically significant (all habitats: Wald = 2.49, df = 2, P = 0.288; only main breeding habitat: Wald = 4.45, df = 2, p = 0.108). Therefore, all interactions were removed from the final models for simplification. All data analyses were performed using the IBM SPSS statistical package, versions 14 (**III**) and 23 (**I**).

2.6 How trustworthy is the dataset?

Before moving on to the results and discussion sections of this thesis, I would like to address the issue of the reliability of the dataset, specifically with respect to how sampling errors were measured. This question has been discussed in the literature at least since the 1960s by population ecologists concerned first with individual-based data, and then with species detectability.

With respect to the analyses presented in Chapter **I**, data collected by different survey methods may produce different estimates for species richness, and thus different SOFD patterns. Here, different survey methods (collecting larvae, exuviae, and observed adults) were indeed used in different studies and geographical regions (Fig. 1), but all of the methods employed are known to detect the majority of species present at a waterbody, missing only a few rare ones. Previous comparative studies have shown that even small samples are able to produce a fairly reliable species list for any site (Bried et al. 2012). Misidentification is also unlikely, as the studies included here were carried out by researchers highly skilled in odonate species identification (Foster & Soluk 2006; Bried et al. 2012). Larvae of the first instars were omitted from the data because only larvae of the last instars can be reliably identified to species level. Hence, it is unlikely that the analyses were biased by possible artifacts arising from the survey methods. Second, study plot size may also influence SOFD patterns (McGeoch & Gaston 2002). However, in this study, the sizes of the waterbodies only slightly affected the calculated species richness in three of the four latitudinal regions, with the northernmost one, central Finland, being the exception. Third, the sample size (the number of waterbodies) was relatively large within each geographical region (at least 49 waterbodies). In general, samples from large areas are more heterogeneous than samples from smaller areas, and are therefore likely to contain many satellite (rare) species and exhibit unimodal species distributions (McGeoch & Gaston 2002). My analysis partly supports this, as the pooled data exhibit a unimodal satellite-dominated pattern, whereas bimodal SOFDs were often observed in subsamples of the data (Collins & Glenn 1997; Heatherly et al. 2007; Jokimäki et al. 2016). Thus, the magnitude of the effect of possible artifacts due to waterbody size was probably marginal in this study.

In Chapters **II-IV**, which consider species extinction risk, the aim was to detect all species present at previously monitored sites. The field work conducted was extensive and arduous; moreover, Odonata species are conspicuous insects which are easy to monitor in the small freshwater habitats of central Finland. The main method used was monitoring of adult odonates, but small numbers of exuviae were also collected on the shorelines. In almost all cases, also adult individuals were observed at sites where exuviaes were found. Therefore, in this thesis collecting exuviaes was only a complementary method. In the previous studies, the presence of Odonata populations were determined with comparable methods, mainly by confirming the presence of adults. However, it is possible that a few very rare populations were missed. If they were indeed missed here, though, they are likely to be so rare as to be functionally extinct, that is, there are too few members of the species to perform its function in the ecosystem and it is thus ecologically extinct. This problem is common to all ecological surveys: in all natural ecosystems, the detected and identified species can be confidently listed, but the number and identity of extinct species are almost always uncertain. My subjective opinion is that this thesis provides a thorough documentation of the Odonata fauna of each habitat.

3 Results and Discussion

Clear patterns associated with habitats, traits, and extinction risk were discovered among Odonata species as well as differences among populations within the same species. The studies of this thesis summarized in Chapters **II-IV** represent what is to my knowledge the first systematic re-examination of Odonata field work in Finland. Here, extinction risk was found to be high in both types of studied waterbodies, in dynamic streams as well as in more-stable lakes and ponds. This high extinction rate was understandable, because human-caused habitat changes had been extensive in the study area in the years between the earliest and the most-recent surveys examined here. Furthermore, change in small freshwater habitats, local extinction, and colonization have been shown to be frequent natural phenomena associated with Odonata populations. Indeed, broadly speaking, extinction is a common global phenomenon: almost all the species that have ever lived on earth are extinct.

3.1 Core-satellite species in Fennoscandia (I)

In Chapter **I**, a total of 46 odonate species were recorded in 292 lentic waterbodies. An average of 8.4 (± 3.6 SD) species were found per waterbody, ranging from 1 to 18. In the combined dataset, the number of species did not increase with the area of the waterbody. However, there were regional differences in the correlation between species number and waterbody area: in three out of the four regions, there was no such relationship, but in central Finland there was a clear positive relationship between waterbody area and species number. Each species occurred in an average of 54 ± 62.4 (range 1 to 209) waterbodies. Overall, species with a large geographical range occurred in a higher number of waterbodies (Fig. 2). The model that included breeding habitat and geographical range was considered the best of the tested models. Generalists occurred in a larger number of waterbodies than specialists. In the combined dataset, the SOFD of the odonate species followed a unimodal-satellite pattern. All alternative models fit the data less well (ΔAICc > 4). There was a large number of satellite species; half of the species (23 out of 46) occurred in less than 10% of the waterbodies and only six species were found in at least half of the waterbodies.

I found geographical variation in SOFD patterns (Fig. 2). Three northern regions (i.e. central Finland, southern Finland, and central Sweden; Fig. 3a, b, d) showed the best fit with the bimodal core-satellite pattern, whereas southern Sweden followed the unimodal satellite-dominant pattern (Fig. 3c). All alternative models fit the data less well (ΔAICc > 4). In southern Sweden, more than half of the species occurred in less than 10% of the waterbodies (Fig. 3c), but this was true of approximately one-fourth of the species in central Finland (Fig. 3b). Moreover, in Sweden no species occurred in all waterbodies (Fig. 3c, d), whereas a few species, including *Aeshna grandis*, *A. juncea*, and *Coenagrion hastulatum*, occurred in almost all of the studied Finnish lakes (Fig. 3a, b).

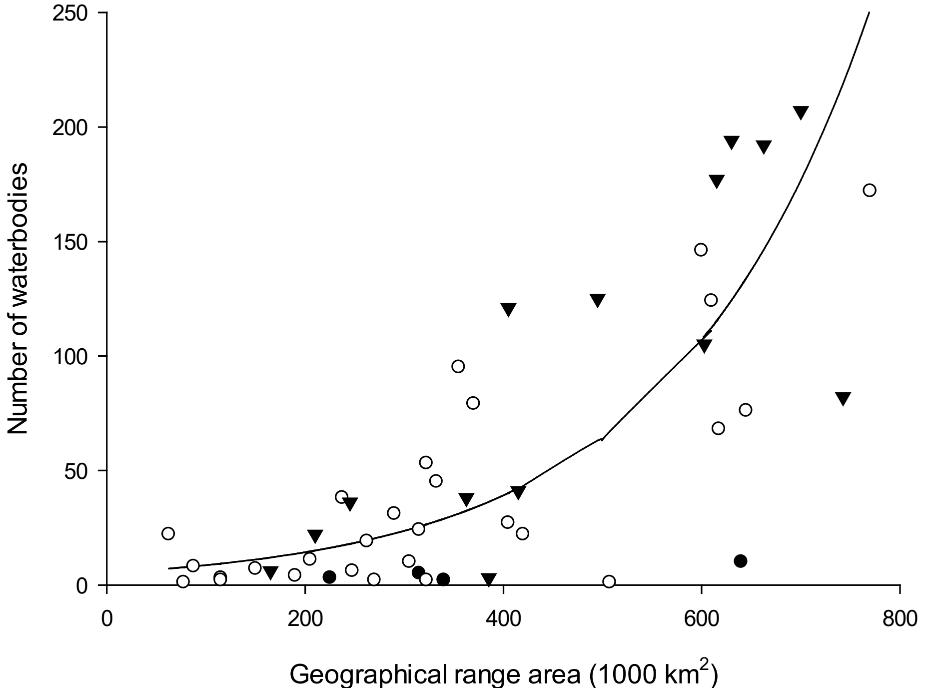

Figure 2. Number of waterbodies occupied by each odonate species (n = 46) in relation to its geographical range in Finland and Sweden. Model prediction curve (continuous line) and 95 % confidence intervals (dotted lines). The curve is based on the combined data set and calculated with Generalized Linear Models. In the model, the number of lakes occupied by each odonate species was negatively binomial distributed with a logarithmic link function. The symbols denote the breeding habitat(s) of the species: generalists (filled triangles) breed in both standing and running waters, specialists (open dots) breed in standing waters and tourists (filled dots) breed mainly in running waters, but occasionally also in standing waters.

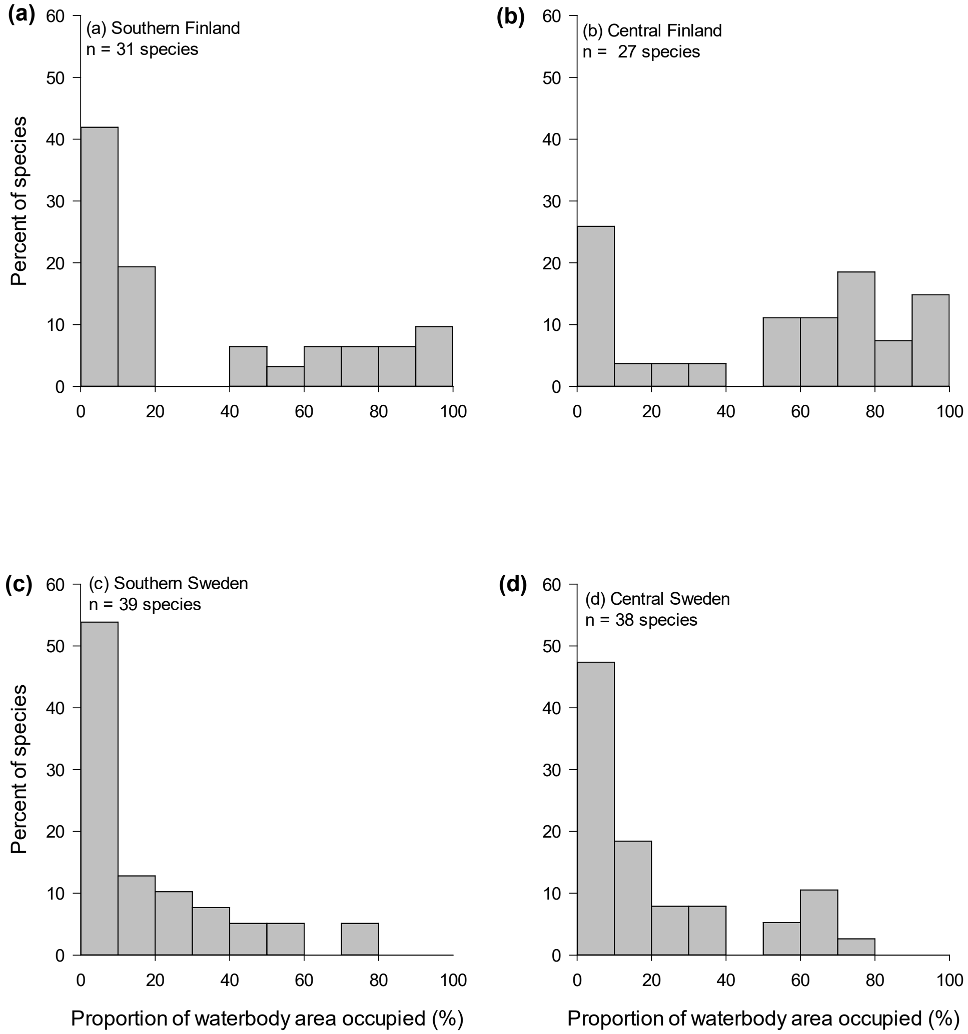

Figure 3. Percentage of odonate species in relation to the proportion of waterbody area (%) occupied in Finland and Sweden. (a) Southern Finland, (b) Central Finland, (c) Southern Sweden and (d) Central Sweden.

As presented in the results of Chapter **I**, no species was found in all southern lakes and ponds, whereas many regionally distributed species were present in all of the studied waterbodies in the north. The number of species did not increase with the area of the waterbody. It has been suggested that larger lakes include more niches, e.g. different structures of aquatic plants, which increases odonate species richness (Honkanen et al. 2011). However, previous studies have also noted that small forest lakes often harbour a larger number of species than large lakes (Flenner & Sahlén 2008). Generalist species with a large geographical range occurred in a higher percentage of waterbodies. Dispersal ability (wing length) seemed to play no major role in shaping distribution and extinction patterns. A potential reason for this observation could be that all studied Odonata species have relatively good dispersal capacity. Therefore, other factors (e.g. Matias et al. 2014) may play a stronger role in distribution.

In Chapter **I**, I found that when I considered Fennoscandia as a whole, the unimodal satellite pattern was predominant. However, on a smaller scale, I found geographical variations in odonate species' SOFD patterns in both Finland and Sweden. Specifically, southern regions had fewer core species and a larger number of satellite species than regions at higher latitudes. For the northern communities, species distributions fit best with bimodal core-satellite patterns, whereas the southern communities followed the unimodal satellite-dominant pattern. It seems that the richer species pool in the southern locations and the larger distribution range of the northern species skewed the unimodal pattern into a bimodal satellite-dominant pattern in the latter assemblages. In this study, many southern Odonata species demonstrated clear limits of tolerance to abiotic factors, beyond which their survival and reproductive success are lowered and range expansion is limited. Indeed, Odonata species richness was lower in northern Fennoscandia, probably due to climatic factors that challenge species' survival. The species that do inhabit northern habitats most likely belong to one of two groups: (i)“peripheral" populations of species with a wide tolerance for conditions in their physical environment and (ii) northern-habitat specialists. The former group may be found in a large number of suitable habitats and benefit from reduced interspecific competition in the north; for these reasons, they are likely to form the core group of common species in northern assemblages. Instead, the latter group of rare satellite species with narrow habitat requirements may become vulnerable to extinction if the number of optimal habitats declines due to climate change or other anthropogenic disturbances.

In conclusion, I found in Chapter **I** that some species are widespread and common, while others exist in only a few populations in the studied geographical area. In the northern parts of their range, rare satellite species inhabit only the highest-quality sites. It is therefore crucial to identify their main habitats in order to identify and protect them throughout the geographical area.

Further empirical and theoretical studies are, however, needed to acquire more detailed information regarding geographical variation in SOFD, and the ways in which range size affect species occupancy frequency. It is likely that species pool size is related to the patterns observed in this study. The number of species encountered at northern latitudes is small, and the variation in community composition will thus be limited. Current global warming is shifting the range of southern odonate species towards the north. As the species pool is larger in central

Europe than in the northern regions (Flenner & Sahlén 2008; Boudot & Kalkman 2015), the geographical range shift possibly increases both the species pool and the proportion of satellite species at the northern locations. This may lead to an unimodal satellite-dominant species pattern. However, if the geographical range of a satellite species shifts towards the north, the species may also shift from a satellite to a core species and, consequently, the proportion of satellite species within a given region may remain unchanged. Even if some species increase their distributional range, populations of rare specialist species within that range may disappear due to environmental changes and increased competition.

3.2 Extinction risk in streams of central Finland (II)

In Chapter **II**, the distribution of each study species and habitat affected the local extinction risk, with a species' distribution in Finland negatively related to the extinction risk of local populations (Fig. 4). Specifically, I found that specialized species with a limited distribution had a greater extinction risk than widely distributed generalist species. When the effects of species' distributions were controlled, there were consistent differences between lotic and lentic species. In general, population survival was higher in lotic species. For example, two specialists of lentic peat bogs in central Finland, *Coenagrion johanssoni* and *Aeshna caerulea*, have disappeared from all stream habitats in which they were previously reported. Furthermore, stream-specialized lotic species were at greater risk of extinction than widely distributed generalist species. Among populations of a given species, the extinction risk was greater in dynamic upstream environments than in more-stable downstream populations within the same catchment area.

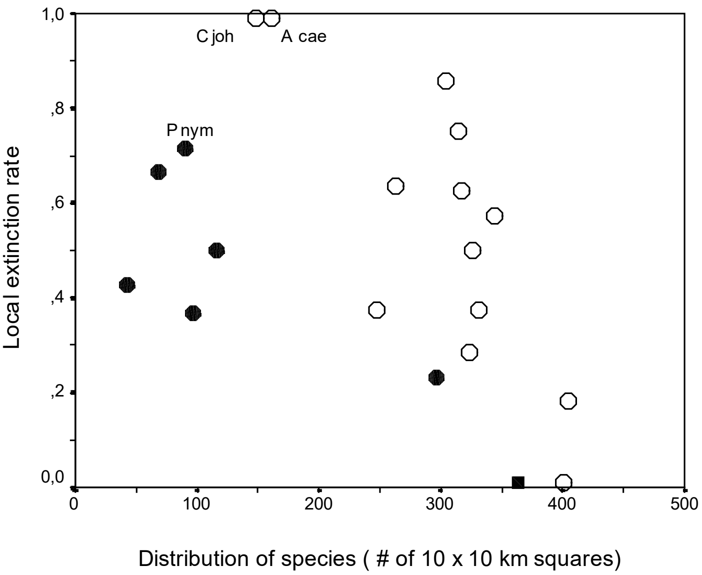

Figure 4. Relationship between the local extinction rate and regional distribution of Odonata species in Finland. Black dots represent running water species and open circles represent standing water species. The filled square represents *Somatochlora metallica*, which is common in both running and standing waters. Standing water species *Coenagrion johanssoni* (C joh) and *Aeshna caerulea* (A cae) were associated with peatlands, whereas *Pyrrhosoma nymphula* (P nym) inhabits slow flowing shadowing peatland associating streams in Central Finland. The data based on odonate populations of the 34 Central Finland streams.

In general, in Chapter **II** I found that the extinction risk of local Odonata populations was high, in particular for species which have only a narrow distribution in Finland (Fig. 4). It is well documented that species with limited ecological and geographical ranges are vulnerable to extinction in both aquatic (Moyle & Williams 1990; Reinthal & Stiassy 1991; Boyle et al. 2017) and terrestrial systems (Terborgh 1974; Hanski 1982; Reid & Miller 1989; Johnson 1998; Harris & Pimm 2008). In insects in particular, local extinction and colonization are frequent phenomena, particularly in running-water habitats (Townsend 1989; Lake 1990; Woodward et al. 2016). Because of this, extinction-prone local populations can only persist regionally if local extinctions are balanced by colonization (Hanski 1998, 1999).

A species' restricted distribution and consequent high extinction rate may stem from its smaller population size and greater environmental sensitivity or lower ability to tolerate enemies compared to widespread species (Angermeier 1995; Genner & Hawkins 2016). Small populations are known to be more prone to extinction than larger ones (e.g. Schoener & Spiller 1987; 1992; Hanski et al. 1995), and this elevated risk is connected with the fact that demographic, genetic and environmental stochasticity affect small populations more severely than larger populations (Lande

1988; Sacceri et al. 1998; Palstra & Ruzzante 2008). Lentic odonates have larger ranges that extend further north than those of lotic species (Hof et al. 2006). Their larger geographical distributions should thus enhance their re-colonization capability compared to lotic species. Many narrowly distributed dragonfly species may also be restricted by their sensitivity to habitat quality. These species may have suffered from deterioration in the water quality of streams, since agriculture, forestry, and construction activities have caused extensive disturbances to dragonfly habitats in the years between the study periods.

In Chapter **II,** I found that, when differences among species distributions were controlled, the extinction risk was lower for stream species than for standing-water species. This result could possibly be explained by source-sink theory (Dias 1996; Thomas et al. 1996; Johnson 2004). Without migration from lakes and ponds, the populations of standing-water species would disappear from streams. The extremely high extinction rates of peatland-associated species gives more support to the idea that sink populations are very vulnerable. In central Finland, the proportion of peatland remaining unditched declined from 80% to 20% over fifty years (Heikurainen 1960; Karjalainen 1991). It is likely that the disappearance of all populations of the peatbog-specialists *C. johanssoni* and *A. caerulea* is linked to the fact that their source habitat was severely degraded in the years between the study periods.

In study streams**,** I found that populations of a given species went extinct more often in upstream sections than in downstream sections of the same catchment area. In general, increasing environmental stochasticity has been found to decrease the lifetime of a population (e.g. Pimm et al. 1988; Benaïm & Schreiber 2019), and small headwater streams undergo extensive fluctuations, which are often regarded as the most important factor regulating the structure of stream communities (Resh et. al 1988; Townsend 1989; Lake 1990). For example, Valle (1945, p. 83) recorded the local extinction of odonates after dry seasons and following disturbances in water velocity. He noted especially the extinctions of peatland species and populations in small headwater habitats. It is also possible that disturbances due to agriculture, forestry, and regulation of water level have had a disproportionate effect on small headwater habitats.

In conclusion, in Chapter **II**, I found that populations of species with limited distributions, and especially those associated with sink habitats and altered peatlands are the most vulnerable to extinction. In addition, the extinction risk in dynamic headwater populations was high. It seems that the effects of species distribution, specialization, and habitat quality all combine to determine the risk of extinction.

3.3 Local extinction and habitat quality (III)

In Chapter **III**, I examined an average of 25 (SD 6) populations of each odonate species (Table 1). On average, 30% (SD = 26; range 0 to 100%) of the populations of each species had become extinct. Across species, the local extinction rate was higher in low-quality than in high-quality habitats. All previously known populations of *Aeshna caerulea* had disappeared (Fig. 5), while few or none of the previously reported populations of the most-common species became extinct. These included the widespread species *Coenagrion hastulatum*, *Aeshna grandis*, and *Somatochlora metallica*. Thus, species with few local populations were those most prone to extinction, while common and widespread species tended to persist.

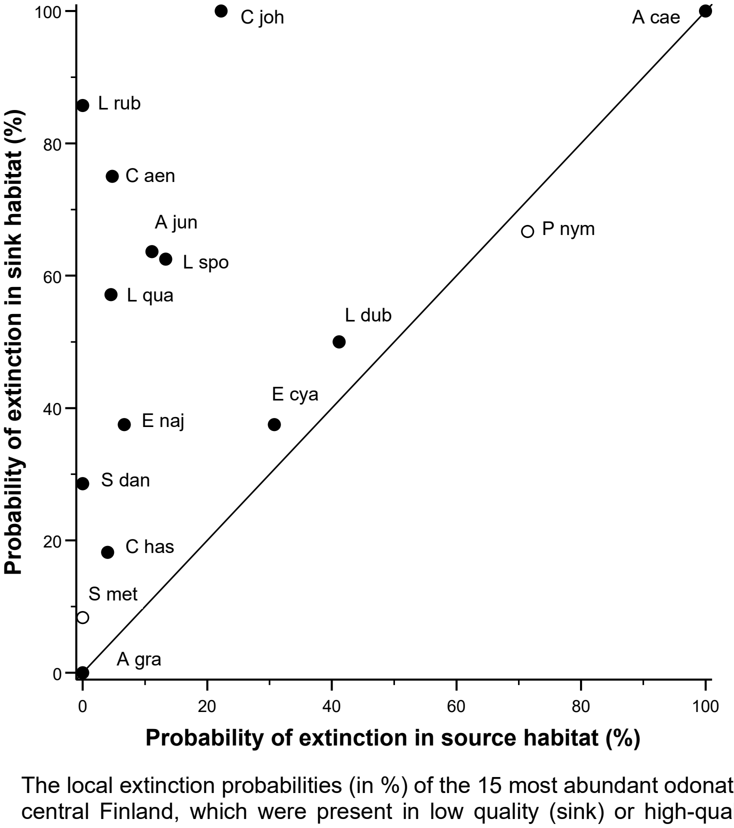

Figure 5. The local extinction probabilities (in %) of the 15 most abundant odonate species in central Finland, which were present in low quality (sink) or high-quality (source) habitats. The continuous line indicates that the probability of local extinction was the same in both habitats. Open dots indicate species with source habitats in running water; filled dots are species with source habitats in standing water. See species abbreviations Chapter **III** original publication from Table 1.

To complement my research on stream habitats (Chapter **II**), Chapter **III** also examined populations in lentic habitats. As noted above, I found that local extinction rates were generally higher in low-quality than in high-quality habitats. In this study, the extinction risk was small (0-20%) for the few most-common species in both lotic and lentic habitat types. Very common species also appeared to be locally abundant and inhabits unfavorable habitats and/or to have high dispersal rates, so that any emigrating individuals are able to quickly re-colonize the few empty source and sink patches. The most common species seem to occupy a wide breadth of suitable niches in the freshwater habitats of central Finland.

In conclusion, Chapter **III** highlights the necessity for conservation biologists to study the quality of freshwater habitats, because this is likely to be an important factor in determining the likelihood of extinction for small populations of aquatic insects. Previous studies have assumed that species distributions are explained solely by habitat characteristics, i.e. a species is assumed to be present because the habitat is suitable, and absent because the habitat it is not suitable. However, this study shows that habitat use, at least in Finnish odonates, is unlikely to be so easy to pin down. For instance, some populations may become locally extinct in ‘pristine’ habitats because they are not well adapted to local conditions. In devising an effective conservation plan for a threatened or endangered population scattered over a heterogeneous habitat, it is not easy to determine the identity of the true sink habitat for that species (Pulliam 1988; Pulliam & Danielson 1991; Watkinson & Sutherland 1995; Thomas et al. 1996; Johnson 2004). My findings indicate, however, that it is important to identify species source habitats even for generalist species.

3.4 Species habitat specialization and extinction risk (IV)

The previous and current lentic and lotic odonate populations were examined in central Finland in Chapter **IV,** on average 35% (SD = 26) (range 0–100%) had become extinct (Fig. 6). All study previously reported populations of *Aeshna caerulea* and *Coenagrion lunulatum* had vanished in the years between surveys, but instead, all populations of *Aeshna grandis* and the lentic species *Coenagrion armatum* survived. This variance in local extinction risk appeared to be at least partly determined by both of the variables studied here: the geographical range size of the species and habitat quality. Specifically, the geographical range size of a species in Finland was negatively related to the probability that local populations would go extinct (Fig. 6 and 7 a,b). There were also consistent differences between the extinction risk of breeding-habitat generalist species (breeding in both running and standing water) and breeding-habitat specialist species (breeding only in running or standing water). When the effects of distribution (covariate) were controlled, the probability of local extinction was lower in specialist species than it was in generalist species. There were no differences in local extinction risk between standing water and running water species, but both species groups had a lower extinction risk than generalist species, which breed in both habitat types. However, when generalist species were categorized with respect to their main breeding habitat, there were no differences between types of species in local extinction risk.

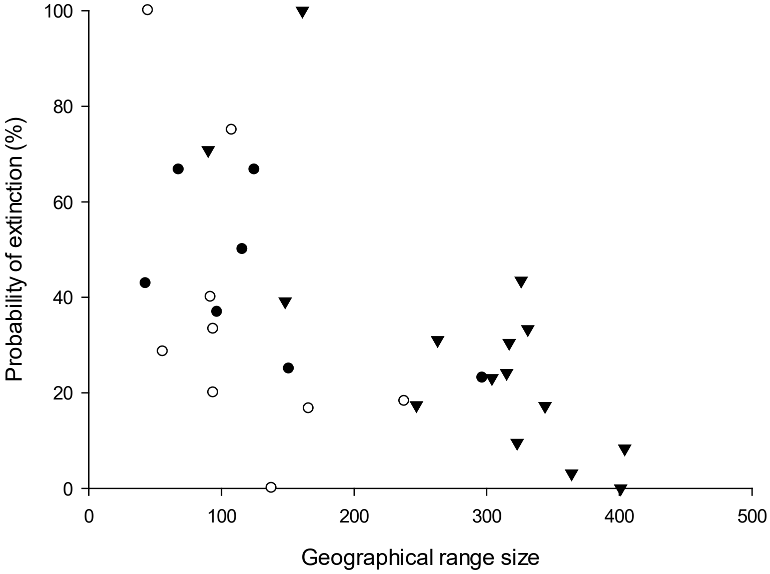

Figure 6. Relationship between the observed local extinction probability (as measured in 34 streams and 23 ponds and lakes in central Finland) of 31 of the most frequently recorded odonate species and the geographical range size (number of 10 km x 10 km squares) of each species in Finland. Open dots represent standing water species, filled dots running water species and the filled triangles represent species, which occur in both running and standing waters.

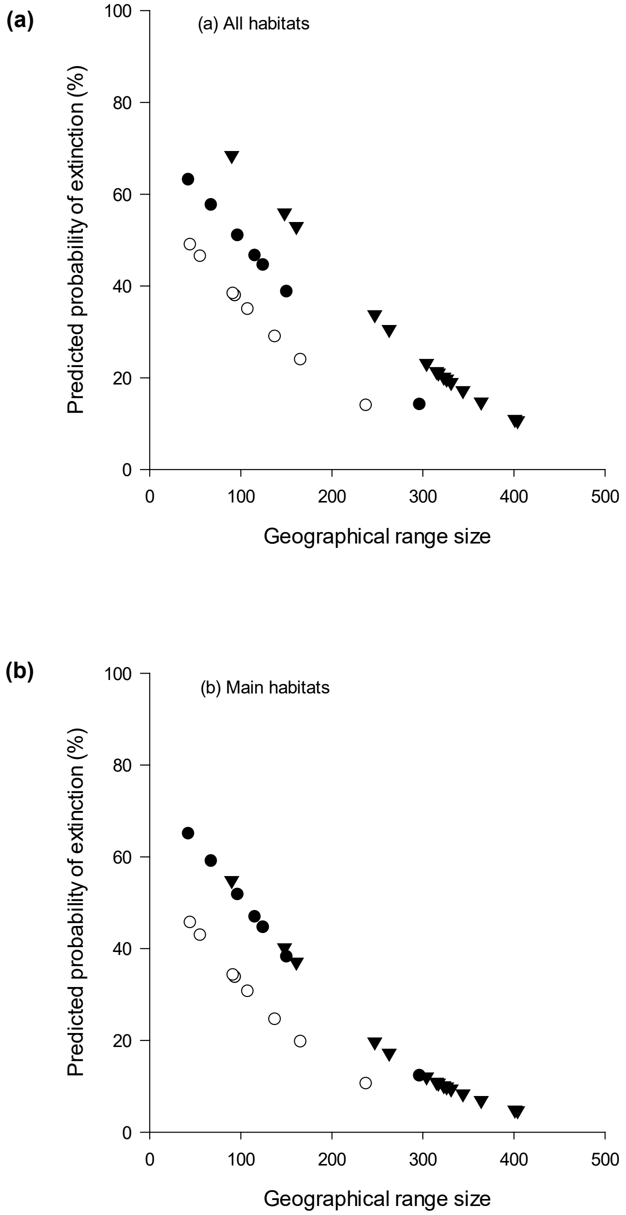

Figure 7. **(a)** Relationship between the predicted local extinction probability in all habitat types of 31 odonate species and the geographical range size (number of 10 km x 10 km squares) of each species in Finland. **(b)** The same as above, but only main breeding habitats of each species. Open dots represent standing water species, filled dots running water species and the filled triangles represent species, which occur in both running and standing waters.

In Chapter **IV,** I combined the datasets obtained from my field surveys of lotic and lentic habitats (see Chapters **II** and **III**) and re-examined extinction risk across a wide variety of habitats. As found in the smaller datasets, the extinction risk of local Odonata populations was again high (see also Chapter **II**), particularly for species that have a narrow distribution in Finland (Fig. 6). In investigating dragonfly and damselfly populations that had been reported in previous surveys, I found that about 30% of these populations had vanished. In general, the extinction risk of local populations was negatively related to the size of the species' geographical range (see Chapter **II**). This result agreed with the published theory that locally common habitat generalist species become widely distributed because of their low extinction rates and high colonization rates (Hanski & Gyllenberg 1997; Chichorro et al. 2019). Indeed, geographical range may be a reliable, easily obtainable indicator of species' and populations' limitations over large spatiotemporal scales (Angermeier 1995).

When the effect of a species' geographical range size was controlled, I found that, in contrast to my prediction, extinction risk was lower in specialist species than in generalist species. This was probably due to the fact that generalist species occur in both low- and high-quality habitats (Fig. 7 a,b); indeed, this phenomenon was detected in generalist species only when populations from both high- and low-quality habitats were pooled together. This result contradicts earlier observations and proposed ecological theory (e.g. Hughes et al. 2000; Harcourt et al. 2002), but here, it can possibly be explained by source-sink theory (Pulliam 1988; Watkinson & Sutherland 1995; Thomas et al. 1996). Habitat degradation may predominately affect sink populations in which reproductive rates are lower compared to source populations. For example, when a species' populations undergo widespread decline due to unusual weather, parasites, or competition from alien species, the remaining individuals (with mobile adult stages) of the reduced sink populations may try to move to another, better mating site. In this, odonate behaviors such as aggregation, territoriality, and dispersion may play an important role (e.g. Corbet 1999; Tynkkynen 2005). On the other hand, in an undisturbed habitat, a species with a highly specialized ecological niche is more effective at competing with other organisms. Therefore, habitat-specialist species may have a small risk of extinction in relatively untouched, stable habitats.

In Chapters **III** and **IV**, an extremely high extinction rate was detected for peatland-associated species in lentic habitats (see lotic habitat study in Chapter **II**), and additional studies on different habitats support the conclusion that sink populations are very vulnerable (Fig. 5). It is likely that most of the previously known populations of the peatland-associated species *Coenagrion johanssoni* and *Aeshna caerulea* disappeared because their source habitat was severely degraded in the years between the study periods. Furthermore, a high extinction risk was detected in both habitat types (source and sink habitats, Fig. 5) for the lentic peatland species

Leucorrhinia dubia and the lotic species *Pyrrhosoma nymphula,* which prefer shadowing slow-flowing peatland-associated streams in central Finland. In southern regions, however, *Pyrrhosoma nymphula* can be found in a wide range of habitats (see introduction). In contrast, the generalist species *Coenagrion hastulatum* is widespread in central Finland, but much more specialized in southern regions, and has been listed on the IUCN Red List due to population declines in parts of central Europe and the British Isles (Dijkstra & Lewington 2006). These examples illustrate the flexibility inherent in species' habitat selection and emphasize that species' ecological traits are occasionally highly localized, with the result that extinction risk is closely linked to limitations in an individual population's resources and geographical range.

3.5 Critical notes

Based on the results and discussion in this thesis, the results of studies focusing on habitat quality may depend on the way how the species are categorized (for example, lentic, lotic, generalists). Habitat quality differ among years, and dispersal is often a highly variable process that can vary seasonally and due to stochastic events, such as storms, droughts and floods (Matias et al. 2014). Critically, without extensive multi-year studies, the relationship between habitat quality and local extinction risk cannot be proven. Future empirical and theoretical studies thus need to incorporate detailed information regarding habitat requirements, habitat quality, geographical range size and dispersal characteristics of populations in order to understand the risk of local population extinction.

3.6 Critical traits associated with extinction

When taken together, my findings indicate that most generalist species with large geographical ranges have some advantages in changing environments (see Chapters **II-IV**). In central Finland, the populations of species with a large geographical range occurred and survived more often than rarer ones. This phenomenon may create communities in which rare species go extinct but common species are sustainably maintained. However, even habitat generalists may not survive if they lose all their source habitats and are left only with sink habitats, in which long-term population survival can be maintained only by immigration from other populations.

According to the results presented in Chapters **II** and **IV**, the relationship between species distribution, specialization, and habitat quality plays an important role in determining extinction risk. It is difficult to fully or even adequately understand which traits and/or factors are critical in causing extinction, because multiple closely linked human-induced and natural drivers will interact with each other (Fig. 8). Moreover, the data analyses have consistently considered species as independent data points while phylogenetic relatedness may play a role in shaping correlations between species` traits. This may go in both directions; real patterns being hidden or misleading patterns being detected.

Species distributions and interactions, with differences in the identities of core and satellite species, migrations, and habitat selection, are determined by highly variable dynamics that are both habitat- and population-specific. The stochastic impact of interspecific competition on the survival of different populations is not easily predictable and poorly understood. For example, Odonata species may be unable to withstand even small amounts of habitat degradation in previously suitable habitats if at the same time they are experiencing synergistic pressures from extreme weather and competition with alien species. Despite this, certain limiting resources, such as suitable water quality and breeding habitats, will always play a critical role.

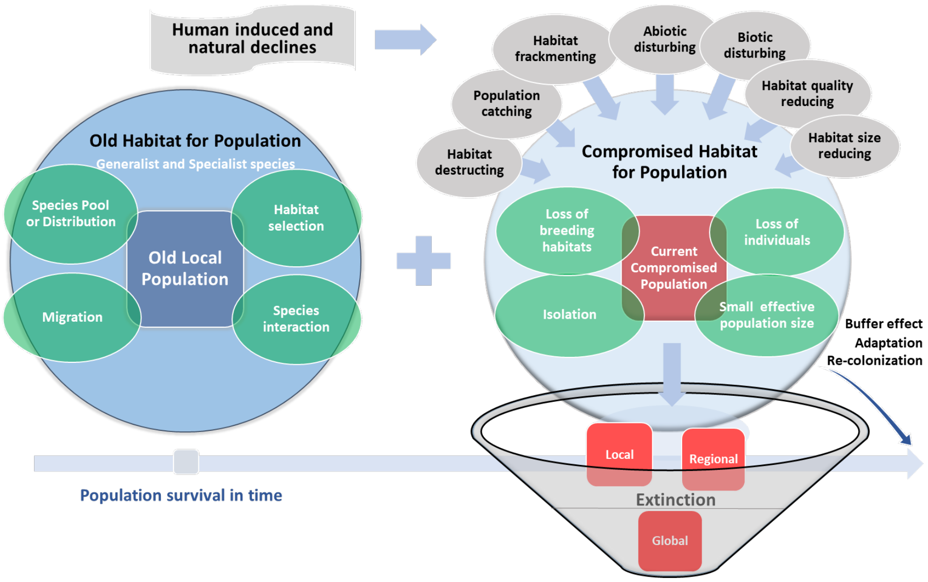

Figure 8. Human induced factors and natural declines drive populations to the extinction trap. The symbols denote old (left large circle) and current (right large circle) habitats. The old (left square) and current (right square) populations are affected many factors (oval circles) that cooperate affecting population survival. Due to anthropogenic disturbances and habitat chancing pressure, the habitat and the population will be compromised. Finally previous known old population fall to local, regional or global extinction (funnel). Population survival time presents population longevity over the time.

Aquatic freshwater habitats experience multiple types of disturbance and degradation (Fig. 8) that may negatively influence resident populations. However, several abiotic (physical-chemical) processes may buffer the habitat changes and allow the decreased habitat to recover. For example, groundwater and sediment can buffer climatic disturbances and changes in water quality in aquatic ecosystems. Moreover, different biotic mechanisms may also buffer threats to a population and therefore limit its decline; these include, among others, expansion of the habitat niche, local adaptations and competitive exclusion. Because of the complicated web of interactions that make up every ecosystem and habitat, the relationship between interspecific competition and population extinction risk is complex and site-specific. Such habitat buffer mechanisms have great potential to reduce population extinction, but the critical environmental factors and population traits will vary depending on habitat sites and the species/populations in question.

Finally, when abiotic and biotic disturbances result in habitat change, a population's stability may be compromised (Fig. 8), and demographic, genetic, and stochastic challenges may influence the persistence of local populations. Small and isolated populations may experience low breeding and feeding success, greatly increasing the risk of local, regional, or global extinction. Global extinction is irreversible, but isolated local extinctions may be merely temporary. When local populations disappear from a habitat, mobile species may be able to re-colonize via immigration from other populations. Ultimately, a population's ability to recover will be determined by the species' ecology, scattered and dynamic habitat traits, and limitations on dispersal distances.

4 Conclusions and implications for conservation

By examining extinction risk among many different species and populations of Odonata, this thesis indicates that species with limited distributions or specialized habitat requirements should be the focus of proactive efforts towards aquatic conservation. Rare species with a limited number of suitable habitats are much more likely to go extinct due to habitat or climate changes and other anthropogenic or natural disturbances. Currently, many human actions are causing a clear decrease in biodiversity; some of the direct drivers include changes in species interactions and species removals. One of the most unambiguous results of the extinction studies presented here is that peatland-associated Odonata populations are increasingly vulnerable due to the destruction of peatland habitats in central Finland. Although many Odonata species have been shown to have a high dispersal ability, re-colonization by rare species is insufficient to maintain a population when the breeding habitat is scarce.

This thesis was specifically concerned with factors that affect Odonata population survival but has many implications for future studies focused on the conservation and ecology of different Odonata species. Further research is needed to identify the abiotic and biotic factors that limit habitat generalism and determine species vulnerability in aquatic communities. In particular, more knowledge is needed on the ecological traits of Odonata species, as these can play an important role in determining species' distributions and their ability to resist environmental change. Ecological knowledge can help to identify extinction-prone species and can provide a basis for proactive conservation efforts. As demonstrated here, existing fauna records can also serve as a good resource for conservation studies.

To protect at risk populations, one appropriate technique is to implement a management plan for water systems that monitors extinction probabilities among species, which may provide the early signals of population decline. Such a program need not be concerned only with rare or protected species; instead, the main focus should to be preserve the ability of an environment to maintain healthy populations and ecosystems over time. It is necessary to have a better understanding of populations' extinction risk if we are to confront the biodiversity crisis and ensure a safe future for the planet.

This thesis presents some useful methods for examining population traits and extinction risk. By making use of previously conducted local studies and performing comparative analyses, I found that some species and populations are more prone to extinction than others due to a variety of factors. However, these results should be considered with the understanding that species habitat requirements, dispersal capabilities, and extinction risk are not fully understood. From a conservation perspective, one implication of these findings is that making predictions about extinction risk from a single trait, such as abundance or population variability, may be risky because traits may act synergistically to render species more or less vulnerable than would be predicted by a single trait.

Finally, this thesis highlights the necessity for conservation biologists to study the quality of freshwater habitats because this is likely to be the key factor affecting small populations. Future conservation activities should provide more information about the ecology of the species in question, although what is truly needed is an extensive study of habitat quality for each species. One practical result of this thesis is the finding that it is not possible to predict a species' survival only with knowledge of its preferred habitat; instead what is needed is information on the population´s habitat quality. For this reason, the current proportions of endangered species might not accurately represent the greater picture of species vulnerability. Further studies that shed light on species' ecology and on the various threats they face, as well as continuous monitoring of at risk habitats, will be essential for the conservation of aquatic species.

Acknowledgements

Firstly, I would like to express my sincere gratitude to my Supervisor Jukka Suhonen. Looking back over three decades, you always gave me encouragement, advice and respect, despite we severally had a little different agenda. When I first time met you in Jyväskylä, you already had early aiming to work something scientific about odonates extinction risk. I also wish to thank Research Director Veijo Jormalainen for his valuable leading methods and my Supervisor Kai Norrdahl for commenting the manuscript. I would also like to thank the staff of the following organizations for enabling this thesis, The University of Turku Graduate School and the Finnish Cultural Foundation, Kymenlaakso Regional Fund for fundings. My special thanks are extended to the staff and board member of Water and Environment Association of The River Kymi.

There are many colleagues who have contributed to my work one way or other. I thank Lindsay Higgins reading and commenting the manuscript and Markku Kuitunen for feedback on my work as well as Göran Sahlén, Merja Elo, Jukka Salmela, Milla Hilli-Lukkarinen, Johanna Kullas and Jouni Penttinen for participating in this thesis. I have been met interesting people while studying and working with biology and odonatology. Especially, Petri Ahlroth, Jari Ilmonen, Sami Karjalainen, Antti Kärkkäinen, Petri Metsälä, Petri Parkko and Jouni Toivola have been provided the views of insects and nature conservation.

My academic career was not ordinary and few kind persons kindly cheer me trust myself. Eija Assola, Aulikki Nygren, Aulis Alatalo and Jukka Suhonen: I understand that without your small supportive words this thesis would not have started or ended. I also thank my good old “pyssyttäjät” friends: Tapsa Rossi, Gusse, Löffe, Ere, Köntsä, Lasse, Säilä, Titus, Jussi and Harri, the Pelli and Tuomas. I am lucky to have you on my side, – and other side of the net you supported me somehow unconsciously. I am very grateful my sister Leena and brothers Janne and Risto, my later godmother Irja and later parents Maila and Kalevi for all kind spirit and support they have given me. Finally, I wish to thank my wife Anne and daughters Aava and Tuuli just for coming in my life.

February 2020

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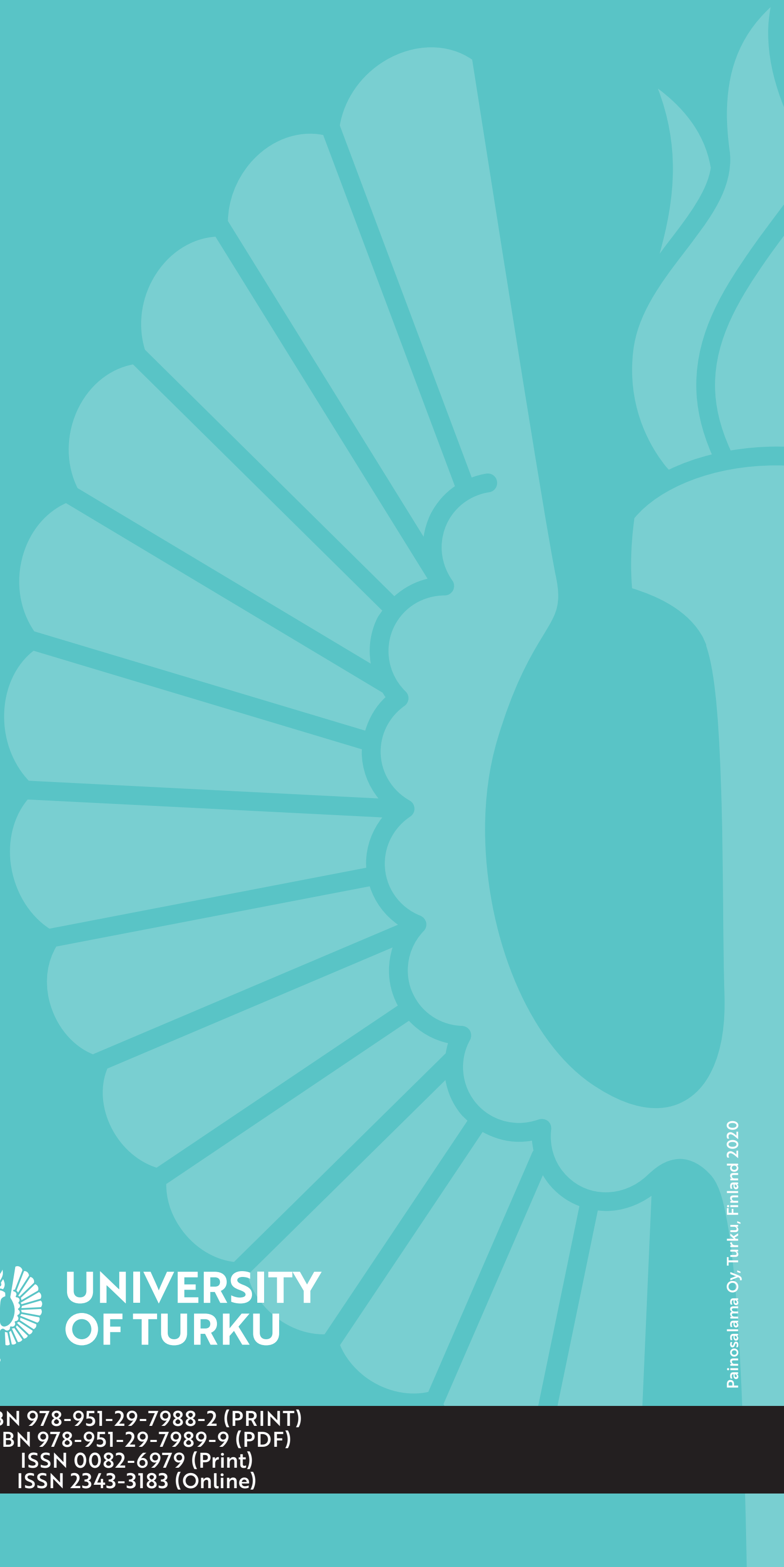

UNIVERSITY
OF TURKU

Painosalama Oy, Turku, Finland 2020

ISBN 978-951-29-7988-2 (PRINT)
ISBN 978-951-29-7989-9 (PDF)
ISSN 0082-6979 (Print)
ISSN 2343-3183 (Online)