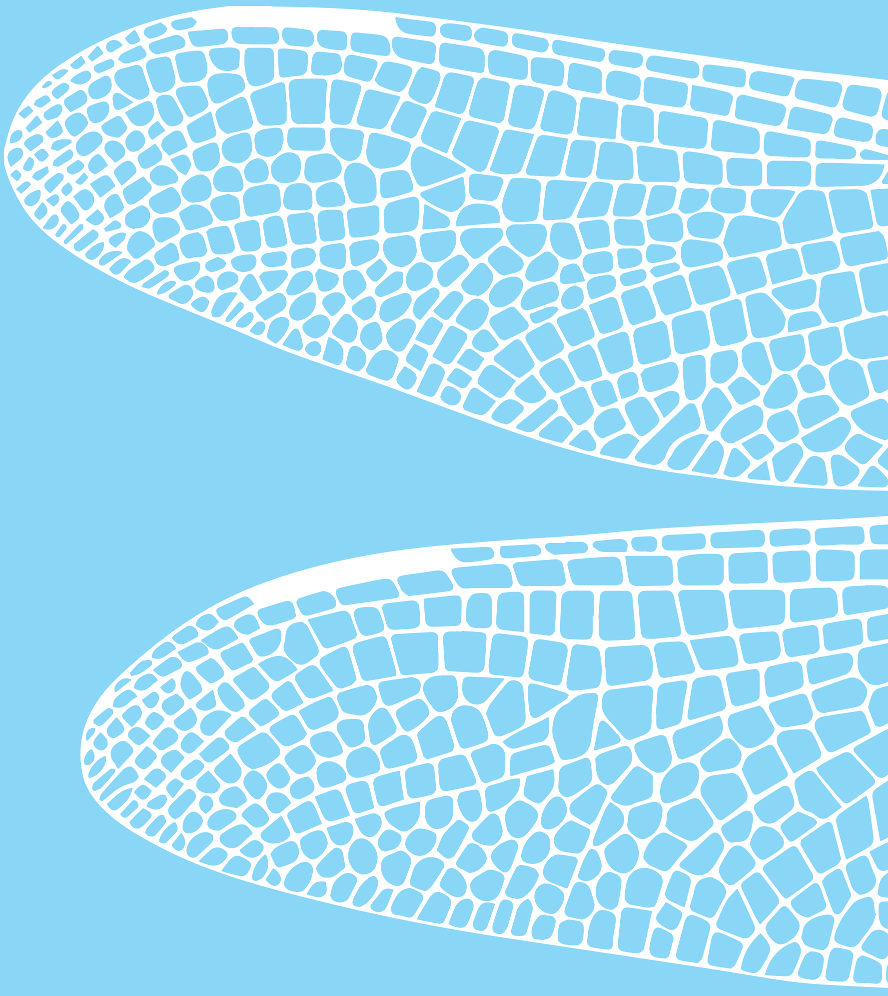
Trending Dragonflies

ASSESSING AND EXPLAINING TRENDS AND THREATS ON DIFFERENT SCALES

Tim Termaat



Propositions

1. Dragonfly communities in the Netherlands have changed profoundly in the last four decades.
   (this thesis)

2. Dragonfly conservation in Europe has become more challenging due to global warming.
   (this thesis)

3. Robust monitoring schemes are essential to oppose the shifting baseline syndrome in our perception of biodiversity.
   Papworth S.K., Rist J., Coad L. & Milner-Gulland E.J. (2009). Evidence for shifting baseline syndrome in conservation. *Conservation Letters* 2: 93-100.

4. Science denialism should be countered more effectively to solve global crises.

5. Farmers should have the same rights and obligations as any other entrepreneur leading a business that is potentially harmful to nature and the environment.

6. Without the European Union we would be left to the wolves, except that there would be no wolves.

Propositions belonging to the thesis, entitled

Trending Dragonflies
assessing and explaining trends and threats on different scales

Tim Termaat
Wageningen, 8 November 2023

Trending Dragonflies

Assessing and explaining trends and threats on different scales

Tim Termaat

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Trending Dragonflies

ASSESSING AND EXPLAINING TRENDS AND THREATS ON DIFFERENT SCALES

Tim Termaat

Thesis
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CONTENTS

Ceriagrion tenellum is a warm-adapted species that occurs in the Netherlands at moorland pools, bogs and mesotrophic ponds.

CHAPTER 1

General introduction

We are in the midst of an unparalleled biodiversity crisis (IPBES, 2019; WWF, 2020). Human-induced changes in Earth's biosphere are causing the sixth mass extinction (Ceballos et al., 2015; Cowie et al., 2022), approximately 66 million years after the Cretaceous–Paleogene extinction event (Schulte et al., 2010), threatening vertebrates, insects and plants alike (Antonelli et al., 2020; Ceballos et al., 2020; Wagner, 2020). The International Union for Conservation of Nature (IUCN) reports that 28% of the approximately 150.300 species currently assessed are threatened with extinction (IUCN, 2022) and future projections are dire (Schipper et al., 2020; Trisos et al., 2020).

In an attempt to slow down the loss of biodiversity, considerable efforts are made by e.g. governments, policy makers, nature conservation organisations and managers of nature reserves. To track the progress of these efforts, and to measure the success of underlying conservation strategies, adequate monitoring is essential (Navarro et al., 2017). This requires large-scale and long-term trend assessments of a representative selection of species, one of the basic units of biodiversity. Unfortunately, most monitoring projects are short-term and focus on small study areas and a limited number of taxonomic groups, typically vertebrates (Proença et al., 2017). This is not due to the lack of awareness that these species groups do not represent total biodiversity, but rather to the lack of available datasets of other taxonomic groups that are suitable for monitoring purposes. After all, adequate monitoring of a taxonomic group requires enough data on species occurrence over a longer period of time, and a scientifically sound method for data analysis to derive robust, non-biased trend information.

In Europe, a substantial number of biodiversity datasets are available for various taxonomic groups (https://monitoring.europabon.org/monitoring), but the majority of these datasets are not suitable or at least not used for large-scale assessments of species trends. Only two taxonomic groups currently have established pan-European indicators: common birds and grassland butterflies (https://biodiversity.europa.eu/track/streamlined-european-biodiversity-indicators). In addition, a prototype indicator for hibernating bats was published in 2014, which may develop into a more comprehensive pan-European bat indicator (Haysom et al., 2014).

Dragonflies and damselflies (order Odonata, hereafter: 'dragonflies') may be a suitable additional indicator group, for several reasons. First of all, dragonflies have fundamentally different life histories than birds, butterflies and bats, and therefore are likely sensitive to other aspects of environmental change. Dragonflies are freshwater invertebrates, which have been indicated as an essential addition to Europe's biodiversity monitoring programme (Feest, 2013; Thomas, 2005). Freshwater ecosystems harbour a relatively high number of species, most of which are insects, and are mentioned as being among the most threatened ecosystems in the world (Davidson, 2014; Reid et al., 2019). On the other hand, it has been suggested that freshwater insects have more positive trends than terrestrial insect (Van Klink et al., 2020). An indicator based on trends of aquatic insects, such as dragonflies, may therefore help to paint a more complete picture of biodiversity developments.

Secondly, dragonflies have often been mentioned as suitable indicators of water quality and freshwater habitat integrity (for a review, see Bried & Samways, 2015). While larvae are sensitive to changes in their aquatic environment, adult dragonflies are airborne insects with good dispersal ability. This enables dragonflies to reach and colonise suitable habitats faster than most other taxonomic groups, potentially giving them an 'early signalling' function.

Furthermore, dragonflies would be a suitable indicator group for practical reasons. Adult dragonflies are relatively easy to find and to identify in the field, as they are large, colourful, terrestrial and diurnal insects, often with a conspicuous behaviour. They are popular with citizen scientists, as the number of species in Europe is manageable and they have vernacular names in many European languages (Bernard et al., 2009; Billqvist et al., 2019; Bos et al., 2007; Dolný & Bárta, 2009; Siesa, 2017). Multiple excellent field guides and distribution atlases are available nowadays and many amateur naturalists have expanded their interest in classical popular taxonomic groups, such as birds and butterflies, to include dragonflies as well. As a result, the number of available dragonfly records ('citizen science data') has sharply risen over the last decades, throughout Europe (Boudot & Kalkman, 2015). In an increasing number of countries or regions these records are stored in central databases, maintained by governmental or non-governmental organisations.

Although many dragonfly data are available in Europe and the usefulness of citizen science data has been widely recognised (Fraisl et al., 2022; Schmeller et al., 2009), these data cannot simply be used for drawing inferences on species trends. This is because the majority of the available records are 'opportunistic data': records collected without a standardised field protocol and without pre-selection of sites. Naively using these opportunistic data to draw inferences on trends in the distribution of species may easily lead to artificial trends or mask existing trends, due to unequal observation efforts across years (Dennis et al., 1999; Dennis & Thomas, 2000; Hassall, 2012).

For this reason, a standardised dragonfly abundance monitoring scheme was started in the Netherlands in 1998, following the successful butterfly monitoring schemes in the UK and the Netherlands (Van Swaay et al., 2008). In the Dutch Dragonfly Monitoring Scheme (DDMS) dragonflies are counted along fixed transects using a standardised field protocol concerning counting method, counting frequency, counting period, weather conditions, etc. (Van Swaay et al., 2018). However, such standardised monitoring schemes require a substantial number of transects, many participating dragonfly observers prepared to perform long-term censuses, and considerable guidance and coordination. This complicates setting up comparable schemes in other countries, that may have proportionally fewer dragonfly observers, or where the study of dragonflies is not centrally organised like in the Netherlands. Therefore, the Dutch initiative has only been followed in France (http://odonates.pnaopie.fr/steli/) and temporarily in the UK (2009-2012; Smallshire & Beynon, 2010), not in other European countries (Bried et al., 2020).

As dragonfly monitoring based on standardised counts is not feasible in most countries, it would be highly desirable to be able to use opportunistic data as an alternative. However, this requires a new method for data analysis that successfully corrects for unequal observation efforts. Furthermore, in order to determine how dragonflies are doing on at European level, and thus enable the use of dragonflies as supranational biodiversity indicators, an additional method is needed to combine distribution indices from different countries or regions into supra-national indices.

Reliable indices and trends of species distributions do not only have value for using dragonflies as biodiversity indicators, but also for protecting dragonflies themselves. After all, negative trends raise concerns regarding a species' regional, European or even global conservation status. To be able to formulate effective protective measures for threatened species the drivers of their declines, such as habitat loss, pollution or climate warming, must be known. One way to identify these drivers may be to group species by common traits or ecological requirements, and look for trend differences between groups. In specific cases however, in-depth autecological research may be necessary to properly understand the requirements and causes for decline of a species.

This thesis investigates whether dragonflies can indeed be monitored by means of opportunistic distribution records, how dragonflies are doing at different spatial scales in Europe, how their trends can be explained, and which consequences this has for dragonfly conservation. Fig. 1.1 gives a conceptual framework for how these topics are interrelated and in which chapters they are treated:

- In Step 1 a suitable, scientifically sound method to derive reliable trend information from available monitoring data is developed and tested. Chapter 2 explores whether this can be achieved by applying site-occupancy models to opportunistic dragonfly data from the Netherlands. Chapters 3 describes a pilot study in which regional occupancy indices of *Calopteryx splendens* are combined into a supra-national index for northwestern Europe. In Chapter 5 this is done at pan-European level, for as many dragonfly species as possible.
- Step 2 involves the application of the acquired method to assess how dragonfly species are doing on different spatial scales. In Chapter 4, this is done at national level for the Netherlands (period 1991-2013), in Chapter 5 at European level (period 1990-2015).
- In Step 3 the resulting species trends are interpreted by exploring the drivers of change. As these drivers may change over time, targeted ecological research may be necessary to identify the currently most relevant pressures. In Chapters 4 and 5 drivers of change are explored by grouping species by habitat and temperature preferences. Chapter 5 also examines the pace in which climate change is altering European dragonfly communities. Chapter 6 zooms in on a smaller scale, by investigating how the Spearhead Bluet (*Coenagrion hastulatum*) in the Netherlands lost more and more populations through the 20th and early 21st century.
- When the most prominent pressures on threatened species are understood, conservation measures can be formulated in Step 4. This is done in Chapter 6 for *C. hastulatum* and in Chapter 7 for species in general, with special emphasis on the consequences of climate warming for dragonfly conservation. The effectiveness of applied conservation measures should be evaluated by repeating steps 2-4 at regular intervals.

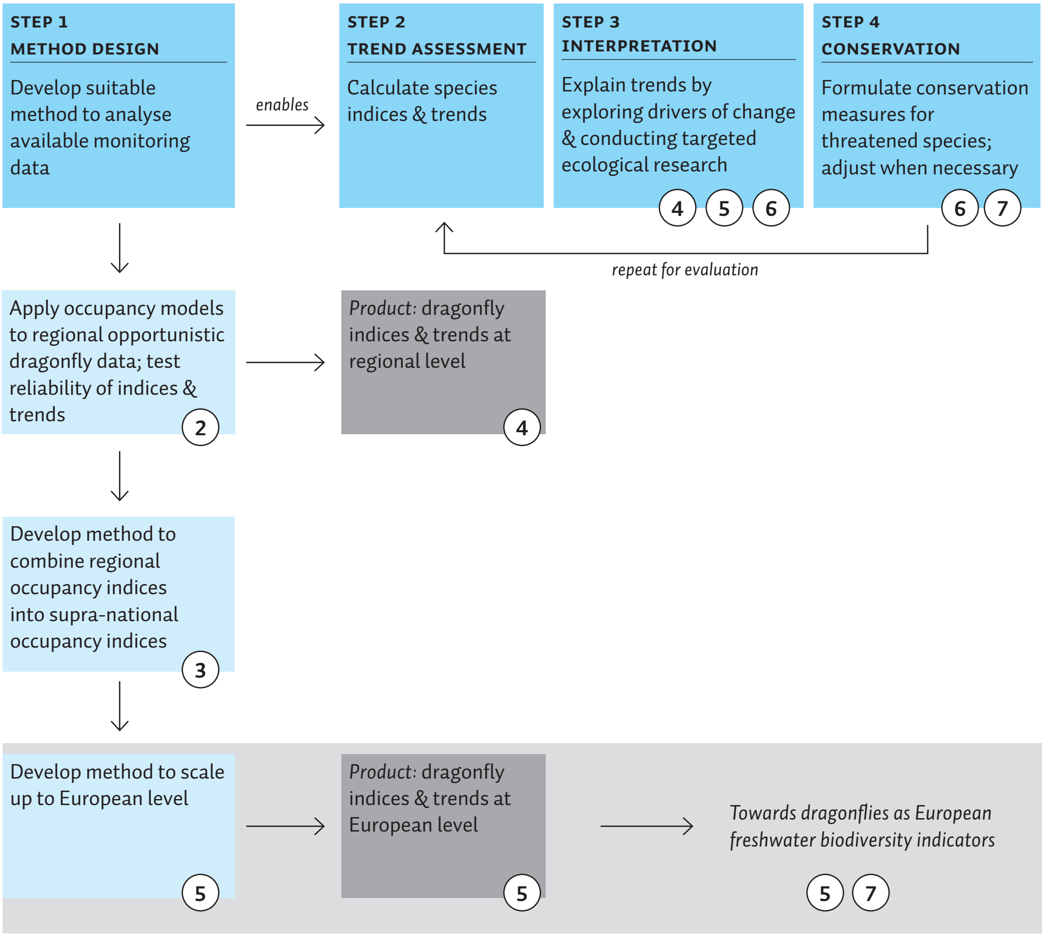

FIG. 1.1: Conceptual framework of topics covered in this thesis and how they interrelate. Numbers refer to thesis chapters.

References

Antonelli A., Fry C., Smith R.J., Simmonds M.S.J., Kersey P.J., … & Qi Y.D. (2020). *State of the World's Plants and Fungi.* PhD thesis. Royal Botanic Gardens, Kew, Sfumato Foundation.

Bernard R., Buczyński P., Tończyk G. & Wendzonka J. (2009). *A distribution atlas of dragonflies (Odonata) in Poland*. Bogucki Wydawnictwo Naukowe, Poznań, Poland.

Billqvist M., Andersson D. & Bergendorff C. (2019). *NordensTrollsländor*. Avium förlag, Stenåsa, Sweden.

Bos F., Wasscher M. & Reinboud W. (2007). *Veldgids Libellen*. 5e druk. KNNV Uitgeverij, Zeist, the Netherlands.

Boudot J.P. & Kalkman V.J. (editors) (2015). *Atlas of the European dragonflies and damselflies*. Zeist, The Netherlands: KNNV Publishing.

Bried J.T. & Samways M.J. (2015). A review of odonatology in freshwater applied ecology and conservation science. *Freshwater Science* 34: 1023-1031.

Bried J., Ries L., Smith B., Patten M., Abbott J., … & White E. (2020). Towards global volunteer monitoring of odonate abundance. *BioScience* 70: 914-923.

Ceballos G., Ehrlich P.R., Barnosky A.D., García A., Pringle R.M. & Palmer T.M. (2015). Accelerated modern human-induced species losses: entering the sixth mass extinction. *Science Advances* 1: e1400253.

Ceballos G., Ehrlich P.R. & Raven P.H. (2020). Vertebrates on the brink as indicators of biological annihilation and the sixth mass extinction. *Proceedings of the National Academy of Sciences of the United States of America* 117: 13596-13602.

Cowie R.H., Bouchet P. & Fontaine B. (2022). The Sixth Mass Extinction: fact, fiction or speculation? *Biological Reviews of the Cambridge Philosophical Society* 97: 640-663.

Davidson N.C. (2014). How much wetland has the world lost? Long-term and recent trends in global wetland area. *Marine and Freshwater Research* 65: 934-941.

Dennis R.L.H., Sparks T.H., Hardy B.P. (1999). Bias in butterfly distribution maps: the effect of sampling effort. *Journal of Insect Conservation* 3: 33-42.

Dennis R.L.H., Thomas C.D. (2000). Bias in butterfly distribution maps: the influence of hot spots and recorders home range. *Journal of Insect Conservation* 4: 73-77.

Dolný A. & Bárta D. (editors) (2009). *Dragonflies of the Czech Republic. Ecology, Conservation and Distribution*. Taita Publishers, Czech Republic.

Feest A. (2013). The utility of the Streamlining European Biodiversity Indicators 2010 (SEBI 2010). *Ecological Indicators* 28: 16-21.

Fraisl D., Hager G., Bedessem B., Gold M., Hsing P.Y., … & Haklay M. (2022). Citizen science in environmental and ecological sciences. *Nature Reviews Methods Primers* 2: 64.

Hassall C. (2012). Predicting the distributions of under-recorded Odonata using species distribution models. *Insect Conservation* and Diversity 5: 192-201.

Haysom K.A., Dekker J., Russ J., van der Meij T. & van Strien A. (2014). *European bat population trends. A Prototype Biodiversity Indicator*. EEA Technical Report No.19/2013. European Environment Agency, Luxembourg.

IPBES (2019). *Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*. Brondizio E.S., Settele J., Díaz S. & Ngo H.T. (editors). IPBES secretariat, Bonn, Germany.

IUCN (2022). *The IUCN Red List of Threatened Species*. Version 2022-2. https://www.iucnredlist.org/. Accessed 28 May 2023.

Navarro L.M., Fernandez N., Guerra C., Guralnick R., Kissling W.D., ... & Pereira H.M. (2017). Monitoring biodiversity change through effective global coordination. *Current opinion in environmental sustainability* 29: 158-169.

Proença V., Martin L.J., Pereira H.M., Fernandez M., McRae L., ... & Van Swaay C.A.M. (2017). Global biodiversity monitoring: from data sources to essential biodiversity variables. *Biological Conservation* 213: 256-263.

Reid A.J., Carlson A.K., Creed I.F., Eliason E.J., Gell P.A., ... & Cooke S. J. (2019). Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biological Reviews* 94: 849-873.

Schipper A.M., Hilbers J.P., Meijer J.R., Antão L.H., Benítez-López A., ... & Huijbregts M.A. (2020). Projecting terrestrial biodiversity intactness with GLOBIO 4. *Global Change Biology* 26: 760-771.

Schmeller D.S., Henry P.Y., Julliard R., Gruber B., Clobert J., ... & Henle K. (2009). Advantages of volunteer-based biodiversity monitoring in Europe. *Conservation Biology* 23: 307-316.

Schulte P., Alegret L., Arenillas I., Arz J.A., Barton P.J., ... & Willumsen P.S. (2010). The Chicxulub asteroid impact and mass extinction at the Cretaceous-Paleogene boundary. *Science* 327: 1214-1218.

Siesa M.E. (2017). *Le libellule delle Alpi: como riconoscerle, dove e quando osservarle*. Blu Edizioni, Torino, Italy.

Smallshire D. & Beynon T. (2010). Dragonfly Monitoring Scheme Manual. British Dragonfly Society. Available at: https://freshwaterhabitats.org.uk/.

Thomas J.A. (2005). Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. *Philosophical Transactions of the Royal Society B: Biological Sciences* 360: 339-357.

Trisos C.H., Merow C., & Pigot A.L. (2020). The projected timing of abrupt ecological disruption from climate change. *Nature*, 580: 496-501.

Van Klink R., Bowler D.E., Gongalsky K.B., Swengel A.B., Gentile A. & Chase J.M. (2020). Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. *Science* 368: 417-420.

Van Swaay C.A.M., Bos-Groenendijk G.I., van Deijk J.R., van Grunsven R.H.A., Kok J.M., … & Poot M. (2018). *Handleiding landelijke meetnetten vlinders, libellen en nachtvlinders*. Report VS2018.011, De Vlinderstichting, Wageningen. Available at: https://www.vlinderstichting.nl/.

Van Swaay C.A.M, Nowicki P., Settele J., & van Strien A.J. (2008). Butterfly monitoring in Europe: methods, applications and perspectives. *Biodiversity and Conservation* 17: 3455-3469.

Van Swaay C.A.M., Plate C.L. & van Strien A. (2002). Monitoring butterflies in the Netherlands: how to get unbiased indices. Proceedings of the section Experimental and Applied Entomology of the Netherlands Entomological Society (N.E.V.) 13: 21-27.

Wagner D.L. (2020). Insect declines in the Anthropocene. *Annual Review of Entomology* 65: 457-480.

WWF (2020). *Living Planet Report 2020 - Bending the curve of biodiversity loss.* Almond R.E.A., Grooten M. & Petersen T. (editors). WWF, Gland, Switzerland.

Aeshna affinis has a positive distribution trend in the Netherlands, while its abundance trend is uncertain.

CHAPTER 2

Site-occupancy models offer new opportunities for dragonfly monitoring based on daily species lists.

Arco J. van Strien, Tim Termaat, Dick Groenendijk, Victor Mensing, Marc Kéry

BASIC AND APPLIED ECOLOGY (2010) 11: 495–503

Abstract

Monitoring biodiversity is necessary but difficult to achieve in practice, in part because standardised field work is often demanding for volunteer field workers. Collecting opportunistic data on presence and absence of species is much less demanding, but such data may suffer from a number of biases, such as variation in observation effort over time. Here we explore whether site-occupancy models may be helpful to reduce such biases in opportunistic data, especially those caused by temporal variation of observation effort and by incomplete reporting of sightings. Site-occupancy models represent a generalisation of classical metapopulation models to account for imperfect detection; they estimate the probability of sites to be occupied (and of the rates of change, colonisation and extinction rates) while taking into account imperfect detection of a species. The models require so-called presence-absence data from replicated visits for a number of sites (e.g., 20–50). We tested whether these models provide reliable trend estimates if collectors of opportunistic data do not report all species detected. We applied the models to three opportunistic datasets of dragonfly species (1999–2007) in the Netherlands: (1) one-species records, (2) short daily species lists and (3) comprehensive daily species lists. Trend estimates based on a fourth dataset from a standardised monitoring scheme were used as a yardstick to judge the results. The analyses showed that occupancy trends based on comprehensive daily species lists in combination with site-occupancy models were generally similar to those based on the monitoring scheme. But trends based on one-species records and short daily lists were too imprecise to be very useful. In addition, site-occupancy models lead to more realistic occupancy estimates than those obtained from conventional logistic regression analysis. We conclude that comprehensive daily species lists can be useful surrogates for monitoring schemes to assess distributional trends.

KEYWORDS: detection, distribution, metapopulation model, monitoring, occupancy, dragonfly, Odonata

2.1 Introduction

Monitoring biodiversity helps in identifying conservation issues and in determining the effects of conservations actions (Vos et al., 2000). Monitoring has become even more important since many countries have committed themselves to reducing biodiversity loss at the Convention on Biological Diversity (Balmford et al., 2005; Schutyser & Condé, 2009). Although the number of country-wide monitoring schemes is steadily increasing in Europe and elsewhere (Gregory et al., 2005; De Heer et al., 2005), large-scale monitoring of many species groups is still scarce and few monitoring schemes exist outside of Europe and North America. This is unfortunate, because commitments to halt biodiversity loss can only be tested if sufficient monitoring data are available.

One reason for the lack of monitoring schemes is their difficulty. Typically, a large-scale monitoring scheme requires searching for species on fixed study sites year after year, using standardised field methods. These requirements make it difficult to recruit many volunteer field workers for large-scale monitoring. Therefore, alternatives for standardised monitoring schemes that require less effort are much needed (Roberts et al., 2007).

Currently an increasing amount of presence-absence data is being collected in the framework of citizen science projects with easy data entry facilities on the internet (see e.g. www.telmee.nl, www.ornitho.ch or www.worldbirds.org). These "opportunistic" data are collected without a standardised field protocol and without using carefully selected sites. It would be helpful if such data could be used to draw inferences on trends in the distribution of species. But without standardisation of field methods, changes in observation efforts across years may easily lead to artificial trends or mask existing trends (Van Swaay, 1990).

Kéry et al. (2010) explored whether site-occupancy models (MacKenzie et al., 2006) may be useful to correct for unequal observation effort in opportunistic data. Their basic idea is that variation in observation effort over the years is directly translated into variation in species detectability. If annual detection probabilities were estimated, one would be able to assess the yearly "true" proportion of occupied sites (occupancy) and thus to assess trends in occupancy. Site-occupancy models are simply an extension of classical metapopulation models to account for imperfect detection. They use presence-absence data arranged in so-called detection histories per site in the season, such as "010" if the study species was detected during the second visit, but not during the first and third visit. These models require data of temporal and spatial replicates, i.e., for at least a number of sites repeated surveys are needed within a so-called period of closure (Kéry et al., 2010). Closure means that a site must stay either occupied or not but must not become permanently abandoned or colonised during the period of surveys within a 'season' (here, year). Here we extend the approach of Kéry et al. (2010) in two ways. First, Kéry et al. (2010) did not compare their results with independent trend information. We compared trends derived from site-occupancy models and opportunistic data with trends based on the Dutch Dragonfly Monitoring Scheme. Second, Kéry et al. (2010) used daily species list of birds in Switzerland as opportunistic data and all observers involved were committed to report any of the species from a fixed set of species. However, many collectors of opportunistic data do not report all species detected, but only those they are interested in for some reason and they ignore others. Here, we tested if incomplete daily lists provide useful trend information when analysed with site-occupancy models. We used opportunistic data of dragonflies (Odonata) differing in the degree of completeness of daily species lists.

2.2 Material and methods

2.2.1 SPECIES

We selected seven dragonfly species, differing in visibility, flight period, commonness, habitat preferences and life span of larvae. Three of them are damselflies (Zygoptera): *Lestes sponsa*, *Coenagrion lunulatum* and *Coenagrion pulchellum*, and four are true dragonflies (Anisoptera): *Aeshna isoceles*, *Brachytron pratense*, *Cordulia aenea* and *Leucorrhinia rubicunda*.

2.2.2 DATA

The opportunistic data were obtained from the Dutch Dragonfly Databank. Many presence records in the databank are stored at a resolution of 1 x 1 km and hence, we use 1 x 1 km squares as our definition of a site for these data. The absence data, or more precisely the non-detection data, as required for the site-occupancy model were created from the information in the database of sightings of other dragonfly species. To create detection histories per site (see above), any observation of a study species was taken as 1 (presence) in the dataset, and as 0 if any other species but not the study species had been reported by the same observer at the same day and site and within the main flight period of the study species. Obviously, the zeroes may be absences, non-detections or non-reported observations of species seen.

We distinguished three levels of completeness of species lists in these data. (1) Single records of species on a particular date without sightings of other species are highly incomplete lists, thus have the strongest underreporting. Such data are usually coincidental observations and are predominant in museum collection data (McCarthy, 1998). (2) Short daily species lists are records of 2-3 species made by one observer on one particular date and site. (3) Comprehensive daily species lists are all records of >3 species per observer, date and site. The high amount (88%) of one or several of the most common ('uninteresting') dragonfly species *Ischnura elegans, Enallagma cyathigerum, Coenagrion puella* or *Coenagrion pulchellum* suggest that comprehensive lists do not substantially suffer from underreporting and thus resemble the data of Kéry et al. (2010).

For each species we assembled three opportunistic datasets that correspond with these levels of completeness. A fourth dataset was based on the Dutch Dragonfly Monitoring Scheme which is a scheme of 200-300 fixed, 250-metre-long transects along waterways surveyed several times per year for all species using a standardised field method (Ketelaar & Plate, 2001). Transect locations in this scheme have not been selected randomly, because the main aim was to achieve data for a number of policy-relevant species which implies that marshland areas that are important for dragonflies are oversampled. A similar oversampling of marshland areas occurs in all three opportunistic datasets.

To meet the closure assumption of the site-occupancy models (see above), we restricted the data to the flight periods of each species, i.e., the yearly period with a continuous stream of sightings, thereby discarding the most extreme dates with sightings. None of the seven species selected had large variations in flight period between years nor had advanced their flight period in response to warmer springs (Dingemans & Kalkman, 2008; Dutch Environmental Data Compendium, 2009). The annual number of sites from which data were received has increased in all three opportunistic datasets from less than 1000 in 1999 to several thousands in 2007 (fig. 2.1). In contrast, the number of sites covered by the monitoring scheme is much lower and more or less stable over time (fig. 2.1).

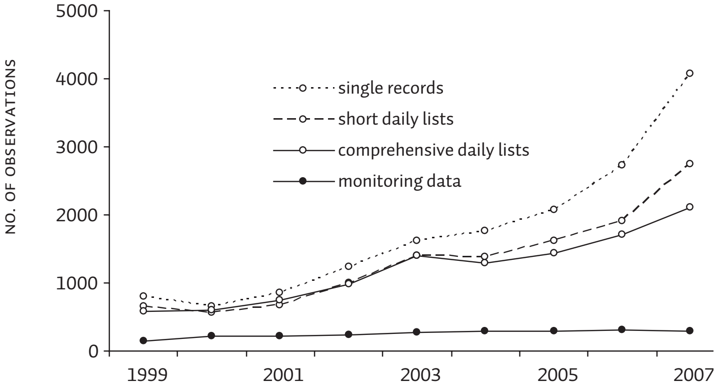

FIG. 2.1 | Annual number of sites in the sets of single records, short daily species lists, comprehensive daily species lists and monitoring data. Data from *Aeshna isoceles* are shown; other species have slightly different numbers of sites (because of their different flight periods) but a similar temporal pattern.

2.2.3 OCCUPANCY DEFINITION

Occupancy is a species' probability to occur at a site at some time during the species-specific flight period. For each dataset we estimated the yearly occupancy ψ, i.e., the proportion of occupied 1 x 1 km squares in the statistical population, of which our sampled squares were representative. To enable use of monitoring data as a yardstick, we restricted the analysis to 1999-2007 because the Dutch Dragonfly Monitoring scheme started in 1999. To some extent occupancy estimation through these monitoring data is comparable to estimation through the opportunistic data. Monitoring transects are smaller than the 1 x 1 km squares applied in collecting opportunistic data, but they are often situated in different 1 x 1 km squares and 1 x 1 km squares are rarely examined entirely while collecting opportunistic data.

2.2.4 STATISTICAL ANALYSIS

We used the dynamic site-occupancy (SO) model as described by Royle & Kéry (2007) and Royle & Dorazio (2008; p. 309) to estimate yearly occupancy ψ, adjusted for detection probability p. Estimating p is only possible if repeated visits are available for at least some sites (MacKenzie et al., 2006). In opportunistic data at most 40% of the sites had a second visit within the same season, and relatively few sites were visited more than three times (fig. 2.2). Often, the subsequent visits were made by different observers. In the monitoring scheme many fieldworkers conducted >5 replicated visits in the season and usually a single observer conducted all repeated surveys within a season. Both components of the model (i.e., ψ and p) may be made a function of covariates, but here we only used a covariate for p. Because detection of dragonflies varies over the season, presumably due to changing population size over the course of a flight period, the Julian date was added as covariate for p via a logit link:

$$\text{logit}(p_{ij}) = \alpha_0 + \beta_1 * \text{date}_{ij} + \beta_2 * \text{date}_{ij}{}^2 ,$$

where p_{ij} is the probability to detect the species at site i during visit j, α_0 is the intercept and β_1 and β_2 are the linear and quadratic effects of the date of visit j at site i.

We fitted the models in a Bayesian mode of inference using the WinBUGS software (Spiegelhalter et al., 2003). We chose conventional vague priors for all parameters: uniform distributions with values between 0 and 1 for all parameters except $\alpha 0$ (values between -5 and 5) and $\beta 1$ and $\beta 2$ (values between -10 and 10). For each analysis, we ran three Markov chains with 6000 iterations each and discarded the first half as burn-in. These specifications were usually sufficient to reach convergence based on the Gelman-Rubin Rhat statistic (Rhat <1.1). The standard deviation of the sample from the posterior distribution of each parameter computed by WinBUGS was interpreted as the standard error of that parameter. Regression coefficients of ψ and p across years were estimated as derived parameters within the WinBUGS model.

For comparison, we used WinBUGS to perform a conventional logistic regression (LR) for each dataset, thus without taking into account detection probability. If a species was not detected in any of the visits per site per year, the species was regarded as absent, else as present. In this simple logistic regression model 1000 iterations were sufficient to achieve convergence for the Markov chains.

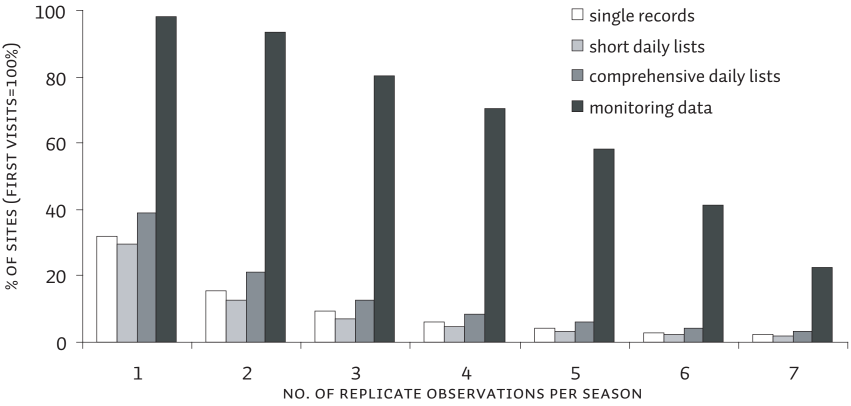

FIG. 2.2: Percentage of replicated visits within the season in 1999-2007 in single records, short daily species lists, comprehensive daily species lists and monitoring data.

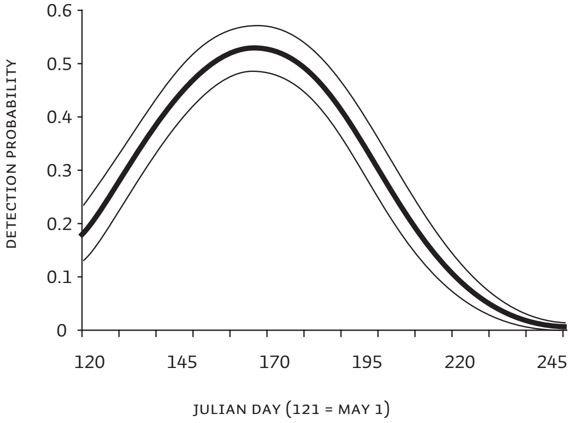

FIG. 2.3: Detection probability (± se) of *Aeshna isoceles* in relation to Julian date in the monitoring data 1999-2007.

2.3 Results

The detection probability *p* of all species was lower at the start and the end of their flight period (see fig. 2.3 for an example). There were also considerable differences in *p* among datasets. As expected, detection probability was especially low in single records due to severe underreporting of species (table 2.1); note that *p* here represents the product of the probability to observe a species and the probability to report a species once detected. Incomplete reporting may also explain the somewhat lower estimates of *p* in short daily lists as compared to comprehensive lists and monitoring data (table 2.1). The latter two datasets did not differ with respect to *p*, except for *C. pulchellum*.

TABLE 2.1: Mean detection probability (± se) per species in four independent datasets based on a site-occupancy model (1999-2007). NA: not available due to lack of data. See fig. 2.1 for the number of sites per year for each dataset.

	Single records	**Short daily lists**	**Comprehensive daily lists**	**Monitoring data**
Lestes sponsa	0.07 ± 0.07	0.22 ± 0.07	0.52 ± 0.02	0.46 ± 0.02
Coenagrion lunulatum	NA	NA	0.34 ± 0.06	0.44 ± 0.07
Coenagrion pulchellum	0.09 ± 0.04	0.33 ± 0.04	0.50 ± 0.02	0.40 ± 0.02
Aeshna isosceles	0.15 ± 0.05	0.24 ± 0.07	0.35 ± 0.03	0.39 ± 0.04
Brachytron pratense	0.10 ± 0.05	0.22 ± 0.05	0.30 ± 0.02	0.30 ± 0.03
Cordulia aenea	0.17 ± 0.09	0.22 ± 0.10	0.37 ± 0.03	0.40 ± 0.03
Leucorrhinia rubicunda	0.17 ± 0.10	0.30 ± 0.08	0.36 ± 0.03	0.45 ± 0.04

In comprehensive daily lists and monitoring data, *p* for individual species varied between about 0.3 and 0.5 (table 2.1). *C. aenea*, *C. pulchellum* and *A. isoceles* showed a significant decline in *p* across years in short daily lists (correlation coefficients with time of *p* -0.77, -0.87 and -0.81 respectively; P<0.05). A decline in *p* was also found in comprehensive daily lists for *L. sponsa* and *C. pulchellum* (correlation coefficients -0.66 and -0.72 respectively; P<0.05; see fig. 2.4 for an example). No significant trends in *p* were found in monitoring data and in single species records. A decline in *p* might be caused by decreasing population numbers which make a species less visible to observers. Indeed, population numbers have declined in 1999-2007 for *C. pulchellum* and *L. sponsa*, but not for *C. aenea* and *A. isoceles* (Dutch Environmental Data Compendium, 2009). Some alternative explanations of the declines in *p* are changes in preferences of observers (though for short daily lists only), in observation effort or in experience of observers (Schmidt, 2004).

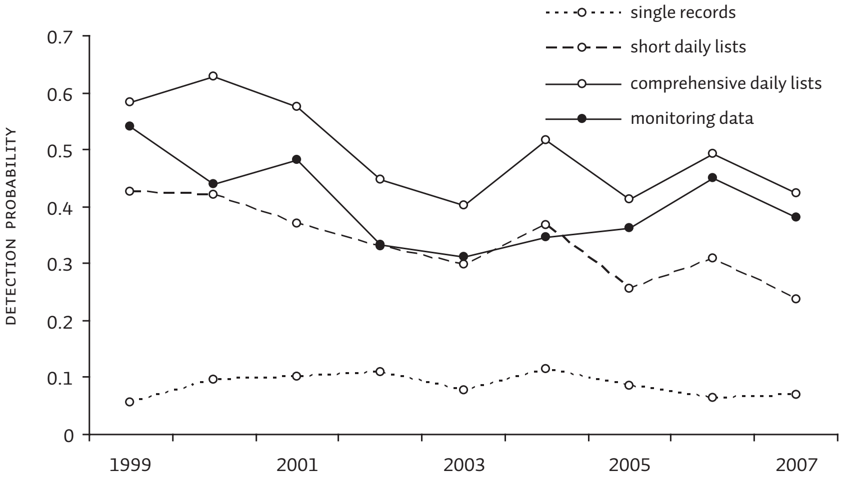

FIG. 2.4: Yearly detection probability (for clarity without se's) of *Coenagrion pulchellum* in single records, short daily species lists, comprehensive daily species lists and monitoring data.

Because p estimates were < 1, a species present at a site is not always detected during a visit. The consequences of $p < 1$ for occupancy estimation do not only depend on the value of p, but also on the number of visits. The probability P_n to assess a species at least once at a site is $1-(1-p)^n$, where n is the number of visits (Kéry et al., 2006). If a site is visited twice and p per visit is equal to 0.4, $P_n = 0.64$ and after four visits $P_n = 0.87$. Because many sites were visited fewer than four times in opportunistic datasets (fig. 2.2), many of the zero values do likely not represent real absences but just non-detections. Without correction this leads to underestimation of occupancy. Site-occupancy models estimate p and by doing so obtain an estimate for each site of the probability that it is occupied considering p and the number of visits. The resulting occupancy estimates thus are necessarily higher than those of the corresponding logistic regression results (table 2.2). The big difference in occupancy estimates between the logistic regression and the site-occupancy model for single records and short species lists is because low values of p (table 2.1) require many visits to detect a species during at least one visit. There are, however, few replicated visits in this dataset (fig. 2.2), thus many sites treated as non-occupied in logistic regression are considered as occupied in the site-occupancy model. In contrast, the difference in occupancy estimates between logistic regression and the site-occupancy model is very small for monitoring data (table 2.2). That is because p estimates were relatively high and many replicated visits are available, leading to detection during one or more visits. Taking into account p and the number of visits in the analysis may then add little to occupancy estimates based on logistic regression (provided *p* is constant in time, which was the case for monitoring data). An additional explanation of the differences in occupancy estimates between LR and SO is bias in estimates under the site-occupancy models when *p* is very low, as was the case for single records (MacKenzie et al., 2006).

TABLE 2.2: Mean occupancy probability (± se) per species in four independent datasets using a logistic regression model (LR) or a site-occupancy model (SO). Data were confined to 2005-2007 because of inaccurate estimates in some early years. NA: not available due to lack of data. See fig. 2.1 for the number of sites per year for each dataset.

		Single records	**Short daily lists**	**Comprehensive daily lists**	**Monitoring data**
Lestes sponsa	LR	0.01 ± 0.002	0.04 ± 0.005	0.25 ± 0.01	0.28 ± 0.02
	SO	0.17 ± 0.07	0.18 ± 0.04 *	0.40 ± 0.02 *	0.31 ± 0.01 *
Coenagrion lunulatum	LR	0.003 ± 0.002	0.006 ± 0.003	0.04 ± 0.01	0.05 ± 0.01
	SO	NA	NA	0.08 ± 0.02	0.07 ± 0.01
Coenagrion pulchellum	LR	0.02 ± 0.003	0.11 ± 0.01	0.30 ± 0.01	0.26 ± 0.02
	SO	0.22 ± 0.07	0.32 ± 0.03	0.49 ± 0.02 *	0.30 ± 0.01 *
Aeshna isosceles	LR	0.04 ± 0.004	0.06 ± 0.005	0.15 ± 0.01	0.26 ± 0.02
	SO	0.20 ± 0.03	0.23 ± 0.03	0.28 ± 0.01	0.26 ± 0.02
Brachytron pratense	LR	0.02 ± 0.004	0.06 ± 0.006	0.17 ± 0.01	0.18 ± 0.02
	SO	0.15 ± 0.06	0.24 ± 0.04	0.40 ± 0.02 *	0.22 ± 0.01 *
Cordulia aenea	LR	0.01 ± 0.002	0.04 ± 0.005	0.21 ± 0.01	0.20 ± 0.02
	SO	0.07 ± 0.02 *	0.25 ± 0.04	0.38 ± 0.02 *	0.22 ± 0.01 *
Leucorrhinia rubicunda	LR	0.01 ± 0.003	0.03 ± 0.004	0.11 ± 0.01	0.11 ± 0.02
	SO	0.04 ± 0.02 *	0.07 ± 0.02	0.21 ± 0.02 *	0.12 ± 0.01 *

** significant difference from monitoring data for the same species P<0.05 (only SO estimates compared)*

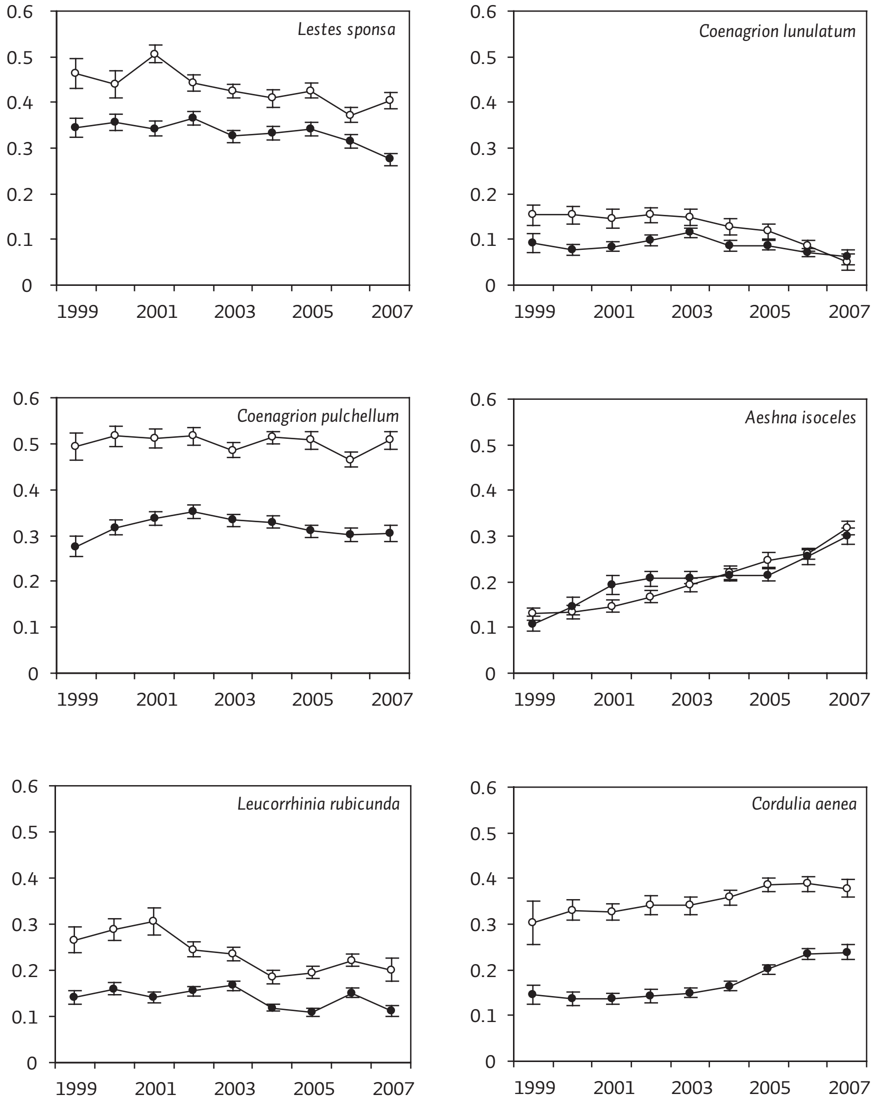

FIG. 2.5: Yearly occupancy probability (± se) of *Lestes sponsa, Coenagrion lunulatum, Coenagrion pulchellum, Aeshna isoceles, Leucorrhinia rubicunda* and *Cordulia aenea* in comprehensive daily species lists (open circles) and monitoring data (closed circles).

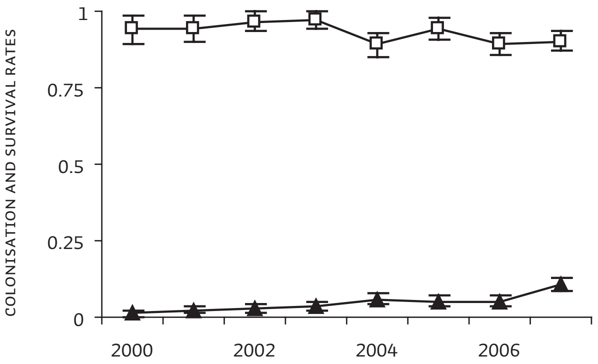

FIG. 2.6: Yearly rates of colonisation (triangles) and survival (± se) (squares) of *Aeshna isoceles*, based on complete daily lists analysed with a dynamic site-occupancy model.

As expected, occupancy estimates based on a site-occupancy model were higher for widespread species as *C. pulchellum* than for rare species as *C. lunulatum* (see SO in table 2.2). Occupancy estimates differed between the opportunistic datasets and monitoring data for a number of species (table 2.2). But trends in occupancy based on comprehensive daily lists and monitoring data were quite similar for most species (fig. 2.5). Only *C. lunulatum* and *L. rubicunda* declined more strongly according to the comprehensive lists than according to the monitoring data (fig. 2.5; appendix 2.1). Trends in occupancy based on single records and short daily lists also corresponded to some degree with the trend based on monitoring data, but the trend estimates were far from precise (see appendix 2.1). Trends based on logistic regression corresponded closely with those based on site-occupancy for monitoring data, but this was frequently not so for the other datasets (see e.g. the difference in trends between LR and SO for *C. pulchellum* in comprehensive species lists in appendix 2.1). This is because the logistic regression does not take into account declines in *p* for some species, resulting in overrated declines in occupancy.

As an interesting by-product in our study, dynamic site-occupancy models yield estimates of annual colonisation and survival rates of sites. As an example, fig. 2.6 shows these estimates for *A. isoceles*. Its positive trend in occupancy (fig. 2.5) is not due to better survival (or persistence) of occupied sites, but to an increased rate of colonising new squares.

2.4 Discussion

The analyses showed that site-occupancy models lead to more realistic occupancy estimates from opportunistic data than did conventional logistic regression analysis (table 2.2). Moreover, trends in occupancy were considered more reliable after using a site-occupancy model, because the model corrected for changes in detection probability. Site-occupancy models were not only useful to reduce bias in comprehensive species lists as Kéry et al. (2010) suggested, but also improved occupancy estimates in single records and short daily lists, by taking into account the low estimates of p in these data. However, the resulting trends in occupancy were hardly informative for single records and short daily lists, because of their large standard errors, in spite of the considerable amount of data (fig. 2.1). One reason for these large standard errors is the uncertainty in p estimation in these datasets. Most models to estimate p in single records did not even converge properly and p estimates smaller than 0.10-0.20 are dubious anyway (MacKenzie et al., 2006). Site-occupancy models are not very useful when p is that small, unless ψ is high and there are many within-year replicates. To a lesser extent short species lists also suffered from imprecise estimates of p. These results confirm the expectation of Kéry et al. (2010) that comprehensive daily species lists in combination with site-occupancy models provide trend estimates that resemble those produced by a monitoring scheme using standardised field methods.

Occupancy estimates based on comprehensive species lists were often higher than those based on monitoring data (fig. 2.5). A possible explanation of this difference is site selection bias. Occupancy estimates are sensitive to the selection of sites by the free choice of observers in both comprehensive daily lists and monitoring data. If observers tend to go mostly to the ‘good’ sites, then the occupancy parameter refers to a statistical population of ‘good’ sites. For this hypothetical statistical population, occupancy may well be higher. But if site selection bias plays a role, we would expect monitoring data to be collected in better sites rather than opportunistic data, and thus expect a higher occupancy in monitoring data. We found the opposite. Another explanation is a possible higher amount of missing zeroes in comprehensive daily species lists than in monitoring data if some observers are disinclined to report that they did not observe any species at all during a field visit. But we judge this risk to be low. A more plausible explanation for the differences in occupancy is a larger search area while collecting opportunistic data. Monitoring data are exclusively sampled at the location of the site and sites usually concern only one type of water (pond, brook, marshland etc.). Species that occur elsewhere in the same 1 x 1 km square may never show up at the monitoring site because they live in another water type. But observers collecting daily species lists data generally cover a larger search area in a 1 x 1 km square and visit several water types, leading to a higher occupancy rate. The most notable exception is *A. isoceles* for which occupancy estimates were similar in both datasets (fig. 2.5). This species is the most mobile of all species studied, and if present in a 1 x 1 km square, it most probably will be observed sooner or later at a monitoring site within the same square.

Although occupancy estimates differed between comprehensive species lists and monitoring data, trends in occupancy were remarkably similar in both datasets for most species. It seems that neither any site selection bias nor a possible different search area affect trend estimation substantially. Important drivers of dragonfly trends are climatic change and large-scale changes in fresh water quality (Corbet, 2004). Because both factors operate at the scale of the Netherlands as a whole, we do not expect large site selection effects on the trends of most dragonfly species.

Because of their lack of standardisation, daily species lists, either complete or incomplete, were supposed to have high risk of bias and the power to detect any trends timely is generally considered low (Weller, 2008). Therefore, monitoring schemes based on standardised methods have been recommended for their high capability to produce unbiased and timely trend information (e.g. Vos et al., 2000). But here we have shown that site-occupancy models are able to correct for bias in comprehensive daily lists and also that comprehensive lists contain sufficient statistical power due to the large amount of data. The standard errors of the trend estimates for comprehensive species lists were only slightly larger than for monitoring data (fig. 2.5; appendix 2.1). The statistical power of daily species lists may be further enhanced if the number of replicates grows or if detection probability can be increased. According to MacKenzie et al. (2006; p. 168) the optimal number of replicates is 4 for $p = 0.4$ and $\psi = 0.3$. Most sites in our daily species lists data had fewer than 4 replicates (fig. 2.2).

If a monitoring scheme with standardised field method is not feasible, one may thus consider the collection of comprehensive species lists as a promising surrogate. Collecting species list data for monitoring purposes has been suggested earlier by Roberts et al. (2007), but especially the combination with site-occupancy models allows achieving trend estimates that are unbiased with respect to observation effort. Furthermore, site selection needs to be taken into account to ensure that the sites are representative for the region about which inference is desired. Though it is better to try to apply a formal sampling design to select sites (Yoccoz et al., 2001), this is often not easy to achieve in practice for monitoring schemes. Collectors of opportunistic data are even less inclined to be directed to pre-selected sites and may easily oversample species-rich areas. A possibility to adjust for any oversampling and undersampling of regions is by applying post-stratification and weighing of sites by surface areas or shares in overall population. This approach has proved successful for butterfly and bird monitoring data in the Netherlands (Van Swaay et al., 2002; Van Turnhout et al., 2008).

The use of site-occupancy models opens new opportunities for large-scale dragonfly monitoring because collecting opportunistic data requires far less effort than setting-up standardised monitoring schemes and it is much less demanding for observers. It also opens new perspectives for monitoring more generally for other species groups that contain at least a few very frequently detected species during field visits.

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References

Balmford A., Bennun L., ten Brink B., Cooper D., Côté I.M., ... & Walther B.A. (2005). The convention on biodiversity's 2010 target. *Science* 307: 212-213.

Corbet P.S. (2004). *Dragonflies: behaviour and ecology of Odonata*. Cornel University Press, Ithaca, New York.

De Heer M., Kapos V. & ten Brink B.J.E. (2005). Biodiversity trends in Europe: development and testing of a species trend indicator for evaluating progress towards the 2010 target. *Philosophical Transactions of the Royal Society B* 360: 297-308.

Dingemans N. & Kalkman V.J. (2008). Changing temperature regimes have advanced the phenology of Odonata in the Netherlands. *Ecological Entomology* 33: 394-402.

Dutch Environmental Data Compendium (2009). http://www.milieuennatuurcompendium.nl/

Gregory R.D., van Strien A., Vorisek P., Gmelig Meyling A.W., Noble D.G., ... & Gibbons D.W. (2005). Developing indicators for European birds. *Philosophical Transactions of the Royal Society B* 360: 269-288.

Kéry M., Spillmann J.H., Truong C. & Holderegger R. (2006). How biased are estimates of extinction probabilities in revisitation studies? *Journal of Ecology* 94: 980-986.

Kéry M., Royle J.A., Schmid H., Schaub M., Volet B., ... & Zbinden N. (2010). Site-occupancy distribution modeling to correct population-trend estimates derived from opportunistic observations. *Conservation Biology* 24: 1388-1397.

Ketelaar R. & Plate C. (2001). *Handleiding Landelijk Meetnet Libellen (Manual monitoring Scheme Dragonflies)*. Rapport VS2001.28. Butterfly Conservation & Statistics Netherlands, Voorburg.

McCarthy M.A. (1998). Identifying declining and threatened species with museum data. *Biological Conservation* 83: 9-17.

MacKenzie D.I., Nichols J.D., Royle J.A., Pollock K.H., Hines J.E. & Bailey L.L. (2006). *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*. Elsevier, San Diego.

Roberts R.L., Donald P.F. & Green R.E. (2007). Using simple species lists to monitor trends in animal populations: new methods and a comparison with independent data. *Animal Conservation* 10: 332-339.

Royle J.A. & Kéry M. (2007). A Bayesian state-space formulation of dynamic occupancy modelling. *Ecology* 88: 813-1823.

Royle, J.A., Dorazio, R.M. (2008). *Hierarchical modeling and inference in ecology*. Academic Press, Amsterdam.

Schmidt B.R. (2004). Declining amphibian populations: the pitfalls of count data in the study of diversity, distributions, dynamics and demography. *Herpetological Journal* 14: 167-174.

Schutyser F. & Condé S. (2009). *Progress towards the European 2010 biodiversity target.* Report No. 4/2009, European Environmental Agency, Copenhagen.

Spiegelhalter D., Thomas A. & Best N.G. (2003). *WinBUGS User Manual.* Version 1.4. MCR Biostatistics Unit, Cambridge.

Van Swaay C.A.M., Plate C.L. & van Strien A. (2002). Monitoring butterflies in the Netherlands: how to get unbiased indices. *Proceedings of the section Experimental and Applied Entomology of the Netherlands Entomological Society (N.E.V.)* 13: 21-27.

Van Swaay C.A.M. (1990). An assessment of the changes in butterfly abundance in The Netherlands during the 20th Century. *Biological Conservation* 52: 287-302.

Van Turnhout C.A.M., Willems F., Plate C., van Strien A., Teunissen W., … & Foppen R. (2008). Monitoring common and scarce breeding birds in the Netherlands: applying a post-hoc stratification and weighting procedure to obtain less biased population trends. *Journal of Catalan Ornithology* 24: 15-29.

Vos P., Meelis E. & ter Keurs W.J. (2000). A framework for the design of ecological monitoring programs as a tool for environmental and nature management. *Environmental Monitoring and Assessment* 61: 317-344.

Weller T.J. (2008). Using occupancy estimation to assess the effectiveness of a regional multiple-species conservation plan: Bats in the Pacific Northwest. *Biological Conservation* 141: 2279-2289.

Yoccoz N.G., Nichols J.D. & Boulinier T. (2001). Monitoring of biodiversity in space and time. *Trends in Ecology and Evolution* 16: 446-453.

Appendix 2.1

Trends in occupancy probability (± se) per species in four independent datasets using a logistic regression model (LR) or a site-occupancy model (SO) in 1999-2007. NA: not available due to lack of data. See fig. 2.1 for the number of sites per year for each dataset.

		Single records	**Short daily lists**	**Comprehensive daily lists**	**Monitoring data**
Lestes sponsa	LR	0.000 ± 0.000	-0.003 ± 0.001 [1]	-0.017 ± 0.002 [1]	-0.006 ± 0.003 [1]
	SO	-0.043 ± 0.022	-0.005 ± 0.016	-0.011 ± 0.004 [1]	-0.007 ± 0.003 [1]
Coenagrion lunulatum	LR	0.000 ± 0.000	-0.001 ± 0.001	-0.009 ± 0.002 [1]	-0.003 ± 0.003
	SO	NA	NA	-0.014 ± 0.004 [1,2]	-0.003 ± 0.002 [2]
Coenagrion pulchellum	LR	-0.002 ± 0.001 [1]	-0.008 ± 0.002 [1]	-0.011 ± 0.002 [1]	-0.001 ± 0.003
	SO	-0.038 ± 0.028	-0.004 ± 0.005	-0.002 ± 0.003	0.000 ± 0.003
Aeshna isoceles	LR	0.004 ± 0.001 [1]	0.007 ± 0.003 [1]	0.015 ± 0.001 [1]	0.020 ± 0.003 [1]
	SO	0.016 ± 0.004 [1]	0.021 ± 0.005 [1]	0.023 ± 0.002 [1]	0.019 ± 0.003 [1]
Brachytron pratense	LR	-0.001 ± 0.001	-0.001 ± 0.001	-0.003 ± 0.002	-0.002 ± 0.003
	SO	-0.062 ± 0.022 1	0.010 ± 0.006	0.008 ± 0.005	0.002 ± 0.003
Cordulia aenea	LR	0.000 ± 0.000	0.004 ± 0.001 [1]	0.005 ± 0.002 [1]	0.011 ± 0.003 [1]
	SO	-0.026 ± 0.020	0.023 ± 0.013	0.010 ± 0.004 [1]	0.014 ± 0.003 [1]
Leucorrhinia rubicunda	LR	0.000 ± 0.000	-0.001 ± 0.001	-0.010 ± 0.002 [1]	-0.006 ± 0.003 [1]
	SO	-0.032 ± 0.018	-0.031 ± 0.024	-0.012 ± 0.003 [1,2]	-0.004 ± 0.002 [1,2]

1 significant trend $P<0.05$

2 significant difference from other datasets for the same species $P<0.05$ (only SO estimates compared)

Calopteryx splendens has increased in distribution in northwestern Europe.

CHAPTER 3

Occupancy modelling as a new approach to assess supranational trends using opportunistic data: A pilot study for the damselfly *Calopteryx splendens*.

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Abstract

There is limited information available on changes in biodiversity at the European scale, because there is a lack of data from standardised monitoring for most species groups. However, a great number of observations made without a standardised field protocol is available in many countries for many species. Such opportunistic data offer an alternative source of information, but unfortunately such data suffer from non-standardised observation effort and geographical bias. Here we describe a new approach to compiling supranational trends using opportunistic data which adjusts for these two major imperfections. The non-standardised observation effort is dealt with by occupancy modelling, and the unequal geographical distribution of sites by a weighting procedure.

The damselfly *Calopteryx splendens* was chosen as our test species. The data were collected from five countries (Ireland, Great Britain, the Netherlands, Belgium and France), covering the period 1990–2008. We used occupancy models to estimate the annual number of occupied 1x1 km sites per country. Occupancy models use presence-absence data, account for imperfect detection of species, and thereby correct for between-year variability in observation effort. The occupancy models were run per country in a Bayesian mode of inference using JAGS. The occupancy estimates per country were then aggregated to assess the supranational trend in the number of occupied 1x1 km squares. To adjust for the unequal geographical distribution of surveyed sites, we weighted the countries according to the number of sites surveyed and the range of the species per country. The distribution of *C. splendens* has increased significantly in the combined five countries. Our trial demonstrated that a supranational trend in distribution can be derived from opportunistic data, while adjusting for observation effort and geographical bias. This opens new perspectives for international monitoring of biodiversity.

KEYWORDS: detection, monitoring, distribution, citizen science data, Odonata, JAGS

3.1 Introduction

Biodiversity is in decline worldwide (Butchart et al., 2010) and this had led to a growing concern for wildlife. Recently, the European Union launched a strategy aimed to halt biodiversity loss in the EU and restore it as far as feasible by 2020 (European Union, 2011). In order to assess whether this target will be met, monitoring data are required on the status of many species, preferably at the European scale. However, data from standardised monitoring yielding information on European trends are scarce. Such information is currently mainly available for birds, some butterflies and some mammal species (de Heer et al., 2005; Gregory et al., 2005; European Environmental Agency, 2007; van Swaay et al., 2008). For these species annual supranational population indices are available with confidence intervals allowing the statistical testing of trends. For birds and butterflies these species trends are combined into biodiversity indicators (European Environmental Agency, 2007).

It seems hardly feasible to collect standardised monitoring data on a large spatial scale for other species groups. Yet, in many countries a great number of opportunistic records is available, i.e., observations collected without standardised field protocol and without a design ensuring the geographical representativeness of sampled sites. The opportunistic records are single records for particular species and day-lists of species, i.e., records of multiple species collected by a single observer on one site and date. In recent years, the number of opportunistic records has increased greatly, with data entry facilitated through internet portals (e.g. https://waarneming.nl/ and https://observation.org/). These data, often labelled as citizen science data, are a potentially valuable source of information on changes in biodiversity (Schmeller et al., 2009; Devictor et al., 2010). However, these data should be used with caution because the non-standardised observation efforts and the often uneven geographical distribution of records make national trend assessments unreliable (Dennis et al., 1999; Dennis & Thomas, 2000; Robertson et al., 2010; Szabo et al., 2010; Hassall, 2012). It is even more challenging to assess supranational trends from such opportunistic data, because the imperfections in the data may differ between countries.

In recent years, dynamic occupancy models (MacKenzie et al., 2006; Royle & Kéry, 2007) have been proposed to derive reliable trend information from opportunistic data (Kéry et al., 2010; van Strien et al., 2010, Chapter 2 of this thesis; 2011). Occupancy models use presence-absence data and yield estimates of the percentage of occupied sites (occupancy), e.g. 1x1 km squares, per year. These models take into account the imperfect detection of species and this characteristic makes them useful for analysing opportunistic data. The basic idea to analyse opportunistic data is that, all else being equal, greater observation effort increases the probability of detecting a species, so variation in observation effort over the years can be translated into variation in species detectability (Kéry et al., 2010). Using such models, Van

Strien et al. (2010, Chapter 2 of this thesis) demonstrated that in the Netherlands the trends for seven dragonfly species derived from opportunistic records during 1999-2007 were similar to trends derived from standardised monitoring data.

To the best of our knowledge, no attempts have so far been made to assess supranational trends from opportunistic data using occupancy modelling. The aim of this study is to explore whether a supranational trend for dragonflies could be generated from opportunistic data while adjusting for the imperfections mentioned. Several European countries have databases with many opportunistic records of dragonflies. We used records of dragonflies from Ireland, Great Britain, the Netherlands, Belgium and France. As a test species we chose *Calopteryx splendens*, which is a widespread species in all five countries.

3.2 Material and methods

3.2.1 DATA

All records used in this study were from adult dragonflies only. Data from Ireland include Northern Ireland and were obtained from the DragonflyIreland dataset managed by the Centre for Environmental Data and Recording (Northern Ireland) with the support of the National Biodiversity Data Centre (Republic of Ireland). Records collected are largely opportunistic and were submitted via email and websites. Data from Great Britain were obtained from the Dragonfly Recording Network of the British Dragonfly Society. Most records are opportunistic and verified by the national network of Vice County Recorders. The opportunistic data from the Netherlands were obtained from the National Database Flora and Fauna, maintained by the National Authority for Data concerning Nature. These data are owned by the Dutch Society for Dragonfly Studies, Dutch Butterfly Conservation, and the European Invertebrate Survey - the Netherlands. Most records are currently collected through the internet portals waarneming.nl and telmee.nl. Data from the Dutch Dragonfly Monitoring Scheme were excluded because these were based on standardised field work. Dragonfly data from Belgium are collected by the Flemish Dragonfly Society and the Walloon Dragonfly Working Group and through the internet portals waarnemingen.be and observations.be which are managed by Natuurpunt and Natagora. Data from France came from the database managed by the French Society of Odonatology (SFO). The French data have been collected within the framework of the Odonata's national surveys, called INVOD (1980-2004) and CILIF (from 2004 onwards) (Dommanget, 2002; 2010).

All data in each country were validated by experts to prevent false positive records. As *Calopteryx splendens* is easy to identify, false positive records are very unlikely.

Data were restricted to 1990-2008, because each of the participating countries had data available in these years. The total amount of dragonfly data in the five countries has increased considerably since 1990 (fig. 3.1). Not only has the amount of single records increased, but also of records of multiple species collected by a single observer at a single site on a single date.

Different geo-reference systems were used in each country for the observations. Hence, all observations were converted to the Universal Transverse Mercator (UTM) system. Because we used 1x1 km as the definition of a site in our analyses, all observations were referenced to 1x1 km UTM squares.

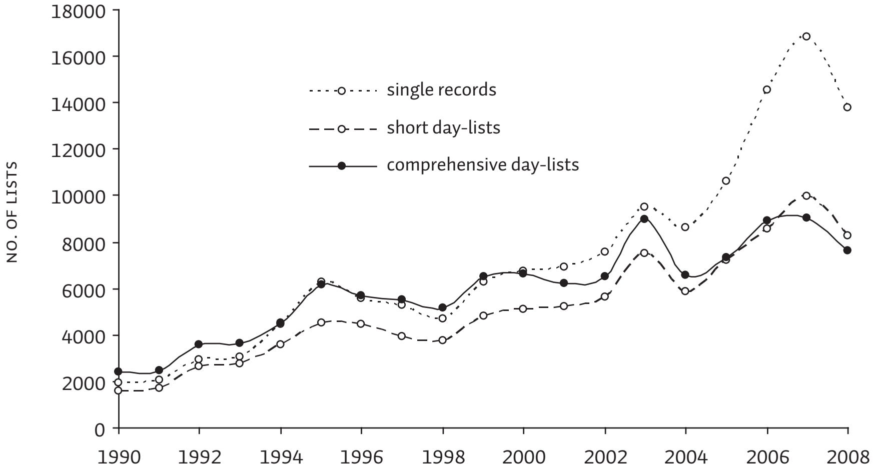

FIG. 3.1: Annual number of day-lists from five countries combined (Ireland, Great Britain, the Netherlands, Belgium and France). Lists were categorised as single records, short day-lists or comprehensive day-lists (see text for explanation). The dip in 2008 is due to a temporary dip in the number of data records in the Netherlands.

3.2.2 GENERATING NON-DETECTION DATA

Almost all data obtained were records of species presence. But occupancy models also require absence data, more precisely non-detection data, to estimate detection probabilities. Detection probability is estimated from the pattern in the detections and non-detections in replicated visits at sites. Valid replicated visits are only those visits made in a period of closure within the year; this is the period during which a site is considered to be either occupied or unoccupied and not abandoned or colonised (MacKenzie et al., 2006).

The non-detection records were generated from the information of sightings of other dragonfly species, following Van Strien et al. (2010, Chapter 2 of this thesis; 2011). Any observation of *C. splendens* was taken as 1 (detection), whereas we rated 0 (non-detection) if any other species but not *C. splendens* had been reported by an observer at a particular 1x1 km site and on a particular date within the closure period. Usually, *C. splendens* is observed between Julian dates 130-250 and we used as closure period Julian dates 150-220. We made an exception for Ireland, where we used Julian dates 160-260 because the species seems to have a later flight period there. Despite many dragonflies having advanced their phenology in recent decades (Dingemans & Kalkman, 2008), data exploration revealed no changes in flight period of our study species during 1990-2008, so the closure period was kept the same for all years.

3.2.3 STATISTICAL ANALYSIS

NATIONAL LEVEL

We applied the same dynamic occupancy model as Van Strien et al. (2010, Chapter 2 of this thesis; 2011) to estimate annual occupancy ψ, adjusted for detection probability p. Because all parameters in the model may differ between countries, the analyses were performed separately for each country and the national results were combined in a second step. The mathematical description of the model is given by Royle & Kéry (2007) and Royle & Dorazio (2008). Here, ψ is the proportion of suitable 1x1 km squares that is occupied. A square is defined as suitable if the species had been recorded there at least once in 1990-2008. The occupancy model consists of two hierarchically coupled submodels, one for occupancy and one for detection, the latter being conditional on the occupancy submodel. The occupancy submodel estimates annual probability of persistence φ_t and of colonisation γ_t and computes the annual occupancy probability per site recursively through:

$$\psi_{it} = \psi_{i,t-1}\,\varphi_{t-1} + (1-\psi_{i,t-1})\,\gamma_{t-1}$$

Thus, whether site *i* occupied in year *t*-1 is still occupied in year *t* is determined by the persistence probability, and whether site *i* unoccupied in year *t*-1 is occupied in year *t* depends on the colonisation probability. All occupancy probabilities per site together yield the estimated annual number of occupied 1x1 km sites per country. The same sites were included in the analysis for all years; estimates for sites not surveyed during some years were derived from sites that were surveyed in those years.

The detection submodel estimates the yearly detection *p*, but in addition *p* is made a function of covariates. We used the Julian date as a covariate for *p* because the detection of the species is expected to vary over the season due to changing population size during the course of the flight period. Detection is also reduced if observers do not report all their sightings. Hence, we include the incompleteness of recording as a covariate for detection. We distinguished: (1) single records of any species on one site and date without records of other species, (2) short day-lists, i.e. records of two or three species made by a single observer on one site and date, and (3) comprehensive day-lists, i.e., records of more than three species per observer, site and date. These lists may or may not include *C. splendens*. These category thresholds are sufficiently low to be not confounded by real differences in species number between sites. In most 1x1 km sites in the countries there are more than three species to be found and often many more. Effects of both covariates were included in the detection submodel via a logit link:

$$\mathrm{logit}(p_{ijt}) = \alpha_t + \beta_1 * \mathrm{date}_{ijt} + \beta_2 * \mathrm{date}_{itj}{}^2 + \delta_1 * (\text{short day-list})_{itj} + \delta_2 * (\text{comprehensive day-list})_{ijt},$$

where p_{ijt} is the probability to detect the species at site i during visit j in year t, α_t is the annual intercept, β_1 and β_2 are the linear and quadratic effects of the date of visit j and δ_1 and δ_2 are the effects of short day-lists and comprehensive day-lists, relative to single records.

We fitted the models in a Bayesian mode of inference using JAGS (Plummer, 2009) on the computer cluster LISA (https://www.surf.nl/en), with essentially the same WinBUGS code (Spiegelhalter et al., 2003) as given by Royle & Dorazio (2008; p. 309), but in addition we estimated the intercept α_t as a random year effect. We chose uninformative priors for all parameters, using uniform distributions with values between 0 and 1 for all parameters except δ_1 and δ_2 (values between -10 and 10), β_1, β_2 (values between -5 and 5) and α_t (values between 0 and 5 for the standard deviation of the normal distribution used as prior for the random year effect; see Kéry (2010) for examples of WinBUGS code for random effects).

For each analysis, we ran three Markov chains with 15,000 iterations to ensure convergence as judged from the Gelman-Rubin Rhat statistic. We discarded the first 10,000 iterations as burn-in and used the remaining iterations for inferences. Model fits were assessed using Bayesian *p*-values. This value is near 0.5 for a fitting model and values close to 0 or to 1 indicate inadequate fits (Kéry, 2010). Our *p*-values varied between 0.44 and 0.59, suggesting that model fits were adequate. The model produced annual estimates of occupancy, persistence and colonisation per country and their regression coefficients across years were estimated as derived parameters (Kéry, 2010).

SUPRANATIONAL LEVEL

The occupancy estimates per country were aggregated in the second step. Countries differ in the number of sites surveyed, so a naive aggregation has the risk of a biased supranational trend. Hence, we developed a procedure to weigh countries according to the sampling intensity in relation to the range of C *splendens* in each country. This procedure is an adaptation of procedures applied by Van Swaay et al. (2002) and Gregory et al. (2005). The range of *C. splendens* in a country is defined as the number of 10x10 km squares where the species has been observed at least once during 1990-2008. We assumed that these ranges are well known, which seems reasonable given the distribution of records (fig. 3.2A). Sampling intensity is defined as the number of 1x1 km squares surveyed at least once in this period within the range of the species. If sampling intensity would be even across countries, the number of surveyed 1x1 km squares is proportional to the range of the species. So, if the range in one country is twice as large as in another country, twice as many 1x1 km squares should have been surveyed to ensure even sampling. When the share of 1x1 km squares surveyed is higher than proportional, the country is considered oversampled. Weights are calculated as the quotient of relative range and relative sampling intensity, to compensate for oversampling and undersampling (table 3.1). Weights per country were similar for each year, because the same sites were in the analysis for all years. The weighted numbers of occupied sites were added across countries and converted into supranational annual occupancy. Similarly, standard errors of national occupancies were combined to achieve standard errors of the supranational annual occupancy.

TABLE 3.1: Ingredients to treat relative oversampling and undersampling of countries with respect to *Calopteryx splendens*.

Country	**Range** (10x10 km squares with *C. splendens*)	**Sampling intensity** (1x1 km squares surveyed within range of *C. splendens*)	**Weight** (% range / % sampling intensity)
Ireland	276 (7.8 %)	1,768 (4.2 %)	1.86
Great Britain	962 (27.4 %)	15,513 (36.6 %)	0.74
The Netherlands	317 (9.0 %)	15,798 (37.3 %)	0.24
Belgium	230 (6.6 %)	3,987 (9.4 %)	0.70
France	1,725 (49.1 %)	5,275 (12.4 %)	3.96

3.3 Results

In each nation, opportunistic records came from all over the country, although some areas were overrepresented, e.g. the southern half of England, and the Netherlands and Belgium as a whole (fig. 3.2A). Great Britain and the Netherlands had relatively large shares of single records in their data, at least for those sites where *C. splendens* occurs (table 3.2). The share of single records was even greater (46.8%) in Ireland. In contrast, databases in France and Belgium held more comprehensive and short lists than single records.

C. splendens is absent in Scotland and south-western France (fig. 3.2B); in the latter region the species is replaced by the related *C. xanthostoma*. Occupancy has significantly increased in Great Britain, the Netherlands and Belgium and remained stable in France (fig. 3.3; table 3.3). In Ireland, the standard errors of the annual occupancy estimates were considerable, except for 1996-2003 when more data were available. As a result, the trend in occupancy is poorly known for Ireland (table 3.3). In none of the countries persistence and colonisation has changed significantly over the years (table 3.3).

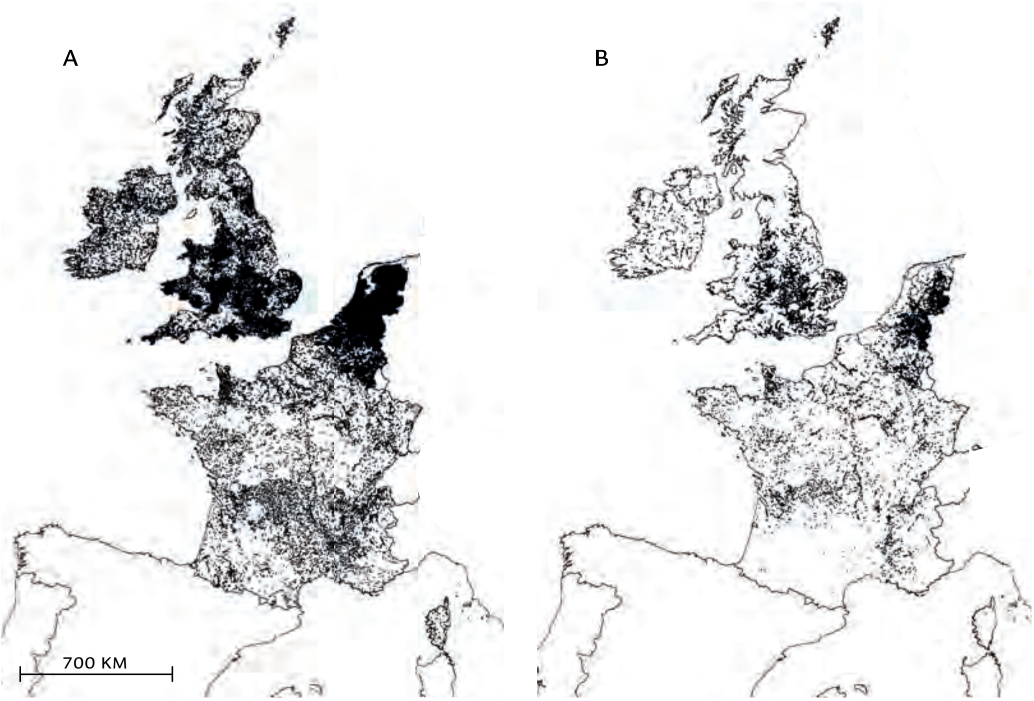

FIG. 3.2: Map of 1x1 km sites with A) opportunistic records of dragonflies in 1990-2008 and B) sites where *Calopteryx splendens* has been observed in the same period.

TABLE 3.2: Number of day-lists per country and day-list category in 1990-2008 in 1x1 km squares where *Calopteryx splendens* has been observed at least once.

Country	Single records data (%)	Short day-lists (%)	Comprehensive day-lists (%)
Ireland	372 (46.8)	223 (28.0)	200 (25.1)
Great Britain	9,543 (30.7)	7,926 (25.5)	13,636 (43.8)
The Netherlands	9,850 (34.9)	7,005 (24.8)	11,378 (40.3)
Belgium	1,391 (23.0)	1,404 (23.2)	3,261 (53.8)
France	1,294 (13.5)	1,642 (17.1)	6,664 (69.4)

TABLE 3.3: Trend in occupancy, colonisation and persistence (± se) of *Calopteryx splendens* per country in 1990-2008. No of sites refers to the 1x1 km squares where *C. splendens* has been observed at least once.

Country (no. of sites)	Trend in occupancy	Trend in colonisation	Trend in persistence
Ireland (409)	-0.002 ± 0.006	-0.001 ± 0.012	0.001 ± 0.011
Great Britain (4,954)	0.007 ± 0.001 [1]	0.004 ± 0.003	0.001 ± 0.001
The Netherlands (3,294)	0.007 ± 0.002 [1]	0.005 ± 0.006	0.003 ± 0.002
Belgium (1,200)	0.014 ± 0.003 [1]	0.003 ± 0.004	0.005 ± 0.003
France (2,666)	0.002 ± 0.002	0.000 ± 0.008	0.001 ± 0.001

[1] *significant* (*P* <0.05)

When the results of all five countries were combined, the species showed a significant increase in occupancy (weighted trend 0.004 with standard error 0.001; P < 0.05; fig. 3.4). Because the stable trajectory in France had more influence in the weighted trend, the unweighted trend is slightly steeper (0.006 with standard error 0.001) than the weighted trend, although the difference in trend is not significant. Weights for France were highest and for the Netherlands lowest, reflecting their respective undersampling and oversampling (table 3.1).

In almost all countries, detection probabilities varied significantly with Julian date. Detection peaks did not differ much between countries and were around Julian date 170, except for Ireland. As expected, in most countries detection in short day-lists and comprehensive day-lists was significantly higher than in single records data (table 3.4). The opposite was true in Ireland, with exceptionally high detections in single records and short day-lists (table 3.4). There was no indication of a trend in detection during 1990-2008 in any of the countries.

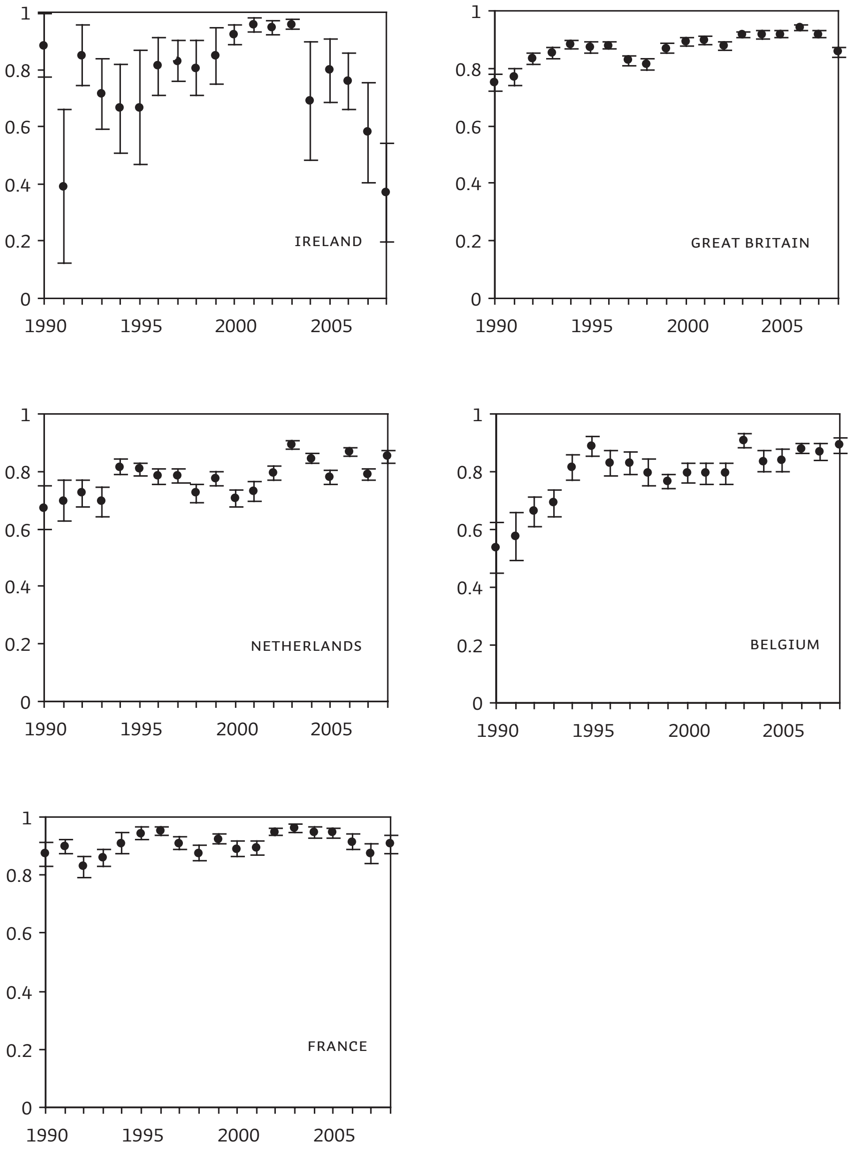

FIG. 3.3. Annual occupancy probability (± se) of *Calopteryx splendens* in Ireland, Great Britain, the Netherlands, Belgium and France, analysed with a dynamic occupancy model.

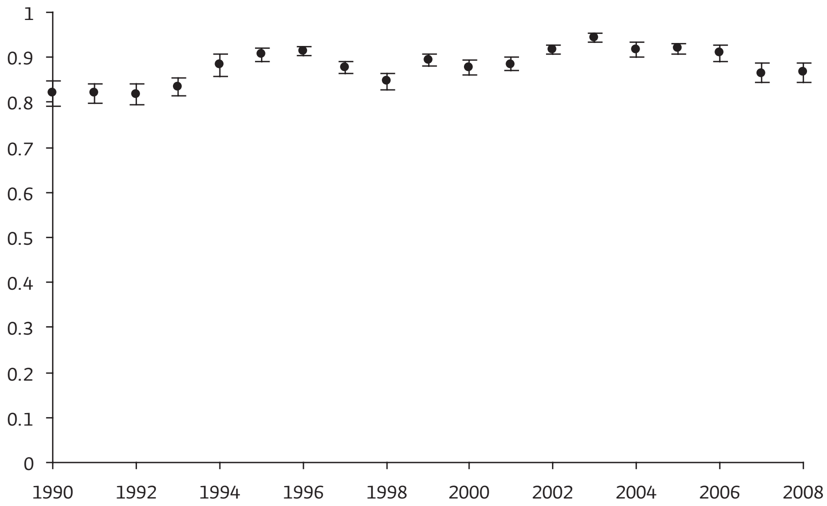

FIG. 3.4. Annual occupancy probability (± se) of *Calopteryx splendens* in five countries combined after countries were given different weights to adjust for different sampling intensity.

TABLE 3.4: Detection probability of *Calopteryx splendens* (± se) per country and day-list category.

Country (no. of sites)	Single records data	Short day-lists	Comprehensive day-lists
Ireland	0.83 ± 0.06	0.75 ± 0.09	0.65 ± 0.10 [1]
Great Britain	0.44 ± 0.03	0.55 ± 0.03 [1]	0.62 ± 0.02 [1]
The Netherlands	0.38 ± 0.03	0.40 ± 0.03	0.50 ± 0.03 [1]
Belgium	0.45 ± 0.04	0.56 ± 0.04 [1]	0.61 ± 0.04 [1]
France	0.19 ± 0.02	0.44 ± 0.03 [1]	0.68 ± 0.03 [1]

[1] *significant difference with detection in single records data (P <0.05)*

Discussion

We have described a new approach to compose supranational trends using opportunistic data. The approach takes into account the two main imperfections in opportunistic data. The non-standardised observation effort is dealt with by occupancy modelling and the unequal geographical distribution of sites by a weighting procedure.

In monitoring schemes variation in observation effort is minimised by adopting a standard field methodology, e.g. reporting all species detected at a site and adhering to a particular field method and timing of visits to a site. In contrast, variation in observation effort is substantial in opportunistic data. Many attempts have been made to extract trend information from opportunistic data, e.g. by comparing only sites that had been equally surveyed (see Hassall & Thompson, 2010) or by a statistical correction method with a proxy for observation effort (Szabo et al., 2010). Occupancy models provide a more general method to control observation effort by assuming that variation in observation effort will result in a different detection probability of species, whatever its source may be. So, the variation in number and timing of field visits, variation in field efforts during a visit and variation in observer skills and in their readiness to report a species after detection are all assumed to be reflected in variation in detection. We adjusted for these sources of variation by taking into account annual detection probability in an occupancy model and we also included day-list category and Julian date as a covariate for detection.

Our trial of the new approach showed an increase of *C. splendens* which agrees well with expert knowledge of the species. As a direct cross-check for the trend in the Netherlands, we used independent monitoring data available for the Netherlands. We selected a subset of squares (n=105) from which both opportunistic data and monitoring data were available and found a similar trend in occupancy in 1999-2010 (trend ± se -0.005 ± 0.006 and -0.004 ± 0.006 respectively). This confirms our earlier findings that opportunistic data may produce reliable trends if analysed by an occupancy model (Van Strien et al., 2010, Chapter 2 of this thesis). Note that the decline found in the data used for comparison contradicts the overall trend found for the Netherlands. This is because the subset of squares was not representative for the whole country.

Sites from which we had opportunistic records were not selected by using a formal sampling design, but instead by the free choice of observers. This might lead to an unequal geographical distribution of sites and to biased results within countries (Yoccoz et al., 2001; Hassall, 2012). We have ignored this potential bias, because we identified no clear skewed geographical distribution within countries (fig. 3.2A). An exception is Great Britain, where England has a higher density of surveyed sites than Scotland. However, this is not relevant in our case because *C. splendens* does not occur in Scotland (fig. 3.2B). Where apparent geographical bias at the national level exists, this could be treated by a post-stratification of sites, e.g. by using regions or habitat types as strata, followed by weighting of strata (Van Swaay et al., 2002; Gregory et al., 2005), much as we did to calculate trends at the supranational level.

Like other dragonflies living in running water, our study species suffered considerably during 1950-1980 from water pollution, deterioration of aquatic vegetation and physical alterations to water bodies. Improvements in these conditions have led to local recovery (Ward & Mill 2004; De Knijf et al. 2006) and here we show that the species has increased on a large spatial scale as well. The lack of any change in France hides a disparity: in several catchments the quality of running waters has improved during the two last decades (Service de l'observation et des statistiques 2010), but in some other catchments water quality has not much or not at all improved (Service de l'observation et des statistiques, 2009). In addition, the species has expanded its range northwards in the UK, probably as the result of a combination of the effects of climate change (Hickling et al., 2005) and of improved water quality of rivers and streams in the northern part of the UK, which acted as a barrier to range expansion due to historic water pollution (Ward & Mill, 2004).

3.4.1 MODEL ASSUMPTIONS

Some additional assumptions which may invalidate our results need to be addressed. First, in the occupancy modelling, we have assumed a period in the season during which no colonisation or extinction of the study species in sites happened. But dragonflies may disperse during the entire season. A lack of closure may lead to low estimates of detection probability and to positive bias in the occupancy estimate (Rota et al., 2009). This is a problem in case occupancy is taken to mean 'permanent presence'. But if random movement occurs to and from sites that are not permanently occupied, as we believe to be the case with mobile organisms like dragonflies, the occupancy parameter should be interpreted as the proportion of sites "used" by the target species during the period over which closure is assumed (MacKenzie et al., 2006).

Secondly, we assumed that sightings of other species were informative about a non-detection of our study species. Some observers might have surveyed running waters in the 1x1 km square, which are possibly inhabited by *C. splendens*, so any detection of another species is indeed informative about a non-detection of *C. splendens*. Others, however, might have surveyed only fens or ditches or other habitats unsuitable for *C. splendens*. In the latter habitat types, the detection of other species is not informative about the detection probability of *C. splendens*. Nevertheless, we expect that this sampling behaviour does not lead to biased occupancy estimates. Kendall & White (2009) demonstrated that sampling of spatial subunits without replacement in a site leads to bias in occupancy estimates, but not sampling with replacement. We consider the collection of opportunistic data by many observers comparable to sampling with replacement, leading to a decent quality of our estimates.

Thirdly, our procedure to generate non-detections for our study species from sighting of other species will not work in practice if there are only a few species in a site or only rare species. Then day-lists will often have length zero, but such informative non-detections rarely enter the databases. In such situations, many records are presences of the study species leading to unlikely high detection estimates. This happens in Ireland, which is naturally poor in dragonfly species and where *C. splendens* is often found on its own (Kalkman et al., 2010; Nelson et al., 2011). Single records data form the largest group of records here (table 3.2) and detection probability is exceptionally high (table 3.4). To a lesser extent this is also true for short day-lists in Ireland. In such cases the mechanism to adjust for variation in observation effort via taking into account detection fails. Some form of standardised monitoring is probably the only option to achieve an unbiased trend estimate for this species in Ireland. Incidentally, any bias in the Irish data will hardly affect the supranational trend estimate, because Ireland contains only a limited share of this species anyway (table 3.1).

3.4.2 PERSPECTIVES

Our trial demonstrated that supranational annual indices with confidence intervals and a supranational trend can be derived from opportunistic data, while adjusting for observation effort bias and geographical bias. The annual indices with confidence intervals allow the formal testing of trends. These characteristics make our approach superior to previous large-scale assessments of changes in species, such as for dragonflies by Clausnitzer et al. (2009).

Occupancy models, however, can only be applied if the data contain a sufficient number of replicated visits at sites within the season (MacKenzie et al., 2006). Outside Europe, the number of dragonfly records seems quite limited (see e.g. Hassall, 2012), so the number of records from replicated visits might be too low for large-scale application of these models. But we suspect that over half of the EU member states currently have useful databases available with considerable amounts of opportunistic dragonfly records. Several other EU countries would be able to join with relatively little extra effort in data collection, for instance by focussing on the collection of records at a limited number of selected sites. This situation might be similar for some other insect groups in the EU, e.g. for grasshoppers, and is likely to be even better for butterflies. We envisage the growing databases of opportunistic data becoming an important source of information to track trends in multiple species groups. When owners of opportunistic data are prepared to cooperate in a Pan-European network, it should be feasible to achieve Pan-European trends in distribution for a number of species groups in the future. The usefulness of databases with opportunistic data can be further enhanced by encouraging the collection of day-lists rather than of single records (Van Strien et al., 2010, Chapter 2 of this thesis). However, trend information derived from opportunistic data will only be reliable if sufficient attention is given to using appropriate methods of analysis.

Our approach could make it possible to compile large-scale multispecies indicators, based on averaging annual indices per species. Such indicators resemble existing indicators for breeding birds and grassland butterflies (Gregory et al., 2005; European Environmental Agency, 2007; van Swaay et al., 2008). But for dragonflies a supranational indicator would be based on changes in distribution rather than in population abundance as in the indicators for birds and butterflies. Finally, occupancy models enable to produce annual species distribution maps from opportunistic data (Kéry, 2011; Van Strien et al., 2011), which may facilitate large-scale studies on climate change, e.g. to compare range shifts of various species groups driven by climatic change (Devictor et al., 2012).

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References

Butchart S.H.M., Walpole M., Collen B., van Strien A., Scharleman J.P.W. … & Watson R. (2010). Global biodiversity: indicators of recent declines. *Science* 328: 1164-1168.

Clausnitzer V., Kalkman V.J., Ram M., Collen B., Baillie J.E.M., … & Wilson K. (2009). Odonata enter the biodiversity crisis debate: The first global assessment of an insect group. *Biological Conservation* 142: 1864–1869.

De Heer M., Kapos V. & ten Brink B.J.E. (2005). Biodiversity trends in Europe: Development and testing of a species trend indicator for evaluating progress towards the 2010 target. *Philosophical Transactions of the Royal Society B* 360: 297–308.

De Knijf G., Anselin A., Goffart P. & Tailly M. (editors) (2006). *De libellen (Odonata) van België: verspreiding - evolutie - habitats*. Libellenwerkgroep Gomphus & Instituut voor Natuur- en Bosonderzoek, Brussel.

Dennis R.L.H., Sparks T.H., Hardy B.P. (1999). Bias in butterfly distribution maps: the effect of sampling effort. *Journal of Insect Conservation* 3: 33-42.

Dennis R.L.H. & Thomas C.D. (2000). Bias in butterfly distribution maps: the influence of hot spots and recorders home range. *Journal of Insect Conservation* 4: 73-77.

Devictor V., Whittaker R.J. & Beltrame C. (2010). Beyond scarcity: citizen science programmes as useful tools for conservation biogeography. *Diversity and Distributions* 16: 354-362.

Devictor V., van Swaay C., Brereton T., Brotons L., Chamberlain D., … & Jiguet F. (2012). Differences in the climatic debts of birds and butterflies at a continental scale. *Nature Climate Change* 1347: 1-4.

Dingemans N. & Kalkman V.J. (2008). Changing temperature regimes have advanced the phenology of Odonata in the Netherlands. *Ecological Entomology* 33: 394-402.

Dommanget J.L. (2002). *Protocole de l'Inventaire cartographique des Odonates de France (Programme INVOD)*. Muséum National d'Histoire Naturelle, Société française d'odonatologie, Paris.

Dommanget J.L. (2010). *Complément à l'inventaire des libellules de France (Programme national de collecte des données odonatologique (Programme CILIF)*, Actualisation janvier 2010. Société française d'odonatologie. http://www.libellules.org/protocole/cilif.html/. Accessed 15 June 2012.

European Environment Agency (2007). *Halting the loss of biodiversity by 2010: proposal for a first set of indicators to monitor progress in Europe*. EEA, Copenhagen.

European Union (2011). Communication from the Commission to the European Parliament, the Council, the Economic and Social Committee and the Committee of the Regions. *Our life insurance, our natural capital: an EU biodiversity strategy to 2020*. COM(2011) 244 final, Brussels.

Gregory R.D., van Strien A., Vorisek P., Gmelig Meyling A.W., Noble D.G., ...& Gibbons, D.W. (2005). Developing indicators for European birds. *Philosophical Transactions of the Royal Society B* 360: 269–288.

Hassall C. (2012). Predicting the distributions of under-recorded Odonata using species distribution models. *Insect Conservation and Diversity* 5: 192-201.

Hassall C. & Thompson D.J. (2010). Accounting for recorder effort in the detection of range shifts from historical data. *Methods in Ecology and Evolution* 1: 343-350.

Hickling R., Roy D.B., Hill J.K. & Thomas C.D. (2005). A northward shift of range margins in British Odonata. *Global Change Biology* 11: 502–506.

Kalkman V.J., Boudot J.P., Bernard R., Conze K.J., De Knijf G., ... & Sahlén G. (2010). *European Red List of Dragonflies*. Publications Office of the European Union, Luxembourg.

Kendall W.L. & White G.C. (2009). A cautionary note on substituting spatial subunits for repeated temporal sampling in studies of site occupancy. *Journal of Applied Ecology* 46: 1182-1188.

Kéry M. (2010). *Introduction to WinBUGS for ecologists – a Bayesian approach to regression, ANOVA, mixed models and related analyses.* Academic Press, Burlington, Massachusetts, USA.

Kéry M. (2011). Towards the modelling of true species distributions. *Journal of Biogeography* 38: 617–618.

Kéry M., Royle J.A., Schmid H., Schaub M., Volet B., ... & Zbinden N. (2010). Site-occupancy distribution modeling to correct population-trend estimates derived from opportunistic observations. *Conservation Biology* 24: 1388-1397.

MacKenzie D.I., Nichols J.D., Royle J.A., Pollock K.H., Hines J.E. & Bailey L.L. (2006). *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*. Elsevier, San Diego.

Nelson B., Ronayne C. & Thompson R. (2011). *Ireland Red List No. 6. Damselflies & Dragonflies (Odonata)*. National Parks and Wildlife Service, Department of the Environment, Heritage and Local Government, Dublin, Ireland.

Plummer M. (2009). *JAGS Version 1.0.3 manual*. http://sourceforge.net/projects/mcmc-jags/. Accessed 15 June 2012.

Robertson M.P., Cumming G.S. & Erasmus B.F.N. (2010). Getting the most out of atlas data. *Diversity and Distributions* 16: 363-375.

Rota C.T., Fletcher R.J., Dorazio R.M. & Betts M.G. (2009). Occupancy estimation and the closure assumption. *Journal of Applied Ecology* 46: 1173–1181.

Royle J.A. & Dorazio R.M. (2008). *Hierarchical modeling and inference in ecology.* Academic Press, Amsterdam.

Royle J.A. & Kéry M. (2007). A Bayesian state-space formulation of dynamic occupancy models. *Ecology* 88: 1813–1823.

Schmeller D.S., Henry P.Y., Julliard R., Gruber B., Clobert J., ... & Henle K. (2009). Advantages of volunteer-based biodiversity monitoring in Europe. *Conservation Biology* 23: 307–316.

Service de l'observation et des statistiques (2009). *Évolution de la qualité des cours d'eau: volet macropolluants*. Études et documents, SOeS et Commissariat général au développement durable, Orléans.

Service de l'observation et des statistiques (2010). *L'environnement en France – edition 2010*. Références, SOeS et Commissariat général au développement durable, Orléans.

Spiegelhalter D., Thomas A. & Best N.G. (2003). *WinBUGS User Manual, Version 1.4*. MCR Biostatistics Unit, Cambridge.

Szabo J.K., Vesk P.A., Baxter P.W.J. & Possingham H.P. (2010). Regional avian species declines estimated from volunteer-collected long-term data using List Length analysis. *Ecological Applications* 20: 2157-2169.

Van Strien A.J., Termaat T., Groenendijk D., Mensing V. & Kéry M. (2010). Site-occupancy models offer new opportunities for dragonfly monitoring based on daily species lists. *Basic and Applied Ecology* 11: 495-503.

Van Strien A.J., van Swaay C.A.M. & Kéry M. (2011). Metapopulation dynamics in the butterfly *Hipparchia semele* changed decades before occupancy declined in The Netherlands. *Ecological Applications* 21: 2510–2520.

Van Swaay C.A.M., Plate C.L. & van Strien A. (2002). Monitoring butterflies in the Netherlands: how to get unbiased indices. *Proceedings of the section Experimental and Applied Entomology of the Netherlands Entomological Society (N.E.V.)* 13: 21-27.

Van Swaay C.A.M., Nowicki P., Settele J. & van Strien A.J. (2008). Butterfly monitoring in Europe: methods, applications. *Biodiversity and Conservation* 17: 3455-3469.

Ward L., Mill, P.J. (2004). Distribution of the Banded Demoiselle *Calopteryx splendens* (Harris) in northern England: an example of range expansion. *Journal of the British Dragonfly Society* 20: 61-69.

Yoccoz N.G., Nichols J.D. & Boulinier T. (2001). Monitoring of biodiversity in space and time. *TREE* 16: 446–453.

Gomphus vulgatissimus is one of the species of running waters that made a remarkable recovery in the Netherlands.

CHAPTER 4

Strong recovery of dragonflies in recent decades in the Netherlands

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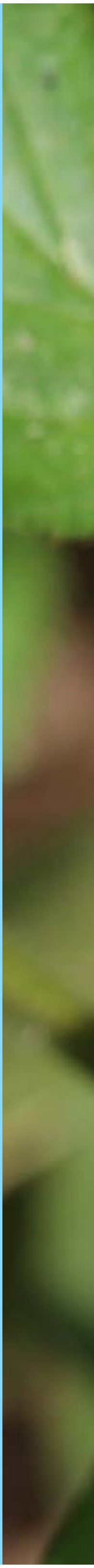

Abstract

Many dragonfly species in the Netherlands declined in the 20th century because of acidification, eutrophication, and desiccation of lotic and lentic habitats and canalisation of streams and rivers. These pressures peaked in the 1970s, when 26 of 65 native species had an unfavourable conservation status on the 1997 Dutch Red List. Since the 1980s, environmental regulations have led to improved water quality, and many habitat restoration projects have been carried out. We used standardised monitoring data (1999–2013) and unstandardised observations (1991–2013) to investigate how dragonflies have changed in the last 20 y on a national scale. We compared trends of dragonfly species from different habitat types and with southern vs northern distribution in Europe. Dragonflies recovered strongly in the Netherlands in a period of ~20 y, probably because of recent habitat improvements. Lotic species have benefitted more than lentic species, and southern species have more positive trends than northern species, suggesting that climate change has contributed to the recovery. Dragonflies were resilient and able to quickly recover when their habitats were restored. Recovery has led to a better conservation status for many species. Unstandardised data delivered results consistent with those from monitoring data and had greater statistical power to detect trends because many more unstandardised data than standardised data were available. Thus, when the goal is to provide a general overview of changes in dragonflies, unstandardised data can outperform standardised abundance data. However, abundance data may deliver complementary information for individual species. Our results support the suitability of dragonflies as indicators of freshwater habitat condition, but they recover more strongly in the Netherlands than many other insects possibly because of their higher dispersal abilities or different habitat requirements.

KEYWORDS: distribution trends, abundance trends, dragonflies, habitat recovery, climate change, conservation

4.1 Introduction

Dragonflies (Insecta: Odonata) are under environmental pressure on a global scale. Clausnitzer et al. (2009) estimated that 10% of all dragonfly species are threatened with extinction, and another 4% are near threatened, based on the criteria used by the International Union for Conservation of Nature Red List (IUCN, 2012). This unfavourable conservation status is explained by various human-induced pressures on freshwater habitats. In western Europe, the most prominent pressures are acidification, eutrophication through N loading, desiccation of both lotic and lentic habitats, and habitat destruction through canalisation of streams and rivers (Kalkman et al., 2010). These pressures have led to alterations in water quality, aquatic vegetation structure, and in the bottom substrate of the water body, thereby negatively affecting the larval stage of many species. In addition, changes in the vegetation along water bodies may affect the adult stage of species (Butler & DeMaynadier, 2008; Corbet 1999; Remsburg & Turner, 2009). As a result, many species have declined in the Netherlands, in particular those in oligotrophic or mesotrophic standing waters. On the Dutch Red List of 1997, which compares the situation in 1950 with the situation in 1996, 26 of all 65 native dragonfly species were classified as threatened (Termaat & Kalkman, 2012).

The environmental pressures increased in the Netherlands during the 20th century and reached their climax in the 1970s (Environmental Data Compendium, 2013a; b). However, since the 1980s, considerable environmental improvements have been achieved. The eutrophying load of NOx and NH3 together has decreased from 2761 mol N/ha in 1981 to 1827 mol N/ha in 2012 (Environmental Data Compendium, 2013a). Acidifying deposition of NOx, NH3, SOx, and other acids has decreased from 5617 mol potential acid/ha to 2514 mol/ha in the same period (Environmental Data Compendium 2013b). The current N load is still well above the critical load threshold for most freshwater habitats (Bobbink & Hettelingh, 2011), but nutrient levels in Dutch rivers and lakes have dropped significantly (Environmental Data Compendium, 2012a; b) and acidification of standing waters has become less severe (Van Dam and Mertens 2011). In addition, numerous restoration projects in streams, moorland pools, bogs, and fens have been carried out during the last 3 decades (Didderen et al., 2009; Natuurmonumenten et al., 2011; Van Duinen et al., 2003 and references therein).

Dragonflies react sensitively to changes in their environment and are well established model organisms for assessing freshwater habitat integrity (Cordoba-Aguilar, 2008; Simaika & Samways, 2009). However, many studies have shown that dragonflies respond negatively to the deterioration of their habitat (e.g., Ferreras-Romero et al., 2009; Martins, 2009; Muller et al., 2003; Sahlén, 1999; Samways & Taylor, 2004; Watson et al., 1982), but only few have addressed their response to habitat improvements (Chovanec & Raab, 1997; D'Amico et al., 2004; Samways

& Sharratt, 2010). These studies were mainly on a local scale or limited to a single habitat type and do not inform about the recovery of the dragonfly fauna on a larger scale. A positive response to environmental improvements on a large scale is not at all self-evident because constraints, such as habitat fragmentation, regional extinction events, and intraguild competition shifts, might hamper dragonflies' ability to reach and colonise restored habitats (Gårdmark et al., 2003). These constraints will vary between species and habitat types, according to their requirements for the physical and chemical conditions of water bodies and their ability to reach restored habitat types.

We investigated whether the reduced environmental pressures and habitat restoration efforts have resulted in the recovery of dragonfly populations on a national scale. We assessed the trends in abundance and distribution over a period of 15 and 23 y, respectively. To assess whether dragonfly species from different habitats have responded differently, we compared groups of species for 3 major habitat types: running waters, moorland pools (including bogs), and fens. These habitat types have undergone different pressures and are not restored to the same extent. Recent climate warming also may affect the abundance and distribution of European dragonflies (Flenner & Sahlén, 2008; Hassall & Thompson, 2008; Hickling et al., 2005; Ott, 2001). Thermophilic species with a southern distribution are expected to have benefitted more from climate warming than less thermophilic species with a northern distribution because they are better adapted to warmer conditions (Rosset & Oertli, 2011). We compared the trends of species with a southern or northern distribution in Europe to examine the extent to which climate change may have contributed to recovery of dragonflies.

4.2 Methods

4.2.1 SPECIES SELECTION AND CLASSIFICATION

We initially included all 60 resident dragonfly species in the Netherlands between 1991 and 2013 (Termaat & Kalkman, 2012). However, we excluded 6 species because of lack of data, leaving 54 species for the analysis. Nomenclature follows Dijkstra (2006), with the exception of *Lestes viridis*, which is now commonly accepted as *Chalcolestes viridis* (Gyulavári et al., 2011).

We classified species by conservation status, habitat preference, and European range (table 4.1). Conservation status was based on the 1997 Dutch Red List, which follows guidelines of the Dutch administration (Termaat & Kalkman, 2012). All species listed as vulnerable, endangered, critically endangered, or regionally extinct were taken together as 'threatened' and species listed as near threatened or least concern as 'nonthreatened'.

Most dragonfly species occur predominantly in a single or a limited number of habitat types. We derived habitat preference from the Dutch dragonfly atlas (Nederlandse Vereniging voor Libellenstudie, 2002), which gives the optimal habitat for each species, i.e., the habitat in which it occurs most in the Netherlands. We distinguished 3 species groups based on habitat: 1) species preferring brooks, streams, and rivers (hereafter 'running waters'); 2) species preferring oligo- to mesotrophic and acidic standing waters mainly fed by rain water, such as moorland pools, shallow soft-water lakes and bogs (hereafter 'moorland pools'); 3) species preferring meso- to eutrophic and alkaline standing waters mainly fed by groundwater, such as fens and lowland peat mires (hereafter 'fens'). Seven species (*Aeshna grandis, Cordulia aenea, Lestes sponsa, Libellula quadrimaculata, Orthetrum cancellatum, Pyrrhosoma nymphula*, and *Sympetrum vulgatum*) occur optimally in both moorland pools and fens. The moorland pools are separated geographically from the fens in the Netherlands, so for abundance trends (DDBS data, see below) and distribution trends (NDFF data, see below), we assessed trends in moorland pools with data from the elevated sandy regions in the Netherlands and trends in fens using data from lowland peat areas.

We based European distribution classification on Sternberg (1998), who characterised species as having a southern distribution (hereafter 'southern' species) or a northern or northeastern distribution (hereafter 'northern' species). The 1st group has its main distribution in the Mediterranean or Africa and probably had glacial refugia there. The 2nd group has a more northern distribution and had glacial refugia in Siberia or in Europe north of the Mediterranean (Schmitt & Varga, 2012). We excluded 9 species with an intermediate distribution pattern from the comparison of southern and northern species.

4.2.2 DATA

DUTCH DRAGONFLY MONITORING SCHEME (DDMS)

This scheme was used to assess trends in abundance from 1999 (the start of the scheme) to 2013. For 17 species, trends could be assessed only over a shorter period (appendix 4.1). The scheme consists of 200–330 fixed, 250-m-long transects along a water body (fig. 4.1A) sampled with a standardised field method (Van Swaay et al., 2011). The number of monitoring transects has increased over the years. Observers recorded all adult dragonflies within 5–7 m, once every 2 wk between 1 May and 30 September. Rare species were counted along additional transects 3 times during their main flight period. All surveys were conducted when weather conditions were suitable for dragonfly activity.

TABLE 4.1: Species classification according to threat status, habitat preference, and European distribution range. Included are all dragonfly species that reproduced in the Netherlands in 1991–2013, except 6 species with too sparse data.

Species	Threatened	Running waters	Moorland pools	Fens	Southern	Northern
Aeshna affinis					x	
Aeshna cyanea						
Aeshna grandis			x	x		x
Aeshna isoceles	x			x	x	
Aeshna juncea			x			x
Aeshna mixta					x	
Aeshna subarctica	x		x			x
Aeshna viridis	x			x		x
Anax imperator					x	
Anax parthenope					x	
Brachytron pratense				x		
Calopteryx splendens		x			x	
Calopteryx virgo	x	x				x
Ceriagrion tenellum	x		x		x	
Chalcolestes viridis				x	x	
Coenagrion hastulatum	x		x			x
Coenagrion lunulatum			x			x
Coenagrion puella			x		x	
Coenagrion pulchellum				x		
Cordulegaster boltonii		x				
Cordulia aenea			x	x		x
Crocothemis erythraea					x	
Enallagma cyathigerum			x			x
Erythromma lindenii					x	
Erythromma najas				x		x
Erythromma viridulum				x	x	
Gomphus flavipes	x	x				
Gomphus pulchellus					x	
Gomphus vulgatissimus	x	x				
Ischnura elegans				x		x
Ischnura pumilio					x	

Species	**Threatened**	**Running waters**	**Moorland pools**	**Fens**	**Southern**	**Northern**
Lestes barbarus			x		x	
Lestes dryas			x			x
Lestes sponsa			x	x		x
Lestes virens	x		x			
Leucorrhinia albifrons	x		x			x
Leucorrhinia dubia	x		x			x
Leucorrhinia pectoralis	x			x		x
Leucorrhinia rubicunda			x			x
Libellula depressa					x	
Libellula fulva	x			x		
Libellula quadrimaculata			x	x		x
Ophiogomphus cecilia	x	x				x
Orthetrum brunneum					x	
Orthetrum cancellatum			x	x	x	
Orthetrum coerulescens	x	x			x	
Platycnemis pennipes		x				
Pyrrhosoma nymphula			x	x		x
Somatochlora arctica	x		x			x
Somatochlora flavomaculata	x		x			x
Somatochlora metallica						x
Sympecma fusca	x		x		x	
Sympecma paedisca	x			x		x
Sympetrum danae			x			x
Sympetrum flaveolum			x			x
Sympetrum fonscolombii					x	
Sympetrum pedemontanum	x	x				x
Sympetrum sanguineum				x	x	
Sympetrum striolatum					x	
Sympetrum vulgatum			x	x	x	

NATIONAL DATABASE FLORA AND FAUNA (NDFF, WWW.NDFF.NL)
Dragonfly records from this database were used to assess trends in distribution (occupancy) in 1991–2013. The NDFF comprises opportunistic data, i.e., observations collected without a standardised field protocol of many different species groups in the Netherlands. The database contains >1.5 million presence records of adult dragonflies for the period 1991–2013 (on average, ~400 records/km2). These data were quantified at a 1- × 1-km resolution (fig. 4.1B) and used to estimate annual occupancy, i.e., the annual proportion of 1- × 1-km grid squares that were occupied.

4.2.3 STATISTICAL ANALYSIS

Abundance and distribution are 2 aspects of the occurrence of species (Shoo et al., 2005; Verberk et al., 2010), and both are acknowledged as relevant variables to assess the threat level of species (IUCN, 2012). Therefore, we assessed trends in abundance and in distribution.

We derived trends in abundance from the standardised monitoring data. We summed counts of separate visits in the DDMS to obtain yearly totals/transect after interpolating missing weekly counts linearly. We produced the abundance indices for each species with TRIM (Pannekoek & Van Strien, 2001), which is a widely used freeware program with an efficient implementation of Poisson regression to analyse time-series of counts (log-linear models). TRIM is equivalent to a conventional Poisson regression model with site and year effects. It estimates ('imputes') missing yearly counts for particular transects from the observations at transects with counts. In a 2nd step, we summarised the overall change over time by fitting a linear regression line via the year effects, with full error propagation (fig. 4.2A).

We derived trends in distribution from the unstandardised NDFF data. However, unstandardised data cannot be analysed in as straight-forward a manner as monitoring data because use of unstandardised data may easily lead to artificial trends or mask existing trends (Van Swaay 1990). However, Van Strien et al. (2013a) showed that data collected without a standardised field protocol yield unbiased trend estimates for dragonflies if analysed with occupancy models. Occupancy models separate occupancy (the presence of a species at a site) from detection (the observation of the species at that site) when analysing field survey data (MacKenzie et al., 2006). The models require detection/nondetection data that are arranged in 'detection histories' per site per year, such as '01' for a site where the species under focus is detected during the 2nd visit, but not during the 1st visit. Occupancy and detection can be inferred from the frequency of the detection histories of the sites. By taking into account imperfect detection, occupancy models estimate the annual 'true' proportion of occupied sites and can produce a trend in occupancy that is corrected for variation in observation effort. Details of the occupancy model applied were given by Van Strien et al. (2013a).

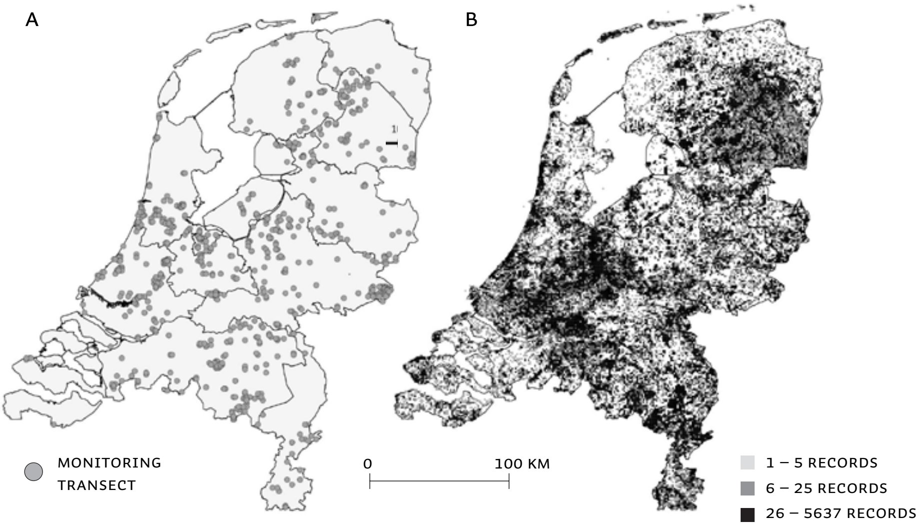

FIG. 4.1: Spatial variation in dragonfly recording effort in the Netherlands. **A:** Locations of monitoring transects where abundance data were collected in 1999–2013 based on a standardised field protocol (1307 transects, data from 200–230 transects annually). **B:** Sites where distribution data were collected in 1991–2013 without standardised field protocol (1- × 1-km resolution).

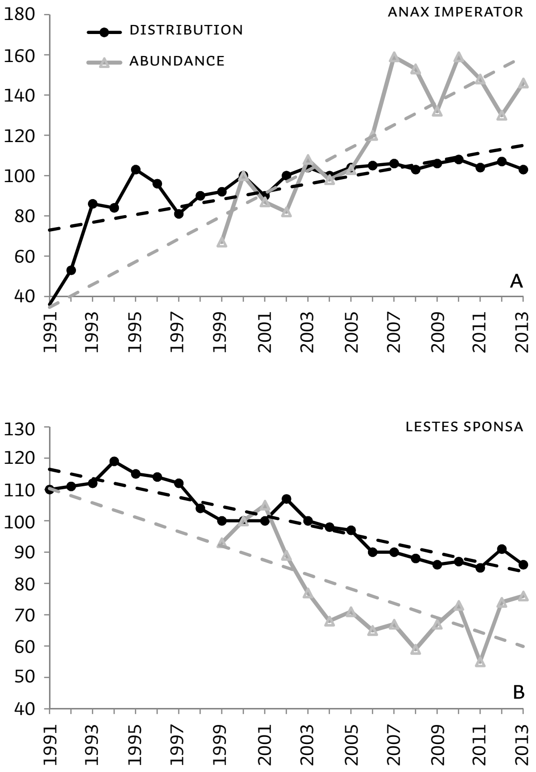

FIG. 4.2: Abundance index (1999–2013) and distribution index (1991–2013) of (A) *Anax imperator* and (B) *Lestes sponsa*. Linear regression lines (dashed lines) are fitted through the year effects to summarise overall change.

A complication is that the NDFF contains almost no nondetection records. We deduced nondetection records from the sightings of all other dragonfly species in the NDFF data, following the procedure described by Van Strien et al. (2013a). Any observation of the species under consideration within a period of closure was taken as a 1 (detection), whereas we rated 0 (nondetection) if any other species but not the species under consideration had been reported by an observer at a particular 1- × 1-km site on a particular date within the closure period. A closure period is the part of the activity period during a year in which we assumed that sites had not undergone colonisation or extinction. This procedure was repeated for all species to obtain detection histories for each species. Similar to the procedure for the abundance data, we estimated the linear regression line in a 2nd step. We first assessed the often nonlinear trajectory of each species over time by estimating annual occupancy probabilities. Thereafter, we summarised the overall change in annual occupancy by fitting a linear regression line through the annual occupancy estimates, again with full error propagation (fig. 4.2B).

To determine the explanatory power of the traits (habitat, northern or southern distribution, Red List category) related to trend, we fitted multiple-regression models using the *dredge* function in the R package *MuMIn* (Bartoń, 2014). Our continuously distributed trend estimates (regression coefficients; appendix 4.1, 4.2) did not meet the assumptions of a parametric test, so we used linear trend categories as ordinal response variables (strong increase: >5%/y, moderate increase: <5%/y, stable: no significant change, moderate decline: <5%/y, strong decline: >5%/y). Trends estimates of species with no significant change and standard errors too large to detect a 5% trend if it had occurred were classified as uncertain and omitted.

We also used χ^2 tests as a more conservative approach than dredge analysis to assess whether the number of increasing and decreasing species differed within species groups (habitat groups and southern and northern species) for abundance and distribution trends. We also conducted Monte Carlo simulations to test whether the frequency of increasing, stable, and declining species differed among the species groups (appendix 4.3).

4.3 Results

4.3.1 MULTIPLE-REGRESSION ANALYSIS

The dredge analyses of traits related to distribution and abundance trend categories identified habitat and range as the best explanatory individual terms, but only Red List category was statistically significant ($p < 0.05$). For both distribution and abundance, the omnibus test for the model with habitat and range as factors was significant ($p < 0.05$) indicating that these factors do have predictive power.

4.3.2 DISTRIBUTION TRENDS

Significantly more species have increased in distribution than have declined (36 vs 10 species; $\chi 2$ test, $p < 0.01$). Eight other species have remained stable. This difference was also found in the group of threatened species ($p < 0.01$; fig. 4.3A) and was nearly significant in the group of nonthreatened species ($p = 0.06$; fig. 4.3A). More species of running waters had positive than negative distribution trends ($p < 0.01$; fig. 4.4A). Species of moorland pools and fens with positive distribution trends outnumbered species with negative distribution trends, but differences were not significant ($p > 0.05$; fig. 4.4A). Last, more species of the southern and northern species groups have increased than have declined, but this pattern was significant only for southern species ($p < 0.01$; fig. 4.4A). Results of the Monte Carlo simulations closely matched those of the χ^2 tests (appendix 4.3).

4.3.3 ABUNDANCE TRENDS

Abundance trends were similar to distribution trends, but the differences within and among species groups were smaller. Estimates of abundance trends were available for only 43 species. Twenty-one of them have increased, 8 have remained stable, and 14 have declined (fig. 4.3B). The species of fens had equal numbers of species increasing and declining in abundance. In all other species groups (threatened, nonthreatened, running waters, moorland pools, southern species and northern species), more species have increased than have declined (fig. 4.4B), but differences were not significant. No significant differences were found between species groups in the Monte Carlo simulations (appendix 4.3).

For most species, the trends in abundance were less apparent than in distribution. However, for some species, abundance trends were stronger than distribution trends. For example, *Lestes virens* increased moderately in distribution but strongly in abundance. *Coenagrion hastulatum* declined moderately in distribution and strongly in abundance (appendix 4.1, 4.2). Some species showed contrasting trends. *Aeshna mixta, Calopteryx virgo, Orthetrum brunneum* and *Orthetrum coerulescens* increased in distribution but declined in abundance.

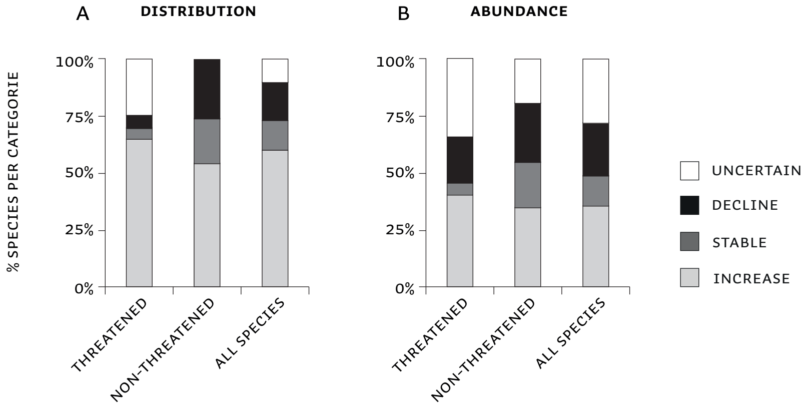

FIG. 4.3: Trends of distribution (1991–2013) (A) and abundance (1999–2013) (B) of threatened (*n* = 20), nonthreatened (*n* = 35), and all (*n* = 60) species, including 5 species without threat-level assessment. Of 6 species with uncertain distribution trends, 1 increased in abundance, 1 declined, and 4 have uncertain abundance trends (appendix 4.1). Of 17 species with uncertain abundance trends, 10 increased in distribution, 1 remained stable, 2 decreased, and 4 have uncertain distribution trends (appendix 4.2).

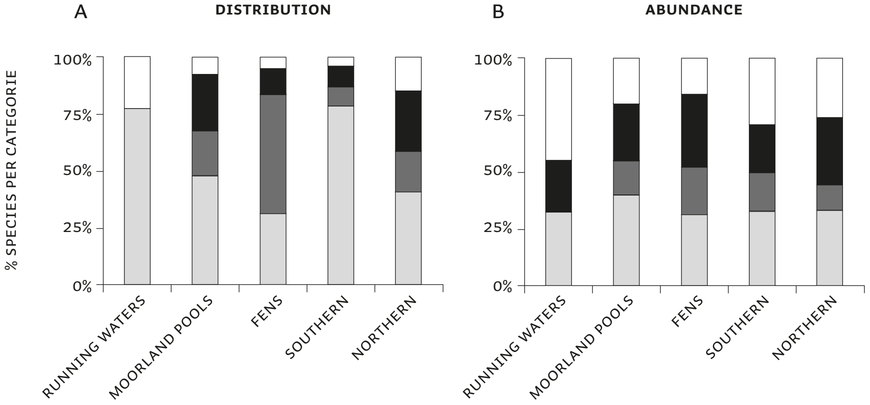

FIG. 4.4: Trends of distribution (1991–2013) (A) and abundance (1999–2013) (B) of species of running waters (n = 9), moorland pools (n = 25), fens (n = 19), southern species (n = 24), and northern species (*n* = 27).

4.4 Discussion

We found evidence of a recovery after the decline of many species in the 20th century (Termaat & Kalkman, 2012). The recovery is especially apparent in the distribution data, where 60% of species had positive trend estimates, whereas 49% of species showed a positive trend in the abundance data. The recovery of species is apparent in all 3 main habitat species groups. Thirteen of the 26 species listed as regionally extinct or threatened on the 1997 Dutch Red List have increased in distribution (19 of 35 nonthreatened species). Five species that had been absent from the Netherlands for decades reappeared after 1990: *Gomphus flavipes* (Kleukers & Reemer, 1998), *Leucorrhinia albifrons* (De Boer & Wasscher, 2006), *Leucorrhinia caudalis* (Muusse & Veurink, 2011), *Onychogomphus forcipatus* (Geraeds & Van Schaik, 2013), and *Ophiogomphus cecilia* (Brekelmans, 2014). Consequently, the Red List threat level of several of these species was reduced (Termaat & Kalkman, 2012).

In general, species of all habitat types have increased, but we found considerable differences in the proportion of increased species among habitat types (appendix 4.3). The recovery of species of running waters is most distinct because all species of streams and rivers showed a positive trend in distribution, abundance, or both. The only exception is the elusive *Gomphus flavipes*, which had an uncertain trend, although some authors have suggested that this species also has become less rare (Bouwman & Kalkman, 2006). Lotic species probably have profited from improvements in water quality and habitat morphology of streams and rivers. Running waters have less legacy effects of past acidification and eutrophication than moorland pools and fens and do not depend on recovery of complex vegetation structures. Therefore, effects might be most rapidly visible in lotic systems.

Species of moorland pools and fens also have increased, most probably because of a combined effect of decreased acidification and eutrophication and numerous habitat restoration projects in moorland pools, bogs, and fens (Natuurmonumenten et al., 2011; Van Duinen et al., 2003 and references therein). However, the ongoing decline of *C. hastulatum*, arguably the most critical species in moorland pools in the Netherlands, indicates that this habitat has not yet fully recovered. The declining abundance of *L. sponsa* (moorland pool populations), *Enallagma cyathigerum*, and *Sympetrum danae* (appendix 4.1) highlights the relevance of reduced acidification and eutrophication for dragonflies. These species can occur in very high densities in strongly acidified standing waters where they are regarded as negative indicators of lake water quality (Van der Molen et al., 2012). The decline of *Ischnura elegans* (appendix 4.1), which may occur in very high densities in hypertrophic waters (Van der Molen et al., 2012), corresponds to the view that improved water quality is important.

The potential effect of phylogenetic autocorrelation should be considered when interpreting differences in trends among species groups (Felsenstein, 1985; Grafen 1989). When species traits (e.g., habitat preference) are more similar within closely than distantly related species the observed response (i.e., trend) might be the result of a shared phylogeny rather than the trait itself. In our study, this risk of pseudoreplication should be taken into account especially for the species group in running waters because 4 of 7 lotic species belong to the families Calopterygidae, Platycnemididae, and Gomphidae, which lack representatives in moorland pools or fens. However, that an external unknown factor has a dominant positive effect on specifically these families in unlikely. Other lotic macroinvertebrates also have increased more strongly than lentic species in the last 2 decades in the Netherlands (Environmental Data Compendium, 2014a), making improved conditions in streams and rivers a more likely explanation.

Our results support the notion that climate change is affecting the distribution of dragonflies. Distribution trends of southern species were more positive than those of northern species. The increase of southern species, such as *Anax parthenope*, *Crocothemis erythraea*, and *Sympetrum fonscolobii*, which used to be very rare in northwestern Europe, is undoubtedly mediated by climate warming. Two other southern species, *C. viridis* and *Gomphus pulchellus*, declined. Range expansions of southern dragonfly species have been reported frequently from other European countries (e.g., Ott, 2001; Hickling et al., 2005; Hassall & Thompson, 2008; De Knijf & Anselin, 2010; De Knijf & Termaat 2010; Khrokalo, 2010; Chelmick, 2011). On the other hand, range contractions of northern species have been predicted by multiple authors (e.g., De Knijf et al., 2011 & Schröter et al., 2012; Jaeschke et al., 2013), but so far, have been found rarely (Grewe et al., 2013). We found that northern species generally increased rather than declined, but a delayed negative response of northern species to climate warming cannot be ruled out (Tilman et al., 1994). Northern species include the most stenotopic species, with critical needs regarding their larval habitat in the Netherlands. Perhaps the improvement of habitat quality counteracts potential negative effects of climate change for northern species. For some stenotopic northern species, the combined effect has led to a decline, e.g., in *C. hastulatum*, *Coenagrion lunulatum*, and *Aeshna juncea*, whereas other stenotypic northern species, like *Somatochlora arctica*, *Somatochlora flavomaculata*, and *Leucorrhinia pectoralis* are favoured.

We found that distribution trends derived from unstandardised data analysed with occupancy models were similar to those derived from standardised monitoring data, but had greater statistical power to detect trends. This result appears counterintuitive because changes in species usually are more easily detected in abundance than in distribution data. Standardised data were available only for 1999–2013 and for a limited number of transects, whereas many more unstandardised data were available and for a longer period (1991–2013) and resulted in much smaller standard errors (SEs) for distribution (mean SE = 0.009; appendix 4.2) than abundance trends (mean SE = 0.08; appendix 4.1). Thus, when the goal is to provide a general overview of the changes in dragonfly fauna, unstandardised dragonfly data appear to be sufficient and even to outperform standardised abundance data. The number of opportunistic, unstandardised dragonfly records (citizen science data) is growing in many countries, which greatly enhances opportunities to monitor dragonflies on a supranational level (Van Strien et al., 2013b). However, abundance data may deliver complementary information for individual species, such as for *C. virgo*, *A. mixta*, *O. brunneum*, and *O. coerulescens*, which increased in distribution but declined in abundance. These results suggest that more suitable sites have become available for these species, e.g., as a result of nature development projects, whereas the suitability of former strongholds has decreased on average.

Dragonflies have proven to be resilient and able to recover quickly when their habitats are restored. After a period of only 23 y, their positive responses are clearly notable. Our study supports the suitability of dragonflies as indicators of freshwater habitat condition (Sahlén & Ekestubbe, 2001; Briers & Biggs, 2003; Kutcher & Bried, 2014) and advocates their potential use for monitoring the effectiveness of water-quality management and wetland-restoration efforts. However, good biological indicators should be useful surrogates of other taxa (McGeoch, 1998). Dragonflies may not fully meet this demand, since they seem to have recovered more strongly than other aquatic invertebrates in the Netherlands (Environmental Data Compendium, 2014b). They have a more positive Red List assessment than other aquatic insects, such as stoneflies, caddisflies, and mayflies (Environmental Data Compendium, 2014a), and many terrestrial insects, like butterflies (Van Swaay, 2006), moths (Ellis et al., 2003), and bees (Biesmeijer et al., 2006). These differences may be explained by the high dispersal ability of dragonflies. They are among the most mobile insects and are able to colonise suitable habitats quickly over long distances (Corbet, 1999), a beneficial trait, especially in the strongly fragmented Dutch landscape. Positive responses of less mobile insects might take longer to become apparent, although some species with more critical habitat requirements may still be limited by the availability of suitable habitat patches rather than their ability to reach them (Wood & Pullin, 2002).

Dragonflies in the Netherlands have shown that loss of biodiversity can, at least partly, be reversed within a short period of time. Whether less mobile and more critical species will benefit from habitat improvements in the future also can be assessed thanks to the increasing availability of opportunistic citizen science data.

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References

Bartoń K. (2014). MuMIn: *Multi-model inference. R package version 1.12.1.* R Project for Statistical Computing, Vienna, Austria. (Available from: http://cran.r-project.org/web/packages/MuMIn/)

Biesmeijer J.C., Roberts S.P.M., Reemer M., Ohlemüller R., Edwards M., … & Kunin W.E. (2006). Parallel declines in pollinators and insect-pollinated plants in Britain and The Netherlands. *Science* 313: 351-354.

Bouwman J.H. & Kalkman V.J. (2006). Verspreiding van de libellen van de Habitatrichtlijn in Nederland. *Brachytron* 9: 3-13.

Brekelmans F. (2014). Gaffellibellen (*Ophiogomphus cecilia*) in de Dommel. *Brachytron* 16: 18-28.

Briers R.A. & Biggs J. (2003). Indicator taxa for the conservation of pond invertebrate diversity. *Aquatic Conservation: Marine and Freshwater Ecosystems* 13: 323-330.

Bobbink, R. & Hettelingh J.P. (editors) (2011). Review and revision of empirical critical loads and dose-response relationships. *Proceedings of an Expert Workshop*, Noordwijkerhout (The Netherlands), 23–25 June 2010. RIVM, Bilthoven, The Netherlands. (Available from: www.rivm.nl)

Butler R.G. & deMaynadier P.G. (2008). The significance of littoral and shoreline habitat integrity to the conservation of lacustrine damselflies (Odonata). *Journal of Insect Conservation* 12: 23-36.

Chelmick D. (2011). Range expansion of European dragonflies: the appearance of African species in Iberia. *Atropos* 43: 13-24.

Chovanec A. & Raab, R. (1997). Dragonflies (Insecta, Odonata) and the ecological status of newly created wetlands: examples for long-term bioindication programmes. *Limnologica* 27: 381-392.

Clausnitzer V., Kalkman V.J., Ram M., Collen B., Baillie J.E.M., … & Wilson, K. (2009). Odonata enter the biodiversity crisis debate: the first global assessment of an insect group. *Biological Conservation* 142: 1864-1869.

Corbet P.S. (1999). *Dragonflies: behaviour and ecology of Odonata*. Harley Books, Colchester, UK.

Cordoba-Aguilar A. (editor) (2008). *Dragonflies and damselflies. Model organisms for ecological and evolutionary research*. Oxford University Press, Oxford, UK.

D'Amico F., Darblade S., Avignon S., Blanc-Manel S. & Ormerod S.J. (2004). Odonates as indicators of shallow lake restoration by liming: comparing adult and larval responses. *Restoration Ecology* 12: 439-446.

De Boer E.P. & Wasscher M.T. (2006). Oostelijke witsnuitlibel (*Leucorrhinia albifrons*) herontdekt in Nederland. *Brachytron* 9: 14-20.

De Knijf G. & Anselin A. (2010). When south goes north: Mediterranean dragonflies (Odonata) conquer Flanders (North-Belgium). Pages 141–153 *in* Ott J. (editor). Monitoring climatic change with dragonflies. *BioRisk* 5. Pensoft, Sofia, Bulgaria.

De Knijf G., Flenker U., Vanappelghem C., Manci C.O., Kalkman V.J. & Demolder H. (2011). The status of two boreo-alpine species, *Somatochlora alpestris* and *S. arctica*, in Romania and their vulnerability to the impact of climate change (Odonata: Corduliidae). *International Journal of Odonatology* 14: 111-126.

De Knijf G. & Termaat T. (2010). De Zuidelijke heidelibel (*Sympetrum meridionale*) in België en Nederland: herkenning, verspreiding en status in Noordwest-Europa. *Brachytron* 13: 4-17.

Didderen K., Verdonschot P.F.M, Knegtel B.P.F.J.M. & Besse-Lototskaya A.A. (2009). Enquête beek(dal) herstelprojecten 2004-2008. *Evaluatie van beekherstel over de periode 1960-2008 en analyse van effecten van 9 voorbeeldprojecten.* Rapport 1858. Alterra, Wageningen, The Netherlands. (Available from: http://edepot.wur.nl/)

Dijkstra K.-D.B. (2006). *Field guide to the dragonflies of Britain and Europe*. British Wildlife Publishing, Gillingham, UK.

Ellis W.N., Groenendijk D., Groenendijk M.M., Huigens M.E., Jansen M.G.M., … & De Vos R. (2013). *Nachtvlinders belicht.* Dynamisch, belangrijk, bedreigd. De Vlinderstichting, Wageningen en Werkgroep Vlinderfaunsitiek, Leiden, The Netherlands.

Environmental Data Compendium (2012a). *Vermesting in grote rivieren, 1970-2011*. Indicator 0249, version 09. September 2012. Central Bureau of Statistics, The Netherlands Environmental Assessment Agency, and Wageningen University and Research Centre, Den Haag and Wageningen, The Netherlands. (Available from: www.compendiumvoordeleefomgeving.nl)

Environmental Data Compendium (2012b). *Vermesting in meren en plassen, 1980–2010*. Indicator 0503, version 05. September 2012. Central Bureau of Statistics, The Netherlands Environmental Assessment Agency, and Wageningen University and Research Centre, Den Haag and Wageningen, The Netherlands. (Available from: www.compendiumvoordeleefomgeving.nl)

Environmental Data Compendium (2013a). *Vermestende depositie, 1981–2012*. Indicator 0189, version 12. October 2013. Central Bureau of Statistics, The Netherlands Environmental Assessment Agency, and Wageningen University and Research Centre, Den Haag and Wageningen, The Netherlands. (Available from: www.compendiumvoordeleefomgeving.nl)

Environmental Data Compendium (2013b). *Verzurende depositie, 1981–2012*. Indicator 0184, version 13. October 2013. Central Bureau of Statistics, The Netherlands Environmental Assessment Agency, and Wageningen University and Research Centre, Den Haag and Wageningen, The Netherlands. (Available from: www.compendiumvoordeleefomgeving.nl)

Environmental Data Compendium (2014a). *Aantal bedreigde soorten*. Indicator 1052, version 12. September 2014. Central Bureau of Statistics, The Netherlands Environmental Assessment Agency, and Wageningen University and Research Centre, Den Haag and Wageningen, The Netherlands. (Available from: www.compendiumvoordeleefomgeving.nl)

Environmental Data Compendium (2014b). *Natuurkwaliteit van macrofauna in oppervlaktewater, 1990–2010*. Indicator 1435, version 04. May 2014. Central Bureau of Statistics, The Netherlands Environmental Assessment Agency, and Wageningen University and Research Centre, Den Haag and Wageningen, The Netherlands. (Available from: www.compendiumvoordeleefomgeving.nl)

Felsenstein J. (1985). Phylogenies and the comparative method. *American Naturalist* 125: 1-15.

Ferreras-Romero M., Márquez-Rodríguez J. & Ruiz-García A. (2009). Implications of anthropogenic disturbance factors on the Odonata assemblage in a Mediterranean fluvial system. *International Journal of Odonatology* 12: 413-428.

Flenner I.D.A. & Sahlén G. (2008). Dragonfly community re-organisation in boreal forest lakes: rapid species turnover driven by climate change? *Insect Conservation and Diversity* 1: 169-179.

Gårdmark A., Enberg K., Ripa J., Laakso J. & Kaitala V. (2003). The ecology of recovery. *Annales Zoologici Fennici* 40: 131-144.

Geraeds R.P.G. & Van Schaik V. (2013). De status van de Kleine tanglibel langs de Roer. *Natuurhistorisch Maandblad* 102: 170-174.

Grafen A. (1989). The phylogenetic regression. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences* 326: 119-156.

Grewe Y., Hof C., Dehling D.M., Brandl R. & Brändle M. (2013). Recent range shifts of European dragonflies provide support for an inverse relationship between habitat predictability and dispersal. *Global Ecology and Biogeography* 22: 403-409.

Gyulavári H.A., Felföldi T., Benken T., Szabó L.J., Miskolczi M., … & Dévai G. (2011). Morphometric and molecular studies on the populations of the damselflies *Chalcolestes viridis* and *C. parvidens* (Odonata, Lestidae). *International Journal of Odonatology* 14: 329-339.

Hassall C. & Thompson D.J. (2008). The effects of environmental warming on Odonata: a review. *International Journal of Odonatology* 11: 131-153.

Hickling R., Roy D.B., Hill J.K. & Thomas C.D. (2005). A northward shift of range margins in British Odonata. *Global Change Biology* 11: 502-506.

IUCN (International Union for the Conservation of Nature) (2012). *IUCN Red List categories and criteria*. Version 3.1. 2nd edition. International Union for the Conservation of Nature, Gland, Switzerland. (Available from: http://www.iucnredlist.org/)

Jaeschke A., Bittner T., Reineking B. & Beierkuhnlein C. (2013). Can they keep up with climate change? Integrating specific dispersal abilities of protected Odonata in species distribution modelling. *Insect Conservation and Diversity* 6: 93-103.

Kalkman V.J., Boudot J.-P., Bernard R., Conze K.-J., De Knijf G., … & Sahlén G. (2010). *European Red List of dragonflies*. Publications Office of the European Union, Luxembourg. (Available from: http://www.iucnredlist.org/)

Khrokalo L. (2010). Expansion of *Crocothemis erythraea* in Ukraine. Pages 211–223 *in* Ott J. (editor). Monitoring climatic change with dragonflies. *BioRisk* 5. Pensoft, Sofia, Bulgaria.

Kleukers R.M.J.C. & Reemer M. (1998). De terugkeer van de Rivierrombout (*Gomphus flavipes* (Charpentier)) in Nederland. *Brachytron* 2: 52-59.

Kutcher T.E. & Bried J.T. (2014). Adult Odonata conservatism as an indicator of freshwater wetland condition. *Ecological Indicators* 38: 31-39.

MacKenzie D.I., Nichols J.D., Royle J.A., Pollock K.H., Hines J.E. & Bailey L.L. (2006). *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*. Elsevier, San Diego, California.

McGeoch M.A. (1998). The selection, testing and application of terrestrial insects as bioindicators. *Biological Reviews* 73: 181-201.

Martins D.J. (2009). Differences in Odonata abundance and diversity in pesticide-fished, traditionally-fished and protected areas in lake Victoria, Eastern Africa. *Odonatologica* 38: 247-255.

Muller Z., Jakb T., Toth A., Szallassy N., Kiss B. & Horvath R. (2003). Effect of sports fisherman activities on dragonfly assemblages on a Hungarian river floodplain. *Biodiversity and Conservation* 12: 167-179.

Muusse T. & Veurink G. (2011). Sierlijke witsnuitlibel (*Leucorrhinia caudalis*)voortplantend waargenomen in De Weerribben. *Brachytron* 14: 14-27.

Natuurmonumenten, Staatsbosbeheer, Landschap Overijssel & Ministerie van Defensie (2011*). Evaluatie hoogveengebieden in Nederland*. Natuurmonumenten, ’s-Graveland, The Netherlands. (Available from: https://www.wur.nl/en/library.htm)

Nederlandse Vereniging voor Libellenstudie (2002). *De Nederlandse libellen (Odonata)*. Nederlandse Fauna 4. Nationaal Natuurhistorisch Museum Naturalis, KNNV Uitgeverij, and European Invertebrate Survey-Nederland, Leiden, the Netherlands.

Ott J. (2001). Expansion of Mediterranean Odonata in Germany and Europe – consequences of climatic changes. *In:* Walther G.R., Buga C. & Edwards P.J. (editors). *‘Fingerprints’ of climate change: adapted behaviour and shifting species ranges.* Kluwer Academic/Plenum Publishers, New York.

Pannekoek J. & Van Strien A.J. (2005). *TRIM 3 manual (TRends and Indices for Monitoring Data).* Central Bureau of Statistics, Voorburg, The Netherlands. (Available from: https://www.cbs.nl/en-gb)

Remsburg A.J. & Turner M.G. (2009). Aquatic and terrestrial drivers of dragonfly (Odonata) assemblages within and among north-temperate lakes. *Journal of the North American Benthological Society* 28: 44-56.

Rosset V. & Oertli B. (2011). Freshwater biodiversity under climate warming pressure: Identifying the winners and losers in temperate standing waterbodies. *Biological Conservation* 144: 2311-2319.

Sahlén G. (1999). The impact of forestry on dragonfly diversity in central Sweden. *International Journal of Odonatology* 2: 177-186.

Sahlén G. & Ekestubbe K. (2001). Identification of dragonflies (Odonata) as indicators of general species richness in boreal forest lakes. *Biodiversity and Conservation* 10: 673-690.

Samways M.J. & Sharratt N.J. (2010). Recovery of endemic dragonflies after removal of invasive alien trees. *Conservation Biology* 24: 267-277.

Samways M.J. & Taylor S. (2004). Impacts of invasive alien plants on Red-Listed South African dragonflies (Odonata). *South African Journal of Science* 100: 78-80.

Schmitt T. & Varga Z. (2012). Extra-Mediterranean refugia: the rule and not the exception? *Frontiers in Zoology* 9: 22.

Schröter A., Schneider T. Schneider E., Karjalainen S. & Hämäläinen M. (2012). Observations on adult *Somatochlora sahlbergi* – a species at risk due to climate change? (Odonata: Corduliidae). *Libellula* 31: 41-60.

Shoo L.P., Williams S.E. & Hero J.-M. (2005). Potential decoupling of trends in distribution area and population size of species with climate change. *Global Change Biology* 11: 1469-1476.

Simaika J.P. & Samways M.J. (2009). An easy-to-use index of ecological integrity for prioritizing freshwater sites and for assessing habitat quality. *Biodiversity and Conservation* 18: 1171-1185.

Sternberg K. (1998). Die postglaziale Besiedlung Mitteleuropas durch Libellen, mit besonderer Berücksichtigung Südwestdeutschlands (Insecta, Odonata). *Journal of Biogeography* 25: 319-337.

Termaat T. & Kalkman V.J. (2012). Basisrapport Rode Lijst Libellen 2011 volgens Nederlandse en IUCN-criteria. *Brachytron* 14: 75-187.

Tilman D., May R.M., Lehman C.L. & Nowak M.A. (1994). Habitat destruction and the extinction debt. *Nature* 371: 65-66.

Van Dam H. & Mertens A. (2011). *Monitoring herstel verzuring en klimaatverandering vennen 1978-2010; temperatuur, hydrologie, chemie, kiezelwieren.* Rapport AWN 911. Water en Natuur, Amsterdam, The Netherlands. (Available from: https://library.wur.nl/WebQuery/hydrotheek)

Van Duinen G.A., Brock A.M.T., Kuper J.T., Leuven R.S.E.W., Peeters T.M.J., … & Esselink H. (2003). Do restoration measures rehabilitate fauna diversity in raised bogs? A comparative study on aquatic macroinvertebrates. *Wetlands Ecology and Management* 11: 447-459.

Van der Molen D.T., Pot R., Evers C.H.M. & Van Nieuwerburgh L.L.J. (editors) (2012). *Referenties en maatlatten voor natuurlijke watertypen voor de Kaderrichtlijn Water.* Stichting Toegepast Onderzoek Waterbeheer, Amersfoort, The Netherlands. (Available from: https://www.stowa.nl/english).

Van Strien A. J., Van Swaay C.A.M & Termaat T. (2013a). Opportunistic citizen science data of animal species produce reliable estimates of distribution trends if analysed with occupancy models. *Journal of Applied Ecology* 50: 1450-1458.

Van Strien A.J., Termaat T., Kalkman V.J., Prins M., De Knijf G., … & Vanreusel W. (2013b). Occupancy modelling as a new approach to assess supranational trends using opportunistic data: a pilot study for the damselfly *Calopteryx splendens*. *Biodiversity and Conservation* 22: 673-686.

Van Swaay C.A.M. (1990). An assessment of the changes in butterfly abundance in The Netherlands during the 20th century. *Biological Conservation* 52: 287-302.

Van Swaay C.A.M. (2006). *Basisrapport Rode Lijst Dagvlinders*. Rapport VS2006.002. De Vlinderstichting, Wageningen, The Netherlands. (Available from: https://www.vlinderstichting.nl/)

Van Swaay C.A.M., Termaat T. & Plate C.L. (2011). *Handleiding Landelijke Meetnetten Vlinders en Libellen (Manual Monitoring Schemes Butterflies and Dragonflies)*. Rapport VS2011.001. De Vlinderstichting, Wageningen and Central Bureau of Statistics, Den Haag, The Netherlands. (Available from: https://www.vlinderstichting.nl/)

Verberk W.C.E.P., Van der Velde G. & Esselink, H. (2010). Explaining abundance–occupancy relationships in specialists and generalists: a case study on aquatic macroinvertebrates in standing waters. *Journal of Animal Ecology* 79: 589-601.

Watson J., Arthington A. & Conrick D. (1982). Effect of sewage effluent on dragonflies (Odonata) of Bulimba Creek, Brisbane. *Marine and Freshwater Research* 33: 517-528.

Wood B.C. & Pullin A.S. (2002). Persistence of species in a fragmented urban landscape: the importance of dispersal ability and habitat availability for grassland butterflies. Biodiversity and Conservation 11: 1451-1468.

Appendix 4.1

Abundance trends for the period 1999-2013 (shorter for 17 species). Species classification according to threat status, habitat preference and European distribution range. Rc = multiplicative regression coefficient of index; se = standard error. See online Supporting Information for index values per year: https://www.journals.uchicago.edu/doi/suppl/10.1086/682669.

Species	Threatened	Running waters	Moorland pools	Fens	Southern	Northern	Stratum	Trend period	n sites	rc	se	Trend category
Aeshna affinis					x		Netherlands	2003-2013	9	0.752	0.259	uncertain
Aeshna cyanea							Netherlands	1999-2013	329	0.957	0.009	decline
Aeshna grandis						x	Netherlands	1999-2013	314	1.035	0.010	increase
Aeshna grandis				x			Lowland peat area	1999-2013	60	0.955	0.019	decline
Aeshna grandis			x				High-lying sandy soils	1999-2013	163	1.061	0.017	increase
Aeshna isoceles	x			x	x		Netherlands	1999-2013	298	1.102	0.008	increase
Aeshna juncea			x			x	Netherlands	1999-2013	98	0.980	0.020	uncertain
Aeshna mixta					x		Netherlands	1999-2013	528	0.979	0.006	decline
Aeshna subarctica	x		x			x	Netherlands	2007-2013	3	3.485	3.035	uncertain
Aeshna viridis	x			x		x	Netherlands	2003-2013	59	0.988	0.013	stable
Anax imperator					x		Netherlands	1999-2013	546	1.052	0.005	increase
Anax parthenope					x		Netherlands	-	-	-	-	uncertain
Brachytron pratense				x			Netherlands	1999-2013	330	1.043	0.007	increase
Calopteryx splendens		x			x		Netherlands	1999-2013	164	1.061	0.009	increase
Calopteryx virgo	x	x				x	Netherlands	1999-2013	58	0.988	0.002	decline
Ceriagrion tenellum	x		x		x		Netherlands	1999-2013	139	1.069	0.021	increase
Chalcolestes viridis				x	x		Netherlands	1999-2013	496	0.957	0.007	decline
Coenagrion hastulatum	x		x			x	Netherlands	1999-2013	20	0.860	0.007	decline
Coenagrion lunulatum			x			x	Netherlands	1999-2013	79	1.007	0.017	stable
Coenagrion puella			x		x		Netherlands	1999-2013	519	1.012	0.004	increase
Coenagrion pulchellum				x			Netherlands	1999-2013	432	1.002	0.005	stable
Cordulegaster boltonii		x					Netherlands	2000-2013	6	0.995	0.046	uncertain
Cordulia aenea						x	Netherlands	1999-2013	265	1.140	0.008	increase

Species	Threatened	Running waters	Moorland pools	Fens	Southern	Northern	Stratum	Trend period	n sites	rc	se	Trend category
Cordulia aenea				x			Lowland peat area	1999-2013	25	1.004	0.036	uncertain
Cordulia aenea			x				High-lying sandy soils	1999-2013	205	1.136	0.011	increase
Crocothemis erythraea					x		Netherlands	2001-2013	71	1.478	0.100	increase
Enallagma cyathigerum			x			x	Netherlands	1999-2013	498	0.986	0.004	decline
Erythromma lindenii					x		Netherlands	2005-2013	7	0.931	0.603	uncertain
Erythromma najas				x		x	Netherlands	1999-2013	386	0.992	0.007	stable
Erythromma viridulum				x	x		Netherlands	1999-2013	363	1.012	0.011	stable
Gomphus flavipes	x	x					Netherlands	-	-	-	-	uncertain
Gomphus pulchellus					x		Netherlands	1999-2013	20	1.107	0.150	uncertain
Gomphus vulgatissimus	x	x					Netherlands	1999-2013	12	0.994	0.032	uncertain
Ischnura elegans				x		x	Netherlands	1999-2013	668	0.935	0.006	decline
Ischnura pumilio					x		Netherlands	1999-2013	72	1.047	0.051	uncertain
Lestes barbarus			x		x		Netherlands	1999-2013	93	0.956	0.023	uncertain
Lestes dryas			x			x	Netherlands	1999-2013	120	1.134	0.031	increase
Lestes sponsa						x	Netherlands	1999-2013	421	0.972	0.005	decline
Lestes sponsa				x			Lowland peat area	2000-2013	31	0.965	0.028	uncertain
Lestes sponsa			x				High-lying sandy soils	1999-2013	261	0.987	0.006	decline
Lestes virens	x		x				Netherlands	1999-2013	188	1.118	0.017	increase
Leucorrhinia albifrons	x		x			x	Netherlands	2007-2013	1	0.683	0.083	decline
Leucorrhinia dubia	x		x			x	Netherlands	1999-2013	129	1.245	0.052	increase
Leucorrhinia pectoralis	x			x		x	Netherlands	1999-2013	84	1.093	0.005	increase
Leucorrhinia rubicunda			x			x	Netherlands	1999-2013	190	1.080	0.012	increase
Libellula depressa					x		Netherlands	2000-2013	321	0.991	0.013	stable

Species	Threatened	Running waters	Moorland pools	Fens	Southern	Northern	Stratum	Trend period	n sites	rc	se	Trend category
Libellula fulva	x			x			Netherlands	1999-2013	90	1.086	0.012	increase
Libellula quadrimaculata						x	Netherlands	1999-2013	547	1.046	0.005	increase
Libellula quadrimaculata				x			Lowland peat area	1999-2013	90	1.089	0.033	increase
Libellula quadrimaculata			x				High-lying sandy soils	1999-2013	300	1.038	0.008	increase
Ophiogomphus cecilia	x	x				x	Netherlands	2000-2013	5	1.088	0.014	increase
Orthetrum brunneum					x		Netherlands	1999-2013	4	0.635	0.185	decline
Orthetrum cancellatum					x		Netherlands	1999-2013	608	1.010	0.006	stable
Orthetrum cancellatum				x			Lowland peat area	1999-2013	122	0.969	0.014	decline
Orthetrum cancellatum			x				High-lying sandy soils	1999-2013	279	1.010	0.012	stable
Orthetrum coerulescens	x	x			x		Netherlands	1999-2013	35	0.975	0.009	decline
Platycnemis pennipes		x					Netherlands	2000-2013	57	1.049	0.021	increase
Pyrrhosoma nymphula						x	Netherlands	1999-2013	455	1.025	0.007	increase
Pyrrhosoma nymphula				x			Lowland peat area	1999-2013	52	0.958	0.015	decline
Pyrrhosoma nymphula			x				High-lying sandy soils	1999-2013	293	1.016	0.010	stable
Somatochlora arctica	x		x			x	Netherlands	2000-2013	6	0.988	0.048	uncertain
Somatochlora flavomaculata	x		x			x	Netherlands	2003-2013	3	0.947	0.093	uncertain
Somatochlora metallica						x	Netherlands	1999-2013	60	0.962	0.031	uncertain
Sympecma fusca	x		x		x		Netherlands	2001-2013	108	1.273	0.056	increase
Sympecma paedisca	x			x		x	Netherlands	2003-2013	19	0.961	0.028	uncertain
Sympetrum danae			x			x	Netherlands	1999-2013	318	0.962	0.007	decline
Sympetrum flaveolum			x			x	Netherlands	1999-2013	162	0.823	0.042	decline
Sympetrum fonscolombii					x		Netherlands	1999-2013	82	1.038	0.034	uncertain
Sympetrum pedemontanum	x	x				x	Netherlands	1999-2013	23	1.055	0.094	uncertain

Species	Threatened	Running waters	Moorland pools	Fens	Southern	Northern	Stratum	Trend period	n sites	rc	se	Trend category
Sympetrum sanguineum				x	x		Netherlands	1999-2013	502	1.044	0.008	increase
Sympetrum striolatum					x		Netherlands	1999-2013	427	1.013	0.008	stable
Sympetrum vulgatum					x		Netherlands	1999-2013	478	0.969	0.006	decline
Sympetrum vulgatum				x			Lowland peat area	1999-2013	80	0.944	0.015	decline
Sympetrum vulgatum			x				High-lying sandy soils	1999-2013	229	0.987	0.011	stable

Appendix 4.2

Distribution trends for the period 1991-2013. Species classification according to threat status, habitat preference and European distribution range. Rc = multiplicative regression coefficient of index; se = standard error. See online Supporting Information for index values per year: https://www.journals.uchicago.edu/doi/suppl/10.1086/682669.

Species	Threatened	Running waters	Moorland pools	Fens	Southern	Northern	Stratum	Trend period	n sites	rc	se	Trend category
Aeshna affinis					x		Netherlands	1991-2013	144	1.059	0.053	uncertain
Aeshna cyanea							Netherlands	1991-2013	6936	0.991	0.001	decline
Aeshna grandis						x	Netherlands	1991-2013	5991	1.000	0.001	stable
Aeshna grandis				x			Lowland peat area	1991-2013	630	0.996	0.004	stable
Aeshna grandis			x				High-lying sandy soils	1991-2013	3636	1.001	0.002	stable
Aeshna isoceles	x			x	x		Netherlands	1991-2013	3624	1.048	0.005	increase
Aeshna juncea			x			x	Netherlands	1991-2013	815	0.958	0.005	decline
Aeshna mixta					x		Netherlands	1991-2013	11713	1.003	0.001	increase
Aeshna subarctica	x		x			x	Netherlands	1991-2013	91	1.024	0.026	uncertain
Aeshna viridis	x			x		x	Netherlands	1991-2013	532	1.002	0.011	stable
Anax imperator					x		Netherlands	1991-2013	9192	1.026	0.003	increase
Anax parthenope					x		Netherlands	1991-2013	167	1.188	0.057	increase
Brachytron pratense				x			Netherlands	1991-2013	3457	1.017	0.003	increase
Calopteryx splendens		x			x		Netherlands	1991-2013	5365	1.008	0.001	increase
Calopteryx virgo	x	x				x	Netherlands	1991-2013	427	1.031	0.005	increase
Ceriagrion tenellum	x		x		x		Netherlands	1991-2013	1540	1.057	0.005	increase
Chalcolestes viridis				x	x		Netherlands	1991-2013	7594	0.995	0.001	decline
Coenagrion hastulatum	x		x			x	Netherlands	1991-2013	59	0.979	0.009	decline
Coenagrion lunulatum			x			x	Netherlands	1991-2013	467	0.980	0.004	decline
Coenagrion puella			x		x		Netherlands	1991-2013	8656	1.008	0.001	increase
Coenagrion pulchellum				x			Netherlands	1991-2013	5866	1.000	0.001	stable
Cordulegaster boltonii		x					Netherlands	1991-2013	45	1.023	0.009	increase

Species	Threatened	Running waters	Moorland pools	Fens	Southern	Northern	Stratum	Trend period	n sites	rc	se	Trend category
Cordulia aenea						x	Netherlands	1991-2013	3125	1.025	0.003	increase
Cordulia aenea				x			Lowland peat area	1991-2013	286	1.007	0.004	stable
Cordulia aenea			x				High-lying sandy soils	1991-2013	2317	1.027	0.004	increase
Crocothemis erythraea					x		Netherlands	1991-2013	1153	1.340	0.031	increase
Enallagma cyathigerum			x			x	Netherlands	1991-2013	7058	1.000	0.001	stable
Erythromma lindenii					x		Netherlands	1991-2013	576	1.065	0.012	increase
Erythromma najas				x		x	Netherlands	1991-2013	6144	1.006	0.002	increase
Erythromma viridulum				x	x		Netherlands	1991-2013	4822	1.017	0.004	increase
Gomphus flavipes	x	x					Netherlands	-	-	-	-	uncertain
Gomphus pulchellus					x		Netherlands	1991-2013	730	0.991	0.004	decline
Gomphus vulgatissimus	x	x					Netherlands	1991-2013	436	1.086	0.023	increase
Ischnura elegans				x		x	Netherlands	1991-2013	15311	0.996	0.000	decline
Ischnura pumilio					x		Netherlands	1991-2013	1219	1.041	0.008	increase
Lestes barbarus			x		x		Netherlands	1991-2013	1444	1.063	0.018	increase
Lestes dryas			x			x	Netherlands	1991-2013	1309	1.001	0.004	stable
Lestes sponsa						x	Netherlands	1991-2013	4670	0.985	0.001	decline
Lestes sponsa				x			Lowland peat area	1991-2013	304	0.994	0.004	stable
Lestes sponsa			x				High-lying sandy soils	1991-2013	3444	0.987	0.001	decline
Lestes virens	x		x				Netherlands	1991-2013	1703	1.055	0.009	increase
Leucorrhinia albifrons	x		x			x	Netherlands	-	-	-	-	uncertain
Leucorrhinia dubia	x		x			x	Netherlands	1991-2013	944	1.010	0.004	increase
Leucorrhinia pectoralis	x			x		x	Netherlands	1991-2013	415	1.193	0.031	increase
Leucorrhinia rubicunda			x			x	Netherlands	1991-2013	1498	1.010	0.003	increase
Libellula depressa					x		Netherlands	1991-2013	7437	1.013	0.002	increase

Species	Threatened	Running waters	Moorland pools	Fens	Southern	Northern	Stratum	Trend period	n sites	rc	se	Trend category
Libellula fulva	x			x			Netherlands	1991-2013	991	1.036	0.006	increase
Libellula quadrimaculata						x	Netherlands	1991-2013	6970	1.005	0.001	increase
Libellula quadrimaculata				x			Lowland peat area	1991-2013	602	1.004	0.004	stable
Libellula quadrimaculata			x				High-lying sandy soils	1991-2013	4499	1.004	0.001	increase
Ophiogomphus cecilia	x	x				x	Netherlands	-	-	-	-	uncertain
Orthetrum brunneum					x		Netherlands	1991-2013	102	1.157	0.021	increase
Orthetrum cancellatum					x		Netherlands	1991-2013	11996	1.009	0.001	increase
Orthetrum cancellatum				x			Lowland peat area	1991-2013	1302	0.999	0.002	stable
Orthetrum cancellatum			x				High-lying sandy soils	1991-2013	6137	1.016	0.002	increase
Orthetrum coerulescens	x	x			x		Netherlands	1991-2013	373	1.034	0.008	increase
Platycnemis pennipes		x					Netherlands	1991-2013	2908	1.022	0.002	increase
Pyrrhosoma nymphula						x	Netherlands	1991-2013	7566	1.004	0.001	increase
Pyrrhosoma nymphula				x			Lowland peat area	1991-2013	456	1.000	0.002	stable
Pyrrhosoma nymphula			x				High-lying sandy soils	1991-2013	5305	1.000	0.001	stable
Somatochlora arctica	x		x			x	Netherlands	1991-2013	26	1.097	0.028	increase
Somatochlora flavomaculata	x		x			x	Netherlands	1991-2013	160	1.140	0.024	increase
Somatochlora metallica						x	Netherlands	1991-2013	1736	0.995	0.003	stable
Sympecma fusca	x		x		x		Netherlands	1991-2013	966	1.153	0.031	increase
Sympecma paedisca	x			x		x	Netherlands	1991-2013	127	1.017	0.017	uncertain
Sympetrum danae			x			x	Netherlands	1991-2013	4637	0.984	0.001	decline
Sympetrum flaveolum			x			x	Netherlands	1991-2013	2347	0.935	0.014	decline
Sympetrum fonscolombii					x		Netherlands	1991-2013	1143	1.256	0.029	increase
Sympetrum pedemontanum	x	x				x	Netherlands	1991-2013	915	1.215	0.035	increase
Sympetrum sanguineum				x	x		Netherlands	1991-2013	7915	0.999	0.001	stable

Species	**Threatened**	**Running waters**	**Moorland pools**	**Fens**	**Southern**	**Northern**	**Stratum**	**Trend period**	**n sites**	**rc**	**se**	**Trend category**
Sympetrum striolatum					x		Netherlands	1991-2013	7223	1.012	0.002	increase
Sympetrum vulgatum					x		Netherlands	1991-2013	8724	1.001	0.001	stable
Sympetrum vulgatum				x			Lowland peat area	1991-2013	723	0.999	0.005	stable
Sympetrum vulgatum			x				High-lying sandy soils	1991-2013	4781	0.999	0.001	stable

Appendix 4.3

We conducted Monte Carlo simulations (50,000 iterations; PopTools, available online) to test whether the frequency of species in 3 trend categories (significant increase, stable, significant decline) differed between the species groups defined by habitat (running waters, moorland pools and fens) and range (northern and southern species). A trend was classified as stable when there was no significant trend and the 95% confidence of the trend estimate is such that an annual trend of 5% or stronger would have been detected if it had occurred; else the trend was classified as uncertain and omitted from this analysis. The mean trend value was calculated for both categories (decline = –1, stable = 0, increase = 1). The number of Monte Carlo iterations for which the simulated difference is equal or larger than the actual difference was scored. This value divided by the total number of iterations (50,000) represents the 1-sided *p*-value, which was then doubled to obtain the 2-sided *p*-value.

Outcome of Monte Carlo analyses that test whether the distribution of species with positive, stable and negative trends over two groups deviates from random. This is done for both distribution trends (A) and abundance trends (B). The group with the most positive trend is given first for every comparison except for running waters vs moorland pools in abundance trends as these were equal.

A: Distribution trends

Factors	Iterations ≥ data (total = 50,000)	*p*-value (two-sided)
Running waters vs moorland pools	1224	0.049
Running waters vs fens	130	0.005
Moorland pools vs fens	22,255	0.89
Southern vs northern	664	0.027

B: Abundance trends

Factors	Iterations ≥ data (total = 50,000)	*p*-value (one-sided)
Running waters vs moorland pools	26,489	1
Running waters vs fens	17,557	0.70
Moorland pools vs fens	12,892	0.52
Southern vs northern	20,066	0.080

With a Species Temperature Index (STI) of 2.0 °C, *Aeshna caerulea* is among the most cold-adapted dragonfly species in Europe.

CHAPTER 5

Distribution trends of European dragonflies under climate change

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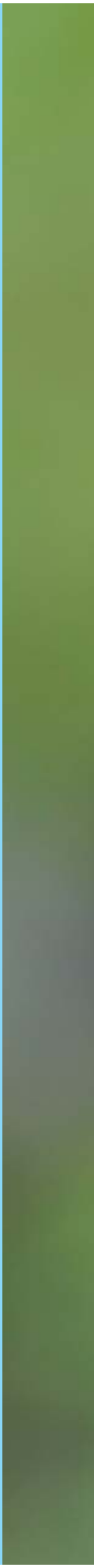


Abstract

Poleward range shifts of species are among the most obvious effects of climate change on biodiversity. As a consequence of these range shifts, species communities are predicted to become increasingly composed of warm-dwelling species, but this has only been studied for a limited number of taxa, mainly birds, butterflies and plants. As species groups may vary considerably in their adaptation to climate change it is desirable to expand these studies to other groups, from different ecosystems. Freshwater macroinvertebrates, such as dragonflies (Odonata), have been ranked among the species groups with highest priority. In this paper, we investigate how the occurrence of dragonflies in Europe has changed in recent decades, and if these changes are in parallel with climate change. We use data from 10 European geographic regions to calculate occupancy indices and trends for 99 (69%) of the European species. Next, we combine these regional indices to calculate European indices. To determine if changes in regional dragonfly communities in Europe reflect climatic warming, we calculate Species Temperature Indices (STI), Multi-Species Indicators (MSI) and Community Temperature Indices (CTI). 55 of 99 considered species increased in occupancy at European level, 32 species remained stable, and none declined. Trends for 12 species are uncertain. MSI of cold-dwelling and warm-dwelling species differ in some of the regions, but increased at a similar rate at European level. CTI increased in all regions, except Cyprus. The European CTI increased slightly. European dragonflies, in general, have expanded their distribution in response to climate change, even though their CTI lags behind the increase in temperature. Furthermore, dragonflies proved to be a suitable species group for monitoring changes in communities, both at regional and continental level.

KEYWORDS: Citizen science data, Climate change, Community Temperature Index, Multi-species Indicator, Odonata, Species Temperature Index

5.1 Introduction

Climate change has a profound impact on the occurrence of many species of plants and animals (Parmesan & Yohe, 2003; Root et al., 2003; Walther et al., 2002). One of the most distinctive consequences is the poleward shift of species distribution ranges as a result of increasing temperatures, resulting in changes in the composition of species communities (Chen et al., 2011; Hickling et al., 2006; Kampichler et al., 2012; Lindström et al., 2013; Mason et al., 2015). Species vary in their response to climate warming, due to different temperature requirements and different dispersal and colonisation capacities. In general. warm-dwelling species and species with good dispersal capacity are more likely to be 'winners' than cold-dwelling species and species with poor dispersal capacity (e.g. Franko et al., 2006; Rosset & Oertli, 2011; Virkkala & Lehikoinen, 2014). As a consequence, communities are predicted to become increasingly composed of warm-dwelling, mobile species.

This may seem straightforward, but the effects of climate change on species' trends and community compositions have only been studied for a limited number of taxa (but see Hickling et al., 2006; Mason et al., 2015), mainly birds, butterflies and plants (Bertrand et al., 2011; Britton et al., 2009; Clavero et al., 2011; Davey et al., 2013; Devictor et al., 2012a; Jiguet et al., 2010; Roth et al., 2014; Virkkala & Lehikoinen, 2014). To gain a better understanding of how climate change affects total diversity, more taxa need to be covered, including taxa from different habitats. Freshwater macroinvertebrates should be ranked among the faunal groups with highest priority, as they have very different life histories from birds and butterflies and occupy very different ecosystems. They are known to react quickly to a wide range of changes in their habitats (Rosenberg & Resh, 1993). Furthermore, fresh water covers only 0.8% of the Earth's surface, while supporting almost 6% of all described species, most of which are insects (Dudgeon et al., 2006). At the same time, they are among the most severely threatened ecosystems in the world, with aquatic species being more threatened than terrestrial species (Collen et al., 2014; Darwall et al., 2018; Dudgeon et al., 2006). For these reasons, freshwater invertebrates have been indicated as an essential future addition to Europe's biodiversity monitoring programme (Thomas, 2005; Feest. 2013).

Unfortunately, monitoring freshwater invertebrates comes with drawbacks. Most groups are so speciose that collecting, sorting, and identifying samples to species level requires much effort and experience. Therefore, the number of specialists studying these groups is, in most countries, limited, which results in an incomplete picture of species' distributions. Dragonflies (Odonata) present an exception to this rule. Adult dragonflies are large, colourful insects, which are easy to spot and relatively easy to identify at species level, making them attractive to a large public. With a manageable 143 species recorded in Europe (Kalkman et al., 2018), they constitute a suitable group for citizen science projects. Furthermore, dragonflies are well-established as useful organisms to assess and monitor aquatic and wetland ecosystem quality (Oertli, 2008), and they are known to react quickly to climate change (Bush et al., 2013; Hassall, 2015).

In most European countries, dragonfly recording has increased in recent decades, mediated by the publication of several good field guides and national distribution atlases. This has resulted in a steep increase in available distribution data from citizen science projects, and the publication of a European distribution atlas in 2015 (Boudot & Kalkman, 2015). The majority of these distribution data refer to records collected without standardisation, which are unsuitable for straightforward calculation of distributions trends. However, previous studies have shown that these 'opportunistic' records can be used to derive reliable trend estimates of dragonflies on a national scale, if occupancy models are applied. These models take the imperfect detection of species into account and thereby they may simultaneously correct for observation and reporting bias as well (Van Strien et al., 2010, Chapter 2 of this thesis; Van Strien et al., 2013; Isaac et al., 2014). Moreover, Van Strien et al. (2013, Chapter 3 of this thesis) showed in a pilot study, using records of a single species from five western European regions, that occupancy indices from multiple regions can be combined to calculate supraregional indices and trends.

In this paper, we investigate how the occurrence of dragonflies in Europe has changed in recent decades, and if these changes are in parallel with climate change. We use distribution data from 10 European geographic regions – ranging from Sweden to Cyprus – to calculate occupancy indices and trends for as many dragonfly species as possible. Next, we combine these regional indices to calculate European indices. To determine if changes in regional dragonfly communities in Europe reflect climatic warming, we calculate Species Temperature Indices (STI), Multi-Species Indicators (MSI) and Community Temperature Indices (CTI). We hypothesise that (i) warm-dwelling species have more positive trends than cold-dwelling species, that, as a consequence, (ii) warm-dwelling species have increased their share in regional communities and (iii) that these effects increase on a south-north gradient through Europe, as the ratio of warm- and cold-dwelling species decreases with increasing latitude.

5.2 Methods

5.2.1 SPECIES RECORDS

We gathered dragonfly distribution records, from 1990 onwards, from the following European geographic regions (countries or lower administrative divisions, hereafter referred to as "regions"): Sweden, Britain (United Kingdom excluding Northern Ireland), the Netherlands, North Rhine-Westphalia (a German state), Bavaria (a German state), Flanders (a Belgian region, including Brussels region), Wallonia (a Belgian region), France, Andalusia (a Spanish autonomous community), and Cyprus (fig. 5.1). The resulting data set included records of 99 species, which equals 69% of all dragonfly species recorded in Europe (Kalkman et al., 2018).

FIG. 5.1: Participating European geographic regions, here considered as countries or lower administrative divisions.

All records used in this study cover adult dragonflies only. The majority of these records are 'opportunistic', i.e., collected without a standardised field protocol and without a design ensuring the geographical representativeness of sampled sites. The period of data coverage and the number of records per unit area vary considerably among regions, depending on data availability (appendix 5.1). All data in each region were validated by experts to prevent false positive records. To standardise the geographic reference system, all observations were mapped in the ETRS89/ETRS-LAEA (EPSG:3035) reference system. Because we used 1 × 1 km grid squares as the definition of a site in our analyses, all observations were referenced to 1 × 1 km ETRS-LAEA squares.

5.2.2 GENERATING NON-DETECTION DATA

Occupancy models require detection/non-detection data collected during replicated visits. Valid replicated visits are only those visits made in a period of closure within the year; this is the period during which a site is considered either to be occupied or unoccupied by the species and not abandoned or colonised (MacKenzie et al., 2006). For dragonflies, we considered the period of closure as the main flight period of a species. Closure periods were defined for each combination of species and region. For each combination, approximately 5% of both the earliest and the latest records were excluded, resulting in the species' main flight period. These main flight periods were expressed in Julian dates. For example, we used Julian dates 125-210 as the closure period of *Pyrrhosoma nymphula* (an early flying species) in France, and Julian dates 200-240 as the closure period of *Aeshna viridis* (a late flying species) in Sweden.

Almost all data obtained were records of species presence. The non-detection records of a given species were generated from the information of sightings of other dragonfly species, following Van Strien et al. (2010, Chapter 2 of this thesis) and Van Strien, et al. (2013). Any observation of a given species was taken as 1 (detection), whereas we rated 0 (non-detection) if any species other than the given species had been reported by an observer at a particular 1 × 1 km site and on a particular date within the species' closure period.

5.2.3 SPECIES TREND ANALYSIS

ANNUAL OCCUPANCY ESTIMATES AND TRENDS: REGIONAL LEVEL

First, we calculated annual occupancy per species, for each region separately. We applied the same dynamic occupancy model as Van Strien et al. (2010, Chapter 2 of this thesis), Van Strien et al. (2013) to estimate annual occupancy ψ, adjusted for detection probability p. Because all parameters in the model may differ between regions, the analyses were performed separately for each region and the regional results were combined in a second step. The description of the model is derived from Royle & Kéry (2007) and Royle & Dorazio (2008). Here, ψ is the proportion of suitable 1 × 1 km squares that is occupied. A square is defined as suitable if the species had been recorded there at least once in 1990-2008. The occupancy model consists of two hierarchically coupled submodels, one for occupancy and one for detection, the latter being conditional on the occupancy submodel. The occupancy submodel estimates annual probability of persistence φ_t and of colonisation γ_t and computes the annual occupancy probability per site recursively through:

$$\psi_{it} = \psi_{i,t-1}\,\varphi_{t-1} + (1 - \psi_{i,t-1})\gamma_{t-1}$$

Thus, whether site *i* occupied in year *t*-1 is still occupied in year *t* is determined by the persistence probability, and whether site *i* unoccupied in year *t*-1 is occupied in year *t* depends on the colonisation probability. All occupancy probabilities per site together yield the estimated annual number of occupied 1 × 1 km sites per region. The same sites were included in the analysis for all years; estimates for sites not surveyed during some years were derived from sites that were surveyed in those years.

The detection submodel estimates the yearly detection *p*, but in addition, *p* is made a function of covariates. We used the Julian date as a covariate for *p* because the detection of the species is expected to vary over the season, due to changing population size during the course of the flight period. Detection is also reduced if observers do not report all their sightings. Hence, we include the incompleteness of recording as a covariate for detection. We distinguished: (1) single records of any species on one site and date without records of other species, (2) short day-lists, i.e. records of two or three species made by a single observer on one site and date, and (3) comprehensive day-lists, i.e., records of more than three species per observer, site and date. These lists may or may not include the species in question. These category thresholds are sufficiently low not to be confounded by real differences in species number between sites. In most 1 × 1 km sites in the regions there are more than three species to be found and often many more. Effects of both covariates were included in the detection submodel via a logit link:

$$\text{logit}(p_{ijt}) = \alpha_t + \beta_1 * \text{date}_{ijt} + \beta_2 * \text{date}_{ijt}^2 + \delta_1 * (\text{short day-list})_{ijt} + \delta_2 * (\text{comprehensive day-list})_{ijt},$$

where p_{ijt} is the probability to detect the species at site *i* during visit *j* in year *t*, αt is the annual intercept implemented as a random effect, β_1 and β_2 are the linear and quadratic effects of the date of visit *j* and δ_1 and δ_2 are the effects of short day-lists and comprehensive day-lists, relative to single records.

We fitted the models in a Bayesian mode of inference using JAGS (Plummer, 2017) on the computer cluster LISA (https://www.surf.nl/en). We chose uninformative priors for all parameters, using uniform distributions with values between 0 and

1 for all parameters except δ_1 and δ_2 (values between -10 and 10), β_1, β_2 (values between -10 and 10) and α_t (values between 0 and 5) for the standard deviation of the normal distribution used as prior for the random year effect.

For each analysis, we ran three Markov chains with sufficient iterations to ensure convergence as judged from the Gelman-Rubin Rhat statistic and saved the last 93 iterations for use at supraregional level. This number of iterations is an empirically obtained compromise between the reliability of the estimates and data handling capacity. The model produced annual estimates of occupancy per region, which were converted into annual indices with first year = 100. The trend in occupancy was considered significant if its confidence interval did not include zero.

ANNUAL OCCUPANCY ESTIMATES AND TRENDS: EUROPEAN LEVEL

In the next step, the annual occupancy estimates per region were aggregated to obtain European occupancy indices and trends for the period 1990-2015. Missing yearly values from a particular region were estimated ('imputed') from averaged year-to-year occupancy ratios in all other regions. For example, 1990 was missing in the Swedish data set. To impute occupancy estimates of Swedish species, we applied the 1991/1990 ratios from all other regions with data from both years. As a consequence of these imputations, confidence intervals increased for years with lacking data from one or more regions, especially when these were large regions (e.g. France).

Regions differ in the number of sites surveyed, so a naive aggregation has the risk of biased European trends. Hence, we developed a procedure to weigh regions according to the sampling intensity in relation to the range of species in each region. This procedure is an adaptation of procedures applied by Van Swaay et al. (2002) and Gregory et al. (2005). Weights were calculated as the quotient of relative range and relative sampling intensity to compensate for oversampling and undersampling. Relative range was defined as the range of a species in a region, as a percentage of its total range in all regions for which an occupancy index could be obtained. Relative sampling intensity was defined as the number of 1 × 1 km squares surveyed at least once in this period within the regional range of the species, relative to the total number of surveyed squares in all regions with indices. Weights per region were similar for each year because the same sites were in the analysis for all years. The weighted numbers of occupied sites were added across regions and converted into European annual indices with 1990 = 100. We took into account the uncertainty of the estimated number of occupied sites per region by adding the number of sites estimated per region for each of the saved 93 iterations and then combining the results of all iterations.

5.2.4 SPECIES TEMPERATURE INDICES

We calculated the Species Temperature Index (STI) for each dragonfly species occurring in Europe (Boudot & Kalkman, 2015). The STI of a given species is the average temperature (expressed in degrees Celsius) of the European part (excluding Russia) of the species' range and is taken as a proxy for species' dependence on temperature. These calculations were based on 2,736 sites with species records underlying the range maps of the European atlas by Boudot & Kalkman (2015; available through Kalkman et al. (2018)) and climate data of WorldClim (http://www.worldclim.org/); accessed March 2017; average monthly temperatures for 1960-1990). The analyses were carried out at a 50 x 50 km grid scale. For each grid square, we calculated the annual mean temperature to estimate the STI as the mean temperature of occupied squares. Although the distribution data covered Europe to a great extent, we found it necessary to correct for differences in sampling intensity between regions. This was achieved by bootstrapping, which consisted of 100 replications of a subset of randomly chosen 50 x 50 grid squares within an area of 250 x 250 km. STI's were estimated as the mean temperature of all occupied squares over all replications.

The period covered by the temperature data from WorldClim (1960-1990) differed from the period covered by the atlas' range maps (> 1990). However, relative differences in STI among species are robust to the time-window considered (Devictor et al., 2012b).

5.2.5 MULTI-SPECIES INDICATORS

To determine whether warm-dwelling species have more positive trends than cold-dwelling species, we calculated Multi-species Indicators (MSI), by combining the trends in occupancy indices of cold-dwelling and of warm-dwelling species respectively. We did this for each region separately and for Europe as a whole. Cold-dwelling species were defined as species with STI lower than 9.8 °C. which is the median STI of all species included in our study. Warm-dwelling species were defined as species with STI > 9.8 °C. Standard deviations of STI did not differ between the two groups (one-way ANOVA, $F(1, 97) = 0.554$, $p = 0.458$).

MSI were calculated including their confidence intervals, using the R script 'MSI-tool' (Soldaat et al., 2017). This method is developed to account for sampling error of species indices in the calculation of multi-species indicators, by calculating confidence intervals using Monte Carlo simulations of annual species indices.

5.2.6 COMMUNITY TEMPERATURE INDICES

Ultimately, we calculated a Community Temperature Index (CTI) for each region, as the average STI of all species in the region, weighted by species occupancies (probabilities of occurrence). CTI is thus expressed in degrees Celsius. Similarly, we calculated European CTI. A temporal increase in CTI directly reflects that the species assemblage is increasingly composed of species that occur at higher temperatures (that is with high STI). With this approach, we follow Devictor et al. (2012a), with the principal difference that we focus on regional communities based on occupancy data from km-squares, instead of local communities based on abundance data from transects (although Devictor et al. (2012a) also included an analysis on presence-absence data which compares with our approach).

5.3 Results

5.3.1 OCCUPANCY INDICES AND TRENDS

The number of species for which a regional trend could be calculated with sufficiently low standard errors, i.e. standard errors low enough to detect a 5% or higher annual increase or decline, ranged from five for Cyprus to 79 for France (table 5.1). In total, we were able to calculate trends with sufficiently low standard errors for 90 of 99 species in our data set, for at least one of the regions (see online Supporting Information for results per region per species: https://doi.org/10.1111/ddi.12913).

In 7 out of 10 regions, more species increased than decreased their occupied range (table 5.1). These regions were Sweden, Britain, the Netherlands, North Rhine-Westphalia, Flanders, Wallonia, and France. No significant difference between increasing and declining species was found for Bavaria, because this region had a high number of stable species (36 of 59 species trends with sufficiently low standard errors). For Andalusia and Cyprus, the number of species trends with sufficiently low standard errors was too small to find significant differences between trend classes.

For all regions combined, 55 species moderately increased in occupancy, indicating that they expanded their distribution at a European level, 32 species remained stable and none declined. As an example, indices of *Sympecma fusca* (a moderately increasing species), and *Gomphus vulgatissimus* (a stable species) are shown in fig. 5.2. Trend estimates of 12 species had too large standard errors. European indices and trends of all species are provided in Appendix 5.2.

5.3.2 SPECIES TEMPERATURE INDICES (STI)

STI ranged from 2.0 °C for the boreo-alpine species *Aeshna caerulea* to 18.3 °C for the Mediterranean (and African) species *Trithemis arteriosa*. (Mean = 9.8 °C; SD = 3.3 °C) (appendix 5.3).

TABLE 5.1: Number of species per trend class per geographic region (from north to south), and for Europe. $\chi2$ = value of Chi-squared test; *p* = probability value. Increase = significant increase ($p < 0.05$); Stable = no significant change; Decline = significant decline ($p < 0.05$); Uncertain = no significant change and standard errors too large to detect a 5% trend if it had occurred.

Region	Trend period	N species	Increase	Stable	Decline	Uncertain	% Increase	$\chi2$	p
Sweden	1991-2014	64	47	1	0	16	73.4	47.0	<0.001
Britain	1980-2012	50	26	12	2	10	52.0	20.6	<0.001
Netherlands	1991-2015	68	39	10	7	12	57.4	22.3	<0.001
North Rhine-Westphalia	1990-2010	67	21	15	0	31	31.3	21.0	<0.001
Flanders	1990-2015	62	27	17	7	11	43.5	11.8	<0.001
Wallonia	1990-2015	65	26	25	0	14	40.0	26.0	<0.001
Bavaria	1990-2013	73	8	36	15	14	11.0	2.1	0.144
France	1990-2012	87	30	45	4	8	34.5	19.9	<0.001
Andalusia	2006-2015	57	1	5	0	51	1.8	NA	NA
Cyprus	2006-2015	35	3	2	0	30	8.6	NA	NA
Europe	1990-2015	99	55	32	0	12	55.6	55.0	<0.001

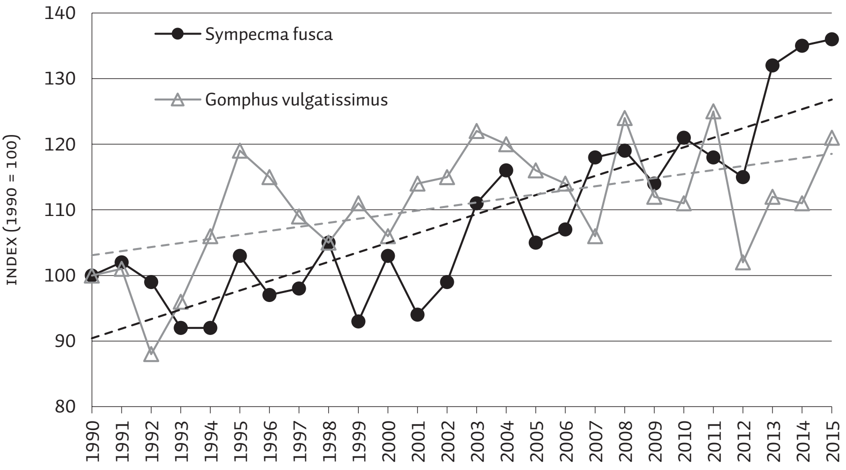


FIG. 5.2: European index (1990-2015) of *Sympecma fusca* and *Gomphus vulgatissimus*. Linear regression lines (dashed lines) were aligned through the year effects to summarise overall change.

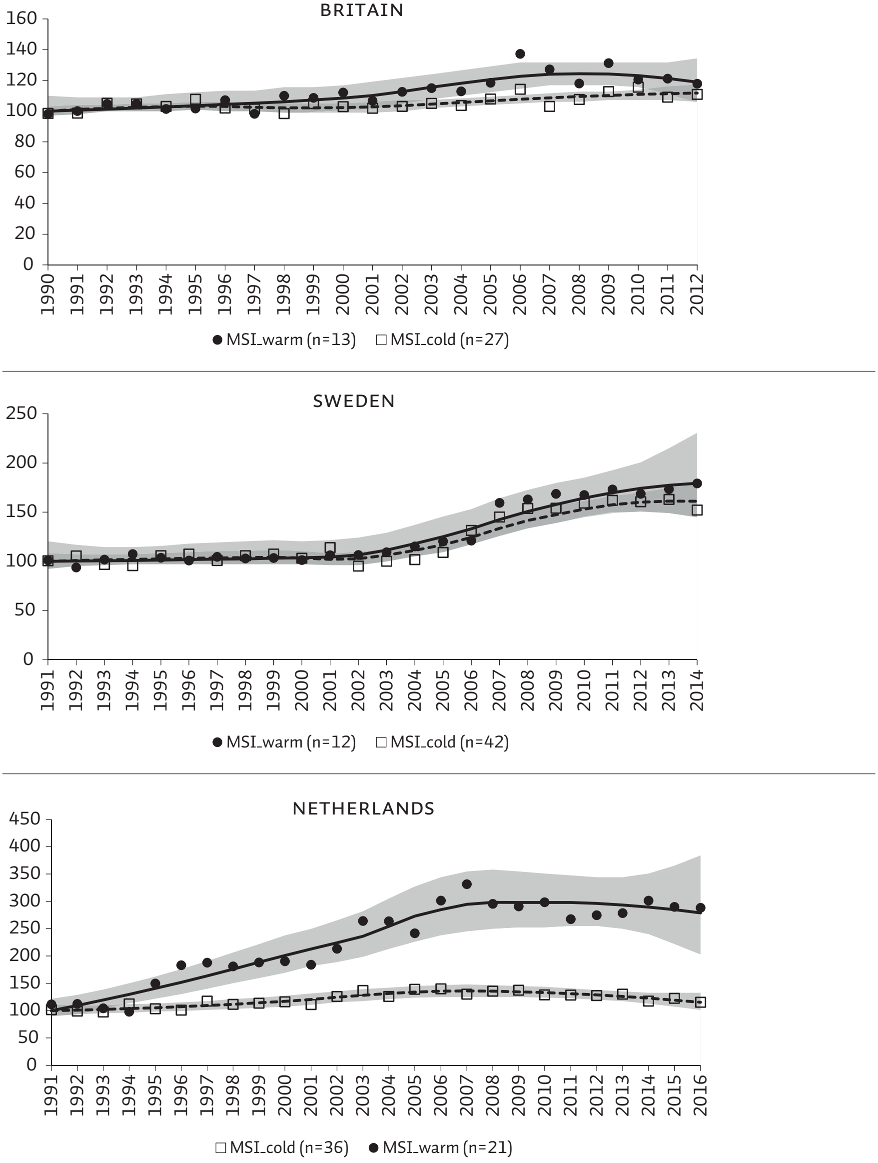
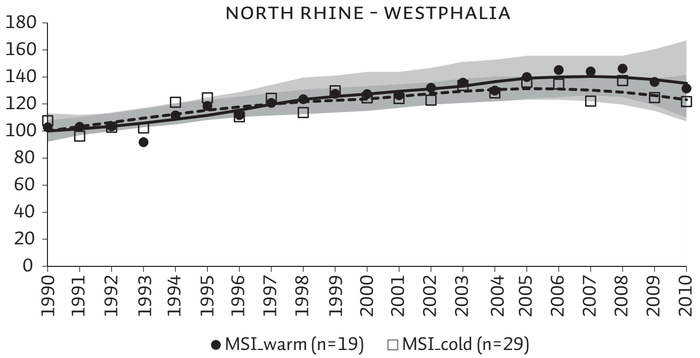
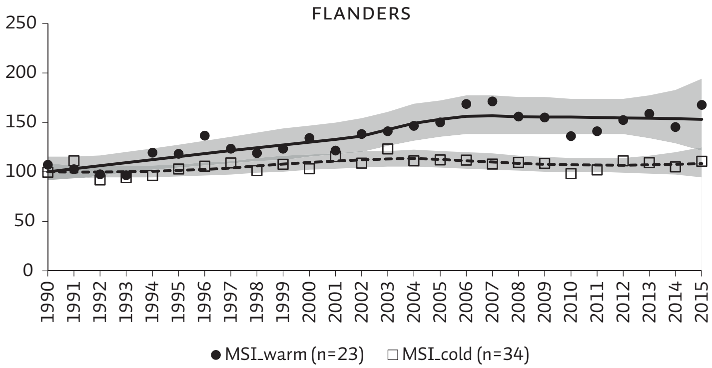


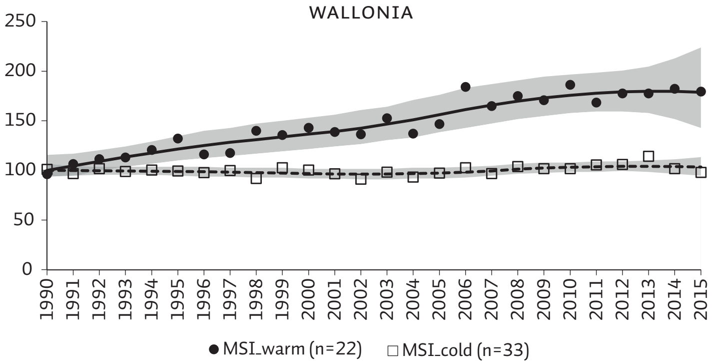
FIG. 5.3: Multi-species Indices (MSI) of warm-dwelling species (Species Temperature Index >9.8°C) and cold-dwelling species (Species Temperature Index <9.8 °C) per geographic region (from north to south), and for Europe. The first year with data was set to 100. Smoothed trend lines were plotted through the year effects to summarise overall change. Shaded areas represent confidence intervals. Please note that Y-axes differ.



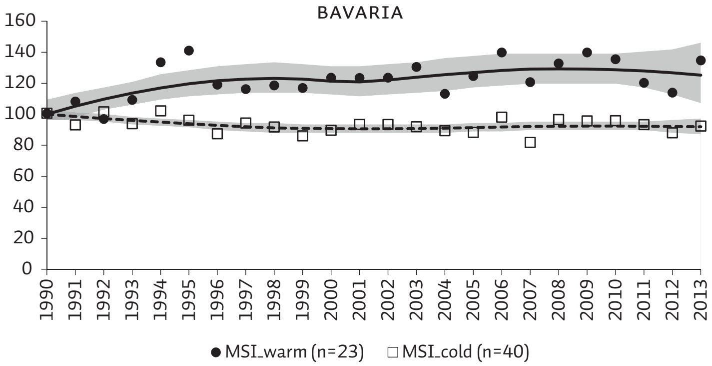
NORTH RHINE - WESTPHALIA



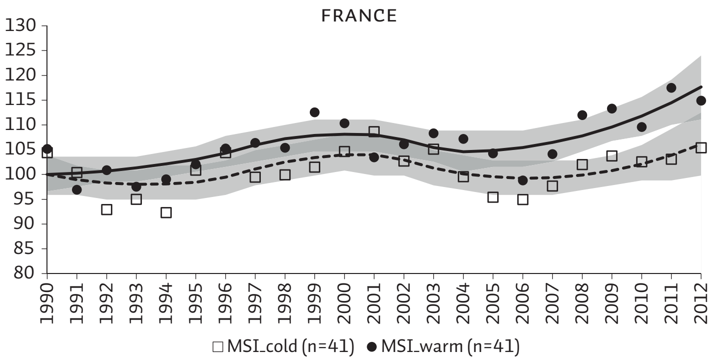
FLANDERS



WALLONIA



BAVARIA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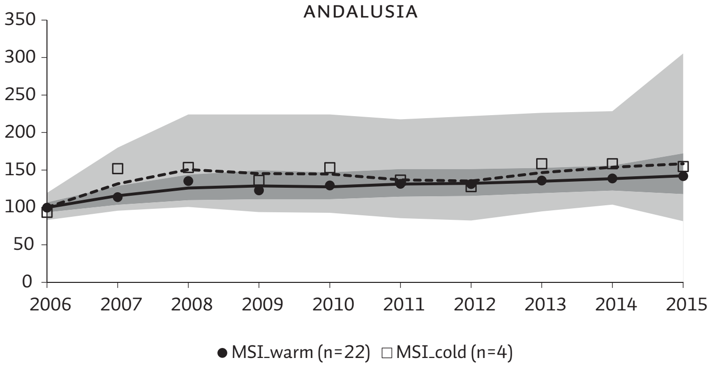
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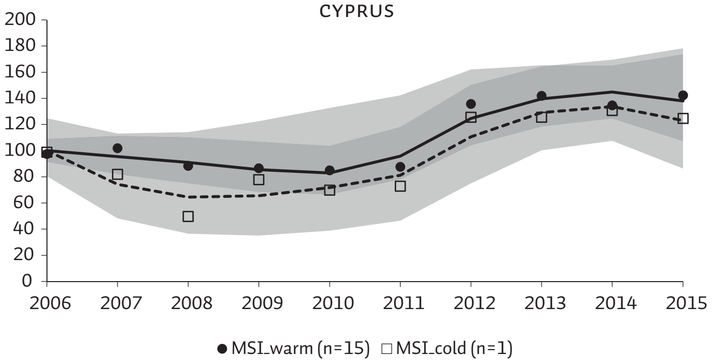
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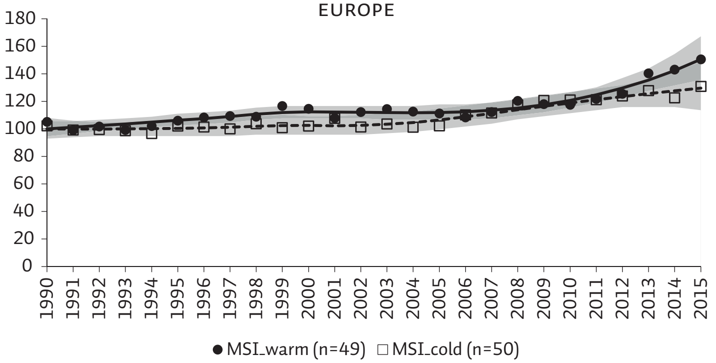
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● MSI_warm (n=49) □ MSI_cold (n=50)

TABLE 5.2: Multi-species Indicator (MSI) trends of cold-dwelling species (Species Temperature Index <9.8°C) and warm-dwelling species (Species Temperature Index >9.8 °C) per geographic region (from north to south), and for Europe. *SE* = standard error; *p* = probability value. Moderate increase = significant increase ≤5% ($p < 0.05$); stable = no significant change; moderate decline = significant decline ≤5% ($p < 0.05$); uncertain = no significant change and standard errors too large to detect a 5% trend if it had occurred.

Region	Trend period	N species	MSI trend ± SE	Classification	p
Sweden cold	1991-2014	42	1.025 ± 0.002	moderate increase	0.177
Sweden warm	1991-2014	12	1.030 ± 0.005	moderate increase	
Britain cold	1990-2012	27	1.005 ± 0.001	moderate increase	0.013
Britain warm	1990-2012	13	1.012 ± 0.003	moderate increase	
Netherlands cold	1991-2015	36	1.010 ± 0.003	moderate increase	<0.001
Netherlands warm	1991-2015	21	1.044 ± 0.006	moderate increase	
North Rhine-Westphalia cold	1990-2010	29	1.012 ± 0.003	moderate increase	0.115
North Rhine-Westphalia warm	1990-2010	19	1.019 ± 0.005	moderate increase	
Flanders cold	1990-2015	34	1.003 ± 0.002	stable	<0.001
Flanders warm	1990-2015	23	1.019 ± 0.004	moderate increase	
Wallonia cold	1990-2015	33	1.002 ± 0.002	stable	<0.001
Wallonia warm	1990-2015	22	1.024 ± 0.004	moderate increase	
Bavaria cold	1990-2013	40	0.998 ± 0.001	moderate decline	<0.001
Bavaria warm	1990-2013	23	1.008 ± 0.003	moderate increase	
France cold	1990-2012	41	1.002 ± 0.001	stable	0.017
France warm	1990-2012	41	1.005 ± 0.001	moderate increase	
Andalusia cold	2006-2015	4	1.029 ± 0.034	uncertain	0.489
Andalusia warm	2006-2015	22	1.030 ± 0.011	moderate increase	
Cyprus cold	2006-2015	1	1.072 ± 0.030	moderate increase	0.694
Cyprus warm	2006-2015	15	1.055 ± 0.015	moderate increase	
Europe cold	1990-2015	50	1.011 ± 0.002	moderate increase	0.362
Europe warm	1990-2015	49	1.012 ± 0.002	moderate increase	

5.3.3 MULTI-SPECIES INDICATORS (MSI)

MSI of warm-dwelling species were increasing in all regions (fig. 5.3). Surprisingly, MSI of cold-dwelling species also increased in Sweden, Britain, the Netherlands and North Rhine-Westphalia. In Flanders, Wallonia and France, MSI of cold-dwelling species was stable, in Bavaria it declined, and in Andalusia it was uncertain (table 5.2). Cyprus has only one cold-dwelling species (*Enallagma cyathigerum*), which increased.

Comparing MSI trends of warm-dwelling and cold-dwelling species (table 5.2) shows the former was significantly more positive in Britain, the Netherlands, Flanders, Wallonia, Bavaria and France. At a European level, however, the MSI of warm-dwelling and cold-dwelling species both increased at a similar rate.

5.3.4 COMMUNITY TEMPERATURE INDICES (CTI)

CTI increased in all regions, except Cyprus (table 5.3; appendix 5.4). The most significantly increasing CTI was found for the Netherlands. The Dutch dragonfly fauna 'warmed' at 9.5 × 10-3 °C y^{-1} over the period 1991-2015 (0.23 °C over the whole period). The weakest increase was found for Britain, at 1.2 × 10-3 °C y^{-1} over the period 1990-2015 (0.03 °C over the whole period). The European CTI increased just as slowly, at 1.2 × 10-3 °C y^{-1} over the period 1990-2015 (0.03 °C over the whole period).

TABLE 5.3: Slope of Community Temperature index (CTI) per geographic region (from north to south), and for Europe. *SE* = standard error; *p* = probability value.

Region	**Trend period**	**CTI slope**	**SE**	**p**
Sweden	1991-2014	2.6 × 10^{-3}	1.5 × 10^{-3}	0.110
Britain	1990-2012	1.2 × 10^{-3}	0.5 × 10^{-3}	0.017
Netherlands	1991-2015	9.5 × 10^{-3}	1.1 × 10^{-3}	<0.001
North Rhine-Westphalia	1990-2010	2.0 × 10^{-3}	0.8 × 10^{-3}	0.025
Flanders	1990-2015	5.4 × 10^{-3}	1.0 × 10^{-3}	<0.001
Wallonia	1990-2015	4.3 × 10^{-3}	0.8 × 10^{-3}	<0.001
Bavaria	1990-2013	1.7 × 10^{-3}	0.7 × 10^{-3}	0.028
France	1990-2012	1.3 × 10^{-3}	0.4 × 10^{-3}	0.011
Andalusia	2006-2015	8.8 × 10^{-3}	8.3 × 10^{-3}	0.325
Cyprus	2006-2015	-26.7 × 10^{-3}	9.5 × 10^{-3}	0.023
Europe	1990-2015	1.2 × 10^{-3}	0.5 × 10^{-3}	0.019

5.4 Discussion

We found clear effects of climate change on several warm-dwelling species, consistent with observed changes in European distributions in the last few decades (Boudot & Kalkman, 2015). In addition, the differences in MSI of warm-dwelling and cold-dwelling species indicate that climate change has changed dragonfly occurrence at the community level as well.

5.4.1 TESTING OF HYPOTHESES

REGIONAL LEVEL

We hypothesised that (i) warm-dwelling species show more positive trends than cold-dwelling species and this was confirmed for 6 of 10 studied regions (Bavaria, Britain, Flanders, France, Netherlands, Wallonia). In Sweden – the most northern region in our study – both MSI of cold-dwelling species and MSI of warm-dwelling species were stable between 1990 and 2001 and both increased in a comparable pace from 2002 onward. This suggests that climatic conditions in the 1990s were probably limiting for most species in Sweden, including cold-dwelling species. With the exception of some extreme cold-tolerant species, such as *A. caerulea* and *Somatochlora sahlbergii*, all Swedish species reach their northern range limit in this region. Recent temperature rises thus appear to have resulted in improved conditions for nearly all species. Furthermore, we expected that (ii) warm-dwelling species had increased their share in regional communities. This was confirmed for all regions except Cyprus, where only one cold-dwelling species occurs. However, with an increasing CTI of 1.2×10^{-3} °C y^{-1} on average, up to 9.5 × 10-3 °C y^{-1} for the Netherlands (table 5.3), this 'warming' of regional communities evolves more slowly than the increase of temperature itself (1.1×10^{-2} °C y^{-1}, after correcting for the difference in latitudinal gradient between CTI and actual temperature; Devictor et al., 2012a), but the difference for the Netherlands is minimal. Thus, dragonflies in Europe are accumulating a substantial 'climatic debt', i.e. the difference between shifts in temperature and shifts in distribution (Devictor et al., 2012a; Menéndez et al., 2006), which varies between regions. Ultimately, our hypothesis that (iii) trends in regional CTI increase on a south-north gradient through Europe is rejected. Highest CTI increases were found for regions on a moderate latitude (the Netherlands, Flanders, Wallonia), and for Andalusia (although measured over a shorter time span), while lowest CTI increases were found for Britain, France and Bavaria. Regions differ in size and subsequently in latitudinal gradient. This may, in theory, affect regional occupancy trends (and thus regional CTI trends) to some extent, possibly limiting the validity of a comparison at the regional level. Calculating CTI across equally sized latitudinal bands would be a preferable approach, but requires a higher data density in some of our regions than is currently available. The MSI trends of cold-dwelling and warm-dwelling species (table 5.2) do not show a structural difference between larger and smaller regions indicating that it is unlikely that CTI trend differences are confounded by differences in region size.

EUROPEAN LEVEL

At European level, MSI of warm-dwelling and cold-dwelling species were similar, both having a slightly positive trend. At community level though, the increase in European CTI of 1.2 × 10^{-3} °C y^{-1} shows that warm-dwelling species have slightly increased their share. To compare this outcome with the trends in CTI of European birds and butterflies (provided by Devictor et al. (2012a), as based on presence-absence data) we re-calculated the European CTI of dragonflies for the same period 1990-2008. Over these 18 years CTI of European dragonflies increased with 2.4 × 10^{-3} °C y^{-1}, which is comparable with the increase in CTI of European butterflies (2.5 × 10^{-3} °C y^{-1}) and considerably greater than the increase in CTI of European birds (1.9 × 10^{-3} °C y^{-1}). This is in line with the well-known ability of dragonflies to quickly colonise new habitats (Corbet, 1999). Dragonflies should probably be considered as more dispersive than butterflies, which, for their part, may show a quicker community response at a local scale, due to their generally shorter life cycle. The net outcome of these opposing differences may have resulted in a similar CTI trend between dragonflies and butterflies. The slower response of bird communities to climatic warming has been suggested by Devictor et al. (2012a) to be a consequence of their slower population turnover.

In conclusion, climate change has a considerable positive impact on the occurrence of dragonflies in several European regions. However, at a continental scale, CTI's are changing only slowly so far, due to the relatively positive response of cold-dwelling species.

LIMITATIONS OF CTI

Several authors have highlighted the CTI as a useful tool for assessing the effect of climate change on the composition of communities (Devictor et al., 2008; Lindström et al., 2013; Roth et al., 2014). However, our results show that a stable CTI does not necessarily mean that climate change is not affecting the occurrence of species. In Sweden, many dragonfly species have benefited from climate warming, including species of cool conditions. This has led to increasing MSI trends for both warm-dwelling and cold-dwelling species, while leaving CTI almost unaffected. We therefore recommend a reviewing of CTI in relation to MSI of warm-dwelling and cold-dwelling species, especially in high-latitude regions where temperatures may have limited species with low STI as well as high STI. In addition, we know that many dragonfly species have substantially expanded their range northwards (Boudot & Kalkman, 2015; Hickling et al., 2005; Ott, 2010). Dragonfly communities have changed as a result of these expansions, yet this is masked by an increase in other species resulting in a quite stable CTI. E.g. it is likely that the reduction of organic pollution and nutrient input in the last quarter of the 20th century has compensated the effects of increasing temperature for species that are sensitive to low oxygen levels (Ketelaar, 2010; Termaat et al., 2015, Chapter 4 of this thesis). These limitations of CTI as an indicator of climate change are also relevant when calculations are based on local abundances instead of regional distributions, even though CTI trends based on abundances show a stronger response to climate change than when based on occupancy (Lindstrom et al., 2013; Virkkala & Lehikoinen, 2014).

THREATS OF CLIMATE CHANGE

We were able to calculate European trends in occupancy for 87 species (88% of species occurring in our data set). Fifty-five of these species have increased from 1990 to 2015, while 32 have remained stable and none have declined. This is a remarkably positive outcome, given the fact that the conservation status of many freshwater organisms is known to have deteriorated globally (Collen et al., 2014; Dudgeon et al., 2006). Although we recognise that some species with a stable trend in occupancy (distribution) may have declined in abundance (population size), we consider it unlikely that this would change the overall picture of range expansion, given that occupancy and population trends show broad similarity (Van Strien et al., 2010). Next to the positive effects of climate change for warm-dwelling species, recent improvements in water quality and the execution of wetland restoration projects are likely to have contributed to the recovery of dragonflies in at least some of the regions (Parkinson et al., 2017; Termaat et al., 2015, Chapter 4 of this thesis).

Jaeschke et al. (2013) combined climate scenarios with the assumed dispersal abilities of six species, to predict changes in their European distributions by 2035. Their model predicted a strong decline for five species (*Coenagrion mercuriale*, -50%; *C. ornatum*, -67%; *Leucorrhinia albifrons*, -39%; *L. caudalis*, -58%; *Ophiogomphus cecilia*, -24%) and an increase for one species (*L. pectoralis*, +21%). These predictions are in sharp contrast with the results of our study over the period 1990-2015, as we found stable trends in European occupancy for *C. mercuriale*, *L. caudalis* and *O. cecilia*, and increasing trends for *C. ornatum*, *L. albifrons* and *L. pectoralis* (appendix 5.2). We explain these differences by the estimations of maximum species dispersal abilities applied by Jaeschke et al. (2013). They used the observed maximum dispersal distances mentioned in the literature, which refer to observations from capture-mark-recapture studies. These studies may give an estimation of distances covered by the majority of the studied population, but undoubtedly miss dispersal events by individuals over much longer distances (see also Suhling et al., 2017), leading to a severe underestimation of maximum dispersal abilities. These extreme dispersal events may be rare and seldom noticed, but they determine the pace at which species distributions may expand. Next to annual estimates of occupancy, occupancy models also provide annual estimates of persistence and colonisation. These parameters may be more informative for future research on the effect of variation in species' dispersal abilities.

The notion that European dragonflies are generally doing rather well and do not appear to be greatly harmed by climate change, does not apply to all species, nor to all regions. Some species, such as the arctic *Somatochlora sahlbergi* and the alpine *S. alpestris*, are in a 'dead end street', as they cannot shift their range further north or to a higher altitude (De Knijf et al., 2011). Other cold-dwelling species, such as *Coenagrion hastulatum*, are doing well in Sweden, while being threatened in more southern regions. Furthermore, indirect effects of climate change may affect dragonflies. Desiccation of habitats such as small streams and ponds is a threat to several species (Kalkman et al., 2010; Kalkman et al., 2018), especially in southern Europe, which is an underrepresented region in our study. Also, changes in communities in central and northern Europe may lead to more interspecific competition between dragonfly species, possibly threatening individual species in the future. Ultimately, dragonflies across Europe face multiple threats other than climate change, such as habitat degradation and destruction, eutrophication (Kalkman et al., 2010) and exposure to pesticides (Jinguji et al., 2013; Van Dijk et al., 2013). The relative contribution of these different environmental changes largely remains to be established.

5.4.2 TRENDS FROM DISTRIBUTION DATA

We based our trend calculations on readily available distribution data from ten European regions, using occupancy models to account for imperfect detection. These records allowed us to assess occupancy indices without the need of a standardised fieldwork programme. As such, our method immediately informs about distribution trends and may serve as an 'early warning system' for species with a deteriorating conservation status and, by proxy, the quality of freshwater habitats (Oertli, 2008). However, our study lacks data from eastern Europe and we have insufficient data from southern Europe to adequately represent that area. Unfortunately, 18 out of 19 dragonfly species considered to be threatened at European level are confined to southern or eastern Europe (Kalkman et al., 2018). Considering this, our European indices and trends may be biased to some degree at pan-European level. However, dragonfly data sets are rapidly growing in many countries, including several eastern and southern European countries (Boudot & Kalkman, 2015). Moreover, a network of European odonatologists has expanded over the past few years and the usefulness of a European dragonfly monitoring scheme is gaining attention. We are therefore confident that European indices will become more robust with future updates, and will have a better geographic coverage.

5.4.3 FUTURE PROSPECTS

Overall, this study has shown that dragonflies present a suitable species group to gain better understanding of biodiversity changes and their causes, including climate change, and that suitable data needed for these analyses are becoming available. Dragonflies may therefore satisfy the need for a biodiversity indicator based on freshwater invertebrates (Feest, 2013). They are likely to represent other taxa which are primarily warm-adapted. Using opportunistic data analysed with occupancy models enables the assessment of species' distribution trends on both regional and European scale. These trends inform about the state of freshwater habitats, which is urgently required (Darwall et al., 2018). Hence, we suggest adding dragonflies as an indicator group to the European biodiversity monitoring programme (European Environmental Agency, 2012), to invest in the extension of a European dragonfly recording network, and to encourage the centralisation of European dragonfly distribution data.

Acknowledgements

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DATA ACCESSIBILITY

Aggregated data used for species' occupancy modelling are available from Dutch Butterfly Conservation (http://www.vlinderstichting.nl/). Climate data used for calculation of Species Temperature Indices are available from http://www.worldclim.org/.

References

Bertrand R., Lenoir J., Piedallu C., Riofrío-Dillon G., de Ruffray P., … & Gégout. J.-C. (2011). Changes in plant community composition lag behind climate warming in lowland forests. *Nature* 479: 517–520.

Boudot J.P. & Kalkman V.J. (editors) (2015). *Atlas of the European dragonflies and damselflies*. KNNV Publishing, Zeist.

Britton A.J., Beale C.M., Towers W. & Hewison R.L. (2009). Biodiversity gains and losses: evidence for homogenisation of Scottish alpine vegetation. *Biological conservation* 142: 1728-1739.

Bush A., Theischinger G., Nipperess D., Turak E., & Hughes L. (2013). Dragonflies: climate canaries for river management. *Diversity and Distributions* 19: 86-97.

Chen I.C., Hill J.K., Ohlemüller R., Roy D.B. & Thomas C.D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science* 333: 1024-1026.

Clavero M., Villero D., & Brotons L. (2011). Climate change or land use dynamics: do we know what climate change indicators indicate? *PLoS ONE* 6: e18581.

Collen B., Whitton F., Dyer E.E., Baillie J.E., Cumberlidge N., … & Böhm. M. (2014). Global patterns of freshwater species diversity, threat and endemism. *Global Ecology and Biogeography* 23: 40-51.

Corbet. P.S. (1999). *Dragonflies: behaviour and ecology of Odonata*. Harley Books, Colchester.

Darwall W., Bremerich V., De Wever A., Dell A.I., Freyhof J., … & Weyl O. (2018). The Alliance for Freshwater Life: A global call to unite efforts for freshwater biodiversity science and conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems* 28: 1015-1022.

Davey C.M., Devictor V., Jonzén N., Lindström Å. & Smith H. G. (2013). Impact of climate change on communities: revealing species’ contribution. *Journal of Animal Ecology* 82: 551-561.

De Knijf G., Flenker U., Vanappelghem C., Manci C.O., Kalkman V.J. & Demolder H. (2011). The status of two boreo-alpine species, *Somatochlora alpestris* and *S. arctica*, in Romania and their vulnerability to the impact of climate change (Odonata: Corduliidae). *International Journal of Odonatology* 14: 111-126.

Devictor V., Julliard R., Couvet D. & Jiguet F. (2008). Birds are tracking climate warming, but not fast enough. *Proceedings of the Royal Society of London B: Biological Sciences* 275: 2743-2748.

Devictor V., Van Swaay C., Brereton T., Chamberlain D., Heliölä J., … & Jiguet. F. (2012a). Differences in the climatic debts of birds and butterflies at a continental scale. *Nature climate change* 2: 121-124.

Devictor V., Van Swaay C., Brereton T., Chamberlain D., Heliölä J., … & Jiguet. F. (2012b). Reply to Rodriguez-Sanchez et al. *Nature Climate Change* 2: 638–639.

Dijkstra K.D.B., Monaghan M.T. & Pauls S.U. (2014). Freshwater Biodiversity and Aquatic Insect Diversification. *Annual Review of Entomology* 59: 143–63.

Dudgeon D., Arthington A.H., Gessner M.O., Kawabata Z.I., Knowler D.J., … & Sullivan C. A. (2006). Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological reviews* 81: 163-182.

European Environmental Agency (2012). *Streamlining European biodiversity indicators 2020: Building a future on lessons learnt from the SEBI 2010 process*. EEA Technical report No. 11/2012, Copenhagen.

Feest A. (2013). The utility of the Streamlining European Biodiversity Indicators 2010 (SEBI 2010). *Ecological Indicators* 28: 16-21.

Franco A.M.A., Hill J.K., Kitschke C., Collingham Y.C., Roy D.B., … & Thomas. C.D. (2006). Impacts of climate warming and habitat loss on extinctions at species' low-latitude range boundaries. *Global Change Biology* 12: 1545-1553.

Gregory R.D., van Strien A., Vorisek P., Gmelig Meyling A.W., Noble D.G., … & Gibbons D.W. (2005). Developing indicators for European birds. *Philosophical Transactions of the Royal Society B* 360: 269–288.

Hassall C. (2015). Odonata as candidate macroecological barometers for global climate change. *Freshwater Science* 34: 1040-1049.

Hickling R., Roy D.B., Hill J.K., Fox R. & Thomas C.D. (2006). The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology* 12: 450-455.

Hickling R., Roy D.B., Hill J.K. & Thomas C.D. (2005). A northward shift of range margins in British Odonata. *Global Change Biology* 11: 502-506.

Isaac N.J.B., van Strien A.J., August T.A., de Zeeuw M.P. & Roy D.B. (2014). Statistics for citizen science: extracting signals of change from noisy ecological data. *Methods in Ecology and Evolution* 5: 1052-1060.

Jaeschke A., Bittner T., Reineking B. & Beierkuhnlein C. (2013). Can they keep up with climate change? – Integrating specific dispersal abilities of protected Odonata in species distribution modelling. *Insect Conservation and Diversity* 6: 93-103.

Jiguet F., Devictor V., Ottvall R., van Turnhout C., van der Jeugd H. & Lindström Å. (2010). Bird population trends are linearly affected by climate change along species thermal ranges. *Proceedings of the Royal Society of London B: Biological Sciences* 277: 3601-3608.

Jinguji H., Thuyet D.Q., Uéda T. & Watanabe H. (2013). Effect of imidacloprid and fipronil pesticide application on *Sympetrum infuscatum* (Libellulidae: Odonata) larvae and adults. *Paddy and Water Environment* 11: 277-284.

Kalkman V.J., Boudot J.-P., Bernard R., Conze K.-J., De Knijf G., … & Sahlén G. (2010). *European Red List of dragonflies*. Publications Office of the European Union, Luxembourg.

Kalkman V.J., Boudot J.P., Bernard R., De Knijf G., Suhling F. & Termaat T. (2018). Diversity and conservation of European dragonflies and damselflies (Odonata). *Hydrobiologia* 811: 269-282.

Kampichler C., van Turnhout C.A.M., Devictor V. & van der Jeugd H.P. (2012). Large-scale changes in community composition: determining land use and climate change signals. *PLoS ONE* 7: e35272.

Kéry M. (2010). *Introduction to WinBUGS for ecologists: a Bayesian approach to regression, ANOVA, mixed models and related analyses*. Academic Press, Burlington.

Ketelaar R. (2010). Recovery and further protection of rheophilic Odonata in the Netherlands and North Rhine-Westphalia. *Brachytron* 12: 38-49.

Lindström A., Green M., Paulson G., Smith H.G. & Devictor V. (2013). Rapid changes in bird community composition at multiple temporal and spatial scales in response to recent climate change. *Ecography* 36: 313–322.

MacKenzie D.I., Nichols J.D., Royle J.A., Pollock K.H., Hines J.E. & Bailey L.L. (2006). *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*. Elsevier, San Diego.

Mason S.C., Palmer G., Fox R., Gillings S., Hill J.K., … & Oliver T.H. (2015). Geographical range margins of many taxonomic groups continue to shift polewards. *Biological Journal of the Linnean Society* 115: 586–597.

Menéndez R., Megías A.G., Hill J.K., Braschler B., Willis S.G., … & Thomas C.D. (2006). Species richness changes lag behind climate change. *Proceedings of the Royal Society of London B: Biological Sciences* 273: 1465-1470.

Oertli B. (2008). The use of dragonflies in the assessment and monitoring of aquatic habitats. In Córdoba-Aquilar A. (editor), *Dragonflies and Damselflies: Model Organisms for Ecological and Evolutionary Research* (pp. 79–95). Oxford University Press, Oxford.

Ott J. (2010). The big trek northwards: recent changes in the European dragonfly fauna. In: Settele J., Penev L.D., Geogiev T.A., Grabaum R., Grobelink. V., … & Kühn I. (editors), *Atlas of Biodiversity Risk* (pp. 82–83). Pensoft Publishers, Sofia.

Parkinson D., Goffart P., Kever D., Motte G. & Schott O. (2017). Réponse des odonates à la restauration des tourbières ardennaises. *Forêt Nature* 142: 47-55.

Parmesan C. & Yohe G.A. (2003). Globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37–42.

Plummer M. (2017). JAGS Version 4.3.0 user manual. Retrieved from http://sourceforge.net/projects/mcmc-jags/.

Root T.L., Price J.T., Hall K.R., Schneider S.H., Rosenzweig C. & Pounds J.A. (2003). Fingerprints of global warming on wild animals and plants. *Nature* 421: 57.

Rosenberg D.M. & Resh V.H. (editors) (1993). *Freshwater biomonitoring and benthic macroinvertebrates*. Chapman & Hall, New York.

Rosset V. & Oertli B. (2011). Freshwater biodiversity under climate warming pressure: identifying the winners and losers in temperate standing waterbodies. *Biological Conservation* 144: 2311-2319.

Roth T., Plattner M. & Amrhein V. (2014). Plants. birds and butterflies: short-term responses of species communities to climate warming vary by taxon and with altitude. *PLoS ONE* 9: e82490.

Royle J.A. & Dorazio R.M. (2008). *Hierarchical modeling and inference in ecology*. Academic Press, Amsterdam.

Royle J.A. & Kéry M. (2007). A Bayesian state-space formulation of dynamic occupancy modelling. *Ecology* 88: 813-1823.

Soldaat L.L., Pannekoek J., Verweij R.J.T., van Turnhout C.A.M. & van Strien A.J. (2017). A Monte Carlo method to account for sampling error in multispecies indicators. *Ecological Indicators* 81: 340-347.

Suhling F., Martens A. & Suhling I. (2017). Long-distance dispersal in Odonata: Examples from arid Namibia. *Austral Ecology* 42: 544-552.

Termaat T., van Grunsven R.H., Plate C.L. & van Strien A.J. (2015). Strong recovery of dragonflies in recent decades in The Netherlands. *Freshwater Science* 34: 1094-1104.

Thomas J.A. (2005). Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. Philosophical Transactions Royal Society of London. *Biological Sciences* 360: 339-357.

Van Dijk T.C., van Staalduinen M.A. & van der Sluijs J.P. (2013). Macro-invertebrate decline in surface water polluted with imidacloprid. *PLoS ONE* 8: e62374.

Van Strien A.J., Termaat T., Groenendijk D., Mensing V. & Kéry M. (2010). Site-occupancy models may offer new opportunities for dragonfly monitoring based on daily species lists. *Basic and Applied Ecology* 11: 495–503.

Van Strien A.J., Termaat T., Kalkman V., Prins M., De Knijf G., … & Vanreusel W. (2013). Occupancy modelling as a new approach to assess supranational trends using opportunistic data: a pilot study for the damselfly *Calopteryx splendens*. *Biodiversity and Conservation* 22: 673–686.

Van Strien A.J., van Swaay C.A.M. & Termaat T. (2013). Opportunistic citizen science data of animal species produce reliable estimates of distribution trends if analysed with occupancy models. *Journal of Applied Ecology* 50: 1450–1458.

Van Swaay C.A.M., Plate C.L. & van Strien A. (2002). Monitoring butterflies in the Netherlands: how to get unbiased indices. *Proceedings of the section Experimental and Applied Entomology of the Netherlands Entomological Society, Amsterdam* 13: 21–27.

Virkkala R. & Lehikoinen A. (2014). Patterns of climate induced density shifts of species: poleward shifts faster in northern boreal birds than in southern birds. *Global Change Biology* 20: 1-9.

Walther G.R., Post E., Convey P., Menzel A., Parmesan C., … & Bairlein F. (2002). Ecological responses to recent climate change. *Nature* 416: 389.

Warren M.S., Hill J.K., Thomas J.A., Asher J., Fox R., … & Thomas C.D. (2001). Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* 414: 65.

Appendix 5.1

Period covered. number of records and data density per geographic region.

Region	**Period covered**	**N records**	**Data density (records/km^2)**
Andalusia	2006-2015	12.140	0.1
Bavaria	1990-2013	115.068	1.6
Britain	1980-2012	848.638	3.7
Cyprus	2006-2015	9.394	1
Flanders	1990-2015	272.435	19.9
France	1990-2012	367.377	0.6
Netherlands	1991-2015	1.858.457	44.7
North Rhine-Westphalia	1990-2010	62.985	1.8
Sweden	1991-2014	96.019	0.2
Wallonia	1990-2015	131.481	7.8

Appendix 5.2

European multiplicative occupancy trends. for the 99 species included in this study. See online Supporting Information for index values per year: https://onlinelibrary.wiley.com/doi/10.1111/ddi.12913

Species	**Index period**	**Multiplicative trend**	**Multiplicative trend se**	**Multiplicative trend category**
Aeshna affinis	1990-2015	1.031	0.010	moderate increase
Aeshna caerulea	1990-2014	1.030	0.012	moderate increase
Aeshna cyanea	1990-2015	1.008	0.002	moderate increase
Aeshna grandis	1990-2015	1.010	0.002	moderate increase
Aeshna isoceles	1990-2015	1.010	0.004	moderate increase
Aeshna juncea	1990-2015	1.012	0.003	moderate increase
Aeshna mixta	1990-2015	1.013	0.003	moderate increase
Aeshna serrata	1991-2014	1.029	0.016	uncertain
Aeshna subarctica	1990-2015	1.034	0.017	uncertain
Aeshna viridis	1991-2015	1.014	0.007	stable
Anax ephippiger	1990-2015	1.001	0.015	stable
Anax imperator	1990-2015	1.009	0.002	moderate increase
Anax parthenope	1990-2015	1.027	0.005	moderate increase
Boyeria irene	1990-2015	1.006	0.004	stable
Brachytron pratense	1990-2015	1.012	0.003	moderate increase
Calopteryx haemorrhoidalis	1990-2015	1.007	0.004	stable
Calopteryx splendens	1990-2015	1.007	0.001	moderate increase
Calopteryx virgo	1990-2015	1.011	0.002	moderate increase
Calopteryx xanthostoma	1990-2012	1.002	0.003	stable
Ceriagrion tenellum	1990-2015	0.101	0.002	moderate increase
Chalcolestes viridis	1990-2015	1.012	0.005	moderate increase
Coenagrion armatum	1991-2014	0.103	0.018	uncertain
Coenagrion caerulescens	1990-2012	0.992	0.012	stable
Coenagrion hastulatum	1990-2015	1.016	0.004	moderate increase
Coenagrion johanssoni	1991-2014	1.030	0.012	moderate increase
Coenagrion lunulatum	1990-2015	1.017	0.010	stable
Coenagrion mercuriale	1990-2015	1.018	0.010	stable
Coenagrion ornatum	1990-2013	1.017	0.008	moderate increase
Coenagrion puella	1990-2015	1.006	0.001	moderate increase
Coenagrion pulchellum	1990-2015	1.002	0.003	stable
Coenagrion scitulum	1990-2015	1.010	0.004	moderate increase
Cordulegaster bidentata	1990-2015	1.007	0.006	stable
Cordulegaster boltonii	1990-2015	1.014	0.003	moderate increase

Species	Index period	Multiplicative trend	Multiplicative trend se	Multiplicative trend category
Cordulia aenea	1990-2015	1.012	0.003	moderate increase
Crocothemis erythraea	1990-2015	1.020	0.003	moderate increase
Enallagma cyathigerum	1990-2015	1.009	0.003	moderate increase
Epallage fatime	2006-2015	1.089	0.071	uncertain
Epitheca bimaculata	1990-2015	1.027	0.013	moderate increase
Erythromma lindenii	1990-2015	1.010	0.004	moderate increase
Erythromma najas	1990-2015	1.010	0.002	moderate increase
Erythromma viridulum	1990-2015	1.008	0.002	moderate increase
Gomphus flavipes	1990-2012	1.023	0.011	moderate increase
Gomphus graslinii	1990-2012	0.102	0.010	moderate increase
Gomphus pulchellus	1990-2015	1.007	0.002	moderate increase
Gomphus simillimus	1990-2012	1.014	0.008	stable
Gomphus vulgatissimus	1990-2015	1.006	0.004	stable
Ischnura elegans	1990-2015	1.004	0.001	moderate increase
Ischnura genei	1990-2012	1.013	0.028	uncertain
Ischnura graellsii	2006-2015	0.100	0.009	stable
Ischnura pumilio	1990-2015	1.003	0.002	stable
Lestes barbarus	1990-2015	1.017	0.010	stable
Lestes dryas	1990-2015	1.004	0.003	stable
Lestes macrostigma	1990-2012	1.030	0.014	moderate increase
Lestes sponsa	1990-2015	1.005	0.002	moderate increase
Lestes virens	1990-2015	1.017	0.008	moderate increase
Leucorrhinia albifrons	1990-2014	1.032	0.016	moderate increase
Leucorrhinia caudalis	1990-2014	1.006	0.009	stable
Leucorrhinia dubia	1990-2015	1.009	0.003	moderate increase
Leucorrhinia pectoralis	1990-2015	1.023	0.007	moderate increase
Leucorrhinia rubicunda	1990-2015	1.020	0.009	moderate increase
Libellula depressa	1990-2015	0.010	0.003	moderate increase
Libellula fulva	1990-2015	1.015	0.003	moderate increase
Libellula quadrimaculata	1990-2015	1.010	0.002	moderate increase
Macromia splendens	1990-2012	0.101	0.008	stable
Nehalennia speciosa	1990-2014	1.000	0.009	stable
Onychogomphus forcipatus	1990-2015	0.101	0.003	moderate increase
Onychogomphus uncatus	1990-2015	1.007	0.004	stable
Ophiogomphus cecilia	1990-2013	0.993	0.005	stable
Orthetrum albistylum	1990-2012	1.007	0.002	moderate increase
Orthetrum brunneum	1990-2015	1.013	0.003	moderate increase
Orthetrum cancellatum	1990-2015	1.010	0.002	moderate increase
Orthetrum chrysostigma	2006-2015	1.039	0.023	uncertain

Species	**Index period**	**Multiplicative trend**	**Multiplicative trend se**	**Multiplicative trend category**
Orthetrum coerulescens	1990-2015	1.012	0.002	moderate increase
Oxygastra curtisii	1990-2015	1.000	0.007	stable
Platycnemis acutipennis	1990-2015	1.005	0.005	stable
Platycnemis latipes	1990-2015	1.004	0.003	stable
Platycnemis pennipes	1990-2015	1.008	0.002	moderate increase
Pyrrhosoma nymphula	1990-2015	1.009	0.002	moderate increase
Selysiothemis nigra	2006-2015	1.026	0.046	uncertain
Somatochlora alpestris	1990-2014	1.012	0.009	stable
Somatochlora arctica	1990-2015	1.016	0.008	stable
Somatochlora flavomaculata	1990-2015	1.010	0.005	moderate increase
Somatochlora metallica	1990-2015	1.008	0.003	moderate increase
Sympecma fusca	1990-2015	1.013	0.002	moderate increase
Sympecma paedisca	1990-2015	1.019	0.009	moderate increase
Sympetrum danae	1990-2015	1.003	0.002	stable
Sympetrum depressiusculum	1990-2015	0.989	0.008	stable
Sympetrum flaveolum	1990-2015	1.011	0.013	stable
Sympetrum fonscolombii	1990-2015	1.022	0.004	moderate increase
Sympetrum meridionale	1990-2015	1.025	0.016	uncertain
Sympetrum pedemontanum	1990-2015	1.005	0.006	stable
Sympetrum sanguineum	1990-2015	1.009	0.002	moderate increase
Sympetrum sinaiticum	2006-2015	1.048	0.059	uncertain
Sympetrum striolatum	1990-2015	1.009	0.002	moderate increase
Sympetrum vulgatum	1990-2015	1.005	0.003	stable
Trithemis annulata	1990-2015	0.100	0.019	stable
Trithemis arteriosa	2006-2015	0.993	0.024	uncertain
Trithemis festiva	2006-2015	1.089	0.065	uncertain
Trithemis kirbyi	2006-2015	1.162	0.086	uncertain

Appendix 5.3

Species Temperature Index (STI) of all European dragonfly species and number of 50 × 50 km grid squares in the species' European range. Blue printed species are included in this study. SD = standard deviation.

Species	STI (°C)	SD	N 50*50 km squares
Somatochlora sahlbergi	-0.636	1.718	9
Aeshna caerulea	2.007	2.975	260
Somatochlora alpestris	2.729	3.515	154
Coenagrion johanssoni	3.180	2.227	154
Coenagrion hylas	4.171	NA	2
Aeshna crenata	4.283	1.264	25
Coenagrion armatum	5.046	2.101	157
Aeshna serrata	5.086	1.421	55
Somatochlora arctica	5.219	3.168	383
Aeshna subarctica	5.405	2.496	321
Leucorrhinia dubia	5.416	3.031	741
Leucorrhinia rubicunda	5.597	3.092	563
Coenagrion hastulatum	5.663	2.621	765
Aeshna juncea	5.860	3.246	1043
Somatochlora metallica	6.412	3.257	1007
Nehalennia speciosa	6.417	1.236	121
Leucorrhinia albifrons	6.454	2.209	343
Aeshna grandis	6.553	2.882	1081
Coenagrion lunulatum	6.739	2.467	294
Sympetrum danae	6.761	2.594	1088
Sympecma paedisca	6.787	1.417	207
Leucorrhinia caudalis	6.898	2.534	292
Aeshna viridis	7.058	1.718	202
Cordulia aenea	7.348	2.772	1135
Epitheca bimaculata	7.494	2.216	339
Ophiogomphus cecilia	7.506	2.589	461
Leucorrhinia pectoralis	7.544	1.963	620
Lestes sponsa	7.572	2.689	1337
Erythromma najas	7.601	2.569	1023
Sympetrum flaveolum	7.661	2.294	961
Sympetrum vulgatum	7.750	2.420	980
Somatochlora flavomaculata	7.769	2.657	652
Libellula quadrimaculata	7.881	3.043	1466

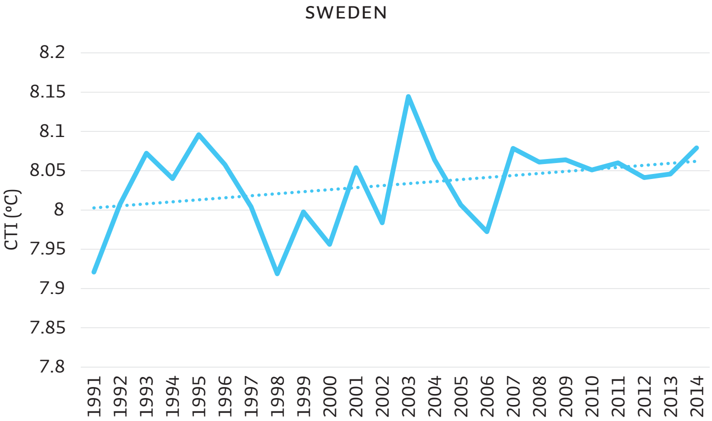
Species	STI (°C)	SD	N 50*50 km squares
Coenagrion pulchellum	8.303	2.765	1157
Enallagma cyathigerum	8.463	3.748	1647
Sympetrum pedemontanum	8.539	2.079	379
Gomphus vulgatissimus	8.606	2.435	872
Cordulegaster boltonii	8.769	3.551	945
Aeshna cyanea	8.813	3.114	1337
Pyrrhosoma nymphula	8.815	3.035	1386
Cordulegaster bidentata	8.831	2.750	390
Calopteryx virgo	8.946	3.743	1436
Brachytron pratense	9.017	2.516	892
Sympetrum depressiusculum	9.040	2.560	256
Lestes dryas	9.067	2.819	919
Gomphus flavipes	9.097	2.012	298
Coenagrion puella	9.297	2.838	1562
Sympetrum sanguineum	9.326	2.664	1394
Calopteryx splendens	9.391	3.041	1354
Platycnemis pennipes	9.427	3.113	1315
Libellula depressa	9.670	3.215	1466
Coenagrion ornatum	9.719	1.876	197
Ischnura elegans	9.815	3.477	1709
Anax junius	9.902	1.248	5
Orthetrum albistylum	9.947	2.311	555
Cordulegaster heros	10.036	2.212	100
Lestes virens	10.193	3.193	879
Aeshna mixta	10.251	3.432	1350
Onychogomphus forcipatus	10.318	3.708	968
Libellula fulva	10.326	3.116	808
Aeshna isoceles	10.379	3.187	832
Orthetrum cancellatum	10.406	3.528	1571
Ischnura pumilio	10.454	3.066	1110
Chalcolestes viridis	10.616	3.066	965
Erythromma viridulum	10.644	3.050	1060
Lestes barbarus	10.741	3.013	930
Sympetrum striolatum	10.817	3.712	1495
Sympecma fusca	10.848	3.338	1045
Aeshna affinis	10.877	2.871	822
Gomphus pulchellus	11.131	2.854	469
Orthetrum coerulescens	11.266	3.533	1180
Anax imperator	11.398	3.803	1559
Coenagrion mercuriale	11.464	2.583	464
Somatochlora meridionalis	11.505	2.515	142

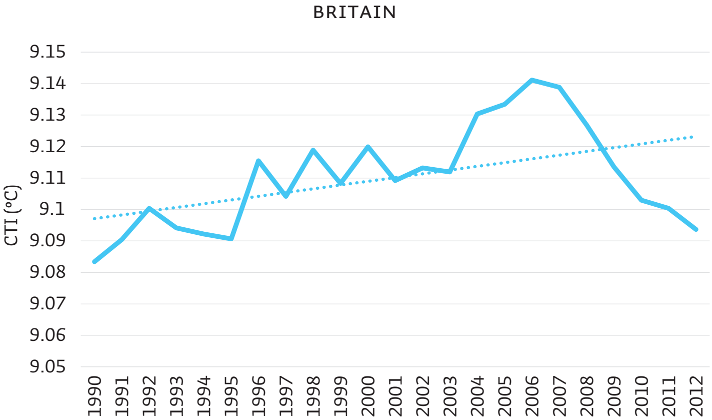
Species	STI (°C)	SD	N 50*50 km squares
Orthetrum brunneum	11.719	3.408	998
Anax parthenope	11.823	3.715	1060
Sympetrum meridionale	11.990	3.257	736
Coenagrion scitulum	12.061	2.685	533
Gomphus simillimus	12.115	2.205	204
Erythromma lindenii	12.123	3.066	712
Ceriagrion tenellum	12.199	2.761	514
Crocothemis erythraea	12.202	3.624	1161
Oxygastra curtisii	12.218	2.390	289
Calopteryx xanthostoma	12.403	2.308	236
Boyeria irene	12.526	2.547	345
Sympetrum fonscolombii	12.590	3.856	1186
Somatochlora borisi	12.698	0.593	8
Onychogomphus uncatus	12.778	2.412	272
Platycnemis acutipennis	12.881	2.381	244
Anax ephippiger	13.050	3.922	476
Cordulegaster insignis	13.236	2.398	29
Chalcolestes parvidens	13.307	2.838	184
Gomphus graslinii	13.321	1.821	97
Platycnemis latipes	13.340	2.531	258
Cordulegaster picta	13.393	1.741	19
Coenagrion caerulescens	13.471	2.404	137
Lindenia tetraphylla	13.492	2.236	44
Caliaeschna microstigma	13.560	2.952	109
Macromia splendens	13.663	1.815	71
Calopteryx haemorrhoidalis	13.733	2.229	322
Pyrrhosoma elisabethae	13.953	0.771	8
Epallage fatime	13.970	3.003	42
Ischnura graellsii	14.204	2.462	195
Cordulegaster trinacriae	14.272	1.301	26
Gomphus schneiderii	14.372	2.297	29
Lestes macrostigma	14.432	3.150	112
Onychogomphus costae	14.551	2.149	34
Selysiothemis nigra	15.159	2.483	96
Ischnura genei	15.311	1.644	44
Sympetrum sinaiticum	15.343	1.995	33
Trithemis annulata	15.378	2.207	284
Cordulegaster helladica	15.527	1.075	14
Paragomphus genei	15.584	1.089	45
Ceriagrion georgifreyi	15.768	NA	2

Species	**STI (°C)**	**SD**	**N 50*50 km squares**
Brachythemis impartita	16.174	1.094	86
Ischnura hastata	16.176	0.245	5
Ischnura senegalensis	16.381	NA	2
Boyeria cretensis	16.539	1.409	4
Coenagrion intermedium	16.632	1.074	7
Orthetrum trinacria	16.681	1.492	86
Pantala flavescens	16.698	1.907	17
Orthetrum nitidinerve	16.719	1.848	28
Trithemis kirbyi	16.723	1.283	40
Diplacodes lefebvrii	16.776	1.052	39
Orthetrum chrysostigma	16.814	1.863	106
Orthetrum taeniolatum	16.967	1.297	13
Orthetrum sabina	17.524	1.215	8
Ischnura fountaineae	17.582	NA	2
Zygonyx torridus	17.818	2.125	16
Anax immaculifrons	17.972	1.137	7
Trithemis festiva	17.977	0.562	8
Ischnura intermedia	18.026	NA	3
Sympetrum nigrifemur	18.172	1.592	12
Ischnura saharensis	18.242	1.093	7
Trithemis arteriosa	18.278	1.594	13

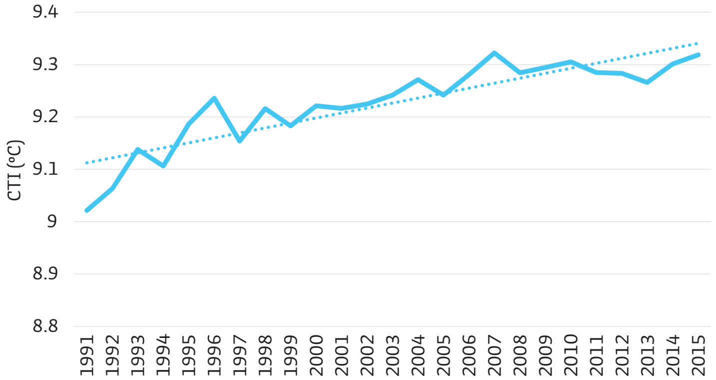
Appendix 5.4

Community Temperature Index (CTI) per geographic region (from north to south), and for Europe. Linear trend lines were plotted through the year effects to summarise overall change. Please note that Y-axes differ.

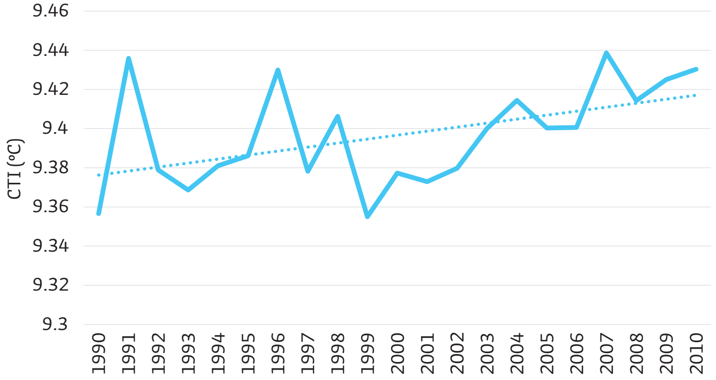




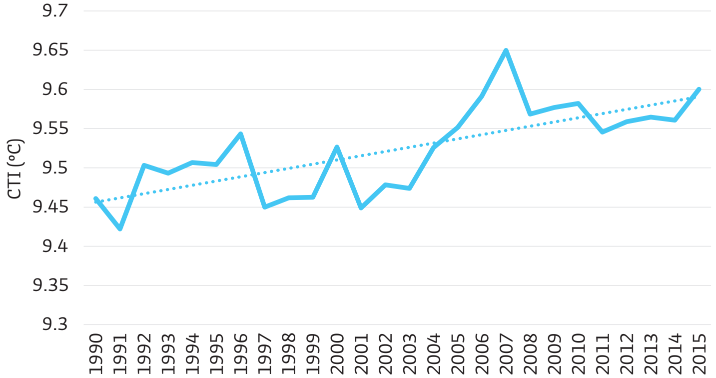
NETHERLANDS

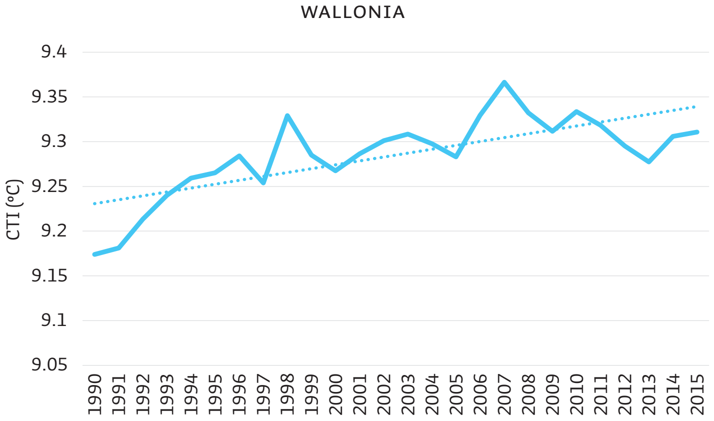


NORTH RHINE - WESTPHALIA



FLANDERS




WALLONIA
CTI (ºC)
9.4
9.35
9.3
9.25
9.2
9.15
9.1
9.05
1990
1991
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
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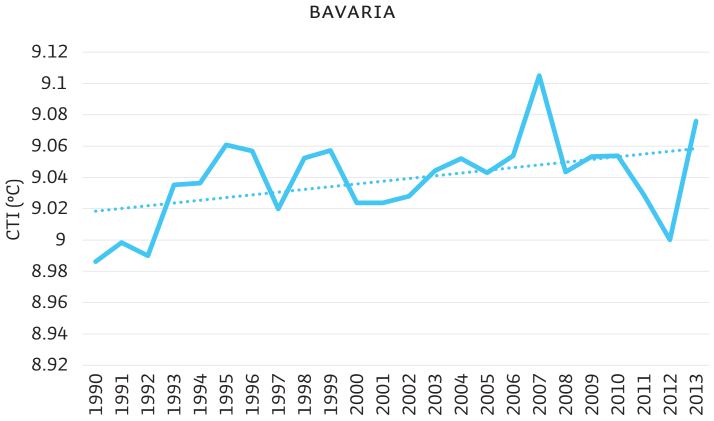
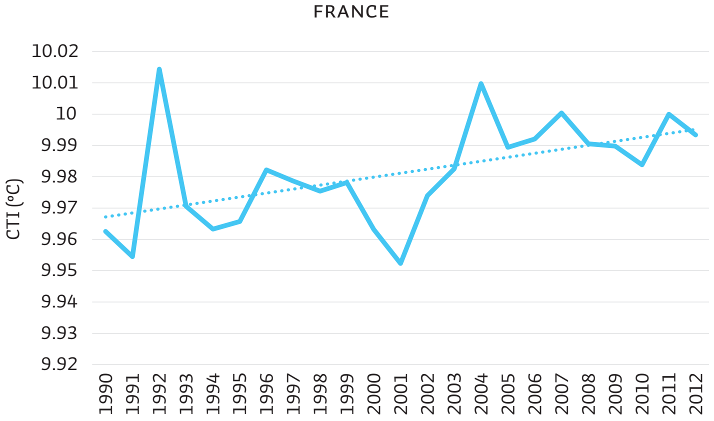
2010
2011
2012
2013
2014
2015


BAVARIA
CTI (ºC)
9.12
9.1
9.08
9.06
9.04
9.02
9
8.98
8.96
8.94
8.92
1990
1991
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013


FRANCE
CTI (ºC)
10.02
10.01
10
9.99
9.98
9.97
9.96
9.95
9.94
9.93
9.92
1990
1991
1992
1993
1994
1995
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1997
1998
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2007
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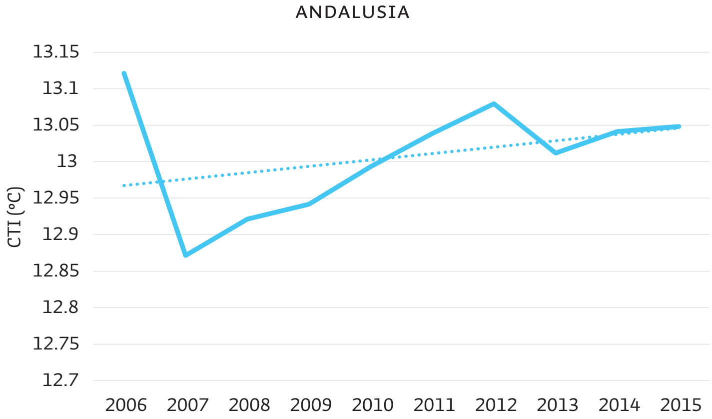
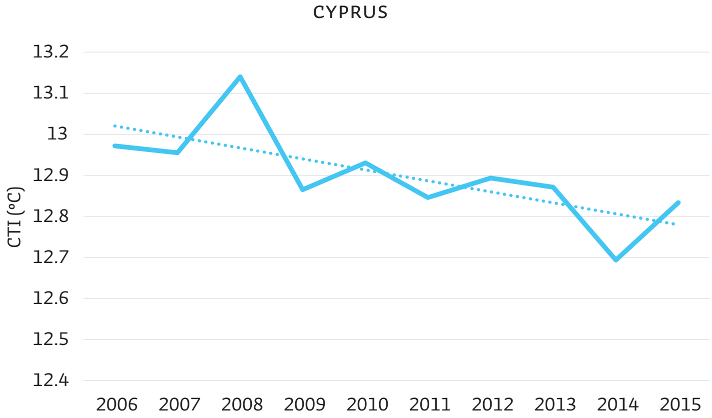
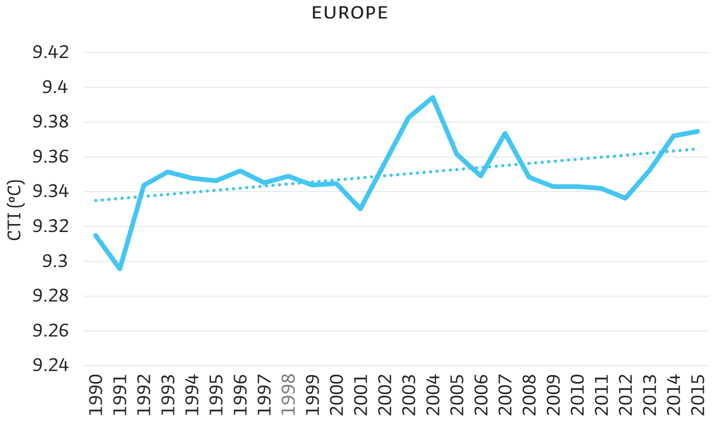

ANDALUSIA
CTI (ºC)
13.15
13.1
13.05
13
12.95
12.9
12.85
12.8
12.75
12.7
2006
2007
2008
2009
2010
2011
2012
2013
2014
2015


CYPRUS
CTI (ºC)
13.2
13.1
13
12.9
12.8
12.7
12.6
12.5
12.4
2006
2007
2008
2009
2010
2011
2012
2013
2014
2015


EUROPE
CTI (ºC)
9.42
9.4
9.38
9.36
9.34
9.32
9.3
9.28
9.26
9.24
1990
1991
1992
1993
1994
1995
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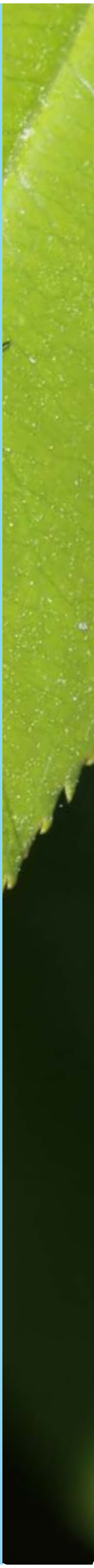
Male *Coenagrion hastulatum* at Klein Hasselsven, one of its last strongholds in the Netherlands.



CHAPTER 6

Spearhead blues: How threats to the damselfly *Coenagrion hastulatum* (Charpentier, 1825) changed over time.

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Roy H.A. van Grunsven, Michiel F. WallisDeVries

SUBMITTED

Abstract

Since insects respond rapidly to environmental changes, their most prominent threats may change quickly as well. For effective insect species conservation it is therefore necessary to discriminate between former and current drivers of decline and to focus conservation efforts on the latter. We investigated how various environmental pressures have affected populations of the regionally endangered damselfly *Coenagrion hastulatum* and how the relevance of these pressures have changed over time. We compared water quality, vegetation properties and population trends in three different time periods: 1921-2000, 2001-2015 and 2016-2021. In our comparison, we included all known reproduction sites in the Netherlands (current and historical), supplemented with nearby, never occupied sites. Suitable ponds were characterised by mesotrophic conditions and high covers of emergent and floating vegetation. Never occupied ponds differed from occupied ponds in being either more acidic or more eutrophic. Ponds where *C. hastulatum* disappeared between 2001 and 2015 had lower covers of mentioned vegetation structures and higher concentrations of various minerals. Ponds where the species disappeared after 2015 were affected by severe droughts in 2018-2020. Most prominent threats to *C. hastulatum* indeed changed over time. Historically, changes in anthropological use of ponds and increased sulphur and nitrogen deposition were the most prominent threats. Recently, severe droughts have become the predominant threat, besides nitrogen deposition. Thus, restoration of groundwater systems and rewetting measures are now first conservation priorities. Our study shows that threats to insect populations can change over short periods of time. Conservation strategies should therefore be evaluated and adjusted regularly.

KEYWORDS: Conservation ecology, Habitat quality, Nitrogen deposition, Climate change, Odonata

6.1 Introduction

The recent recognition that insects are in decline in large parts of the world, precipitated by the hallmark study of Hallman et al. (2017), has highlighted the difficulties in analysing trends in short-lived organisms like insects and attributing declines to possible causes (Wagner et al., 2021). Historically, most conservation efforts have been focused on vegetation and large long-lived animals, primarily birds and mammals (Di Marco et al., 2017). Monitoring these species is not without difficulty, but fluctuations in population sizes are normally modest compared to short lived species such as insects (Fox et al., 2019). Strong yearly fluctuations in abundance are the norm for insects whose lifecycle typically span one or two seasons and this complicates trend assessment for individual insect species and insect communities (Schowalter et al., 2021). For some groups of insects, such as European butterflies and dragonflies, trends are well documented, and while butterflies show strong declines (Warren et al., 2021), this is generally not the case for the dragonflies (Termaat et al., 2019). Van Klink et al. (2020) analysed a broader selection of arthropods and found similar trend difference between terrestrial and aquatic arthropods.

In addition to the difficulties in signalling trends, identifying the causes underlying trends in insect population size is often not straightforward either. Multiple environmental drivers can be involved and even for a single species the relative importance of these drivers can vary across locations and over time. Because of their short generation time, insects tend to react quickly to changes in their environment, which may lead to strong annual fluctuations in abundance. This means that new threats to insect populations may have an immediate impact, and may soon outweigh the relevance of previous threats. From a conservation point of view, changes in the relative importance of threats over time is problematic since the identification of new threats, and deploying conservation efforts to oppose them, take time. If the main threat can change rapidly, we could be fighting the wrong problem. For effective species conservation it is therefore necessary to discriminate between former and current drivers of decline. Both may have affected different shares of the species' reproduction sites and may have led to the loss of different populations. Priority should be given to act against current threats, although restoration of habitats which deteriorated due to former threats may be advantageous as well, provided they can recover from relict or nearby remaining populations.

Dragonflies (Odonata) are among the best studied groups of invertebrates concerning life-history, ecology, distribution and conservation status (Boudot & Kalkman, 2015; Bried et al., 2020; Corbet, 1999; Kalkman et al., 2018). Previous studies have shown substantial shifts in both local population sizes of individual species and their regional distributions. Various environmental drivers have been identified to explain these changes, making dragonflies a suitable insect group to study possible shifts in threats. The geographical scale of these studies co-determine the relative importance of different drivers. In Europe, climate change has been shown to be the prominent driver for dragonfly distribution on a continental scale (Termaat et al., 2019). In the Netherlands, changes in water quality and subsequent changes in vegetation structure and composition are considered to drive dragonfly trends on a national scale, in addition to climate change (Termaat et al., 2015).

In this study, we investigate how environmental pressures have affected populations of the damselfly Spearhead Bluet or Northern Damselfly (*Coenagrion hastulatum* (Charpentier, 1825) (Zygoptera: Coenagrionidae). We chose this species since its range and known habitat requirements may well cause it to be prone to different kinds of pressures. As such it could be a model species to investigate if pressures underlying negative population trends may change over time. Despite efforts to protect this species and its habitats in the Netherlands, there is an ongoing decline. Since past conservation efforts have been closely monitored, both environmental data and data on population trends are available from different periods, allowing us to compare the main threats between time periods.

We hypothesised that the most prominent threats for *C. hastulatum* in the Netherlands have changed during the 20th and beginning of the 21st century, due to different developments influencing its remaining populations, either negatively or positively. Among these developments are changes in the deposition of sulphur and nitrogen compounds (CBS et al., 2019), climate change (CBS et al., 2020b), alterations in local groundwater systems, habitat restoration efforts (Jansen & Grootjans, 2019) and habitat management efforts.

To test our hypothesis, we measured various aspects of water quality and vegetation structures at all ponds in the Netherlands which *C. hastulatum* uses or has used for reproduction. We also included nearby ponds where *C. hastulatum* has never been recorded. These measurements were made in 2001 and repeated in 2015. After 2015 the occurrence of *C. hastulatum* was closely followed at the few ponds where the species was still present, together with developments in water levels and vegetation covers. Thus we compared three time periods: 1921-2000; 2001-2015 and 2016-2021. This enabled us to identify key parameters of habitat suitability and causes for the loss of populations over time.

6.2 Methods

6.2.1 STUDY SPECIES

C. hastulatum is a widespread species in the temporal and boreal parts of Eurasia. In Europe it is predominantly a northern and central species, with scattered populations further south at higher elevations (e.g. Alps, Pyrenees and mountain ranges on the Balkan Peninsula; Boudot & Kalkman, 2015). As a result the Species Temperature Index (STI) of *C. hastulatum*, which expresses the mean annual temperature of its range, is only 5.7 °C. This ranks among the 10% of lowest STI of all European Odonata (Termaat et al. ,2019) and is substantially lower than the mean annual temperature in the Netherlands, which was 10.7 °C in 1999-2019 (CBS et al., 2020b).

C. hastulatum is among the most common damselflies in a large part of Scandinavia, the Baltic States and Russia and is therefore listed as 'Least Concern' on the current European Red List (Kalkman et al., 2010). However, along the southern limit of its European range *C. hastulatum* is rare and has declined during the last decades. In the Netherlands it is Red-Listed as 'Critically Endangered' (Termaat & Kalkman, 2012), due to the small number of occupied sites in combination with a negative trend in abundance (fig. 6.1). In the nearby countries Germany, Belgium, France and Great Britain the species is Red Listed as well (Daguet et al., 2008; De Knijf et al., 2021; Motte et al., 2021; Ott et al., 2015).

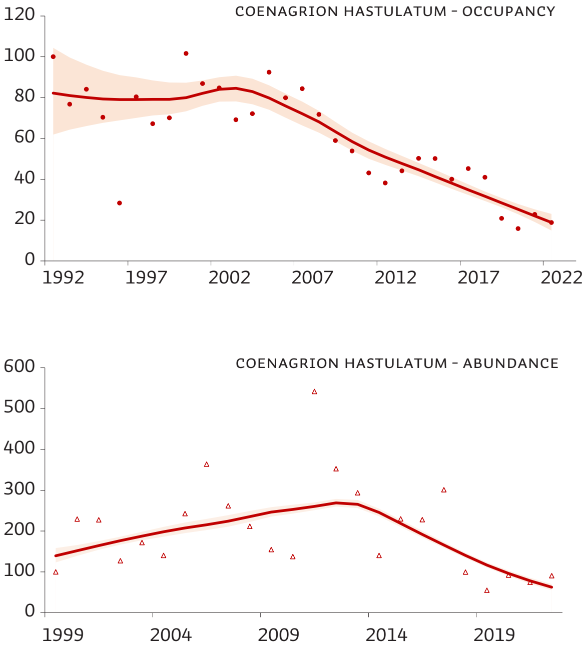


FIG. 6.1: Indices of *Coenagrion hastulatum* in the Netherlands. Above: occupancy index (distribution; 1991 was set to 100), below: abundance index, based on standardised counts (1999 was set to 100). Smoothed trend lines were plotted through the year effects to summarise overall change. Shaded areas represent 95% confidence intervals.

C. hastulatum is largely restricted to standing waters (hereafter: 'ponds') that are relatively poor in nutrients and have ample aquatic and riparian vegetation (Boudot & Kalkman, 2015; Dinning et al., 2022). In the Netherlands these ponds include moorland pools, shallow oligo-mesotrophic lakes, transition mires and other water bodies in peat bogs with a certain groundwater influence and, occasionally, man-made ditches with dense stands of the Pondweeds *Potamogeton polygonifolius* or *P. natans*. All former and current populations are situated in the east and southeast of the country, in areas with Pleistocene aeolian sand deposits. Ponds occupied by *C. hastulatum* are usually rich in other dragonfly species as well (Nederlandse Vereniging voor Libellenstudie, 2002).

6.2.2.SELECTION OF DATA AND STUDY SITES

The Netherlands has the highest density of dragonfly records of any country in the world (Bried et al., 2020) and has a long history of dragonfly recording. The current and historical distribution of *C. hastulatum* is therefore well known. All available dragonfly records are currently stored and validated in the National Database Flora and Fauna (www.ndff.nl). Dubious recent records of *C. hastulatum* (from new sites and without a photograph) have been omitted in this study, as have older records that were considered implausible. Field studies to find unknown populations of *C. hastulatum* and reconfirm its presence at known sites have been performed regularly (Ketelaar, 2001; Nederlandse Vereniging voor Libellenstudie, 2002; Termaat, 2006; Termaat & Van Kleef, 2016). As a result there is good knowledge on the status of (former) reproduction sites of *C. hastulatum*.

In this study we selected all ponds where reproduction occurred or still occurs (appendix 6.1). We assigned these ponds to the following categories: 1) ponds where *C. hastulatum* once occurred, but disappeared prior to 2001 (year with last record lies within period 1921-2000; n=12); 2) ponds where *C. hastulatum* disappeared in the period 2001-2015 (n=8); and 3) ponds where *C. hastulatum* was present in 2015 (n=13), including 7 ponds where *C. hastulatum* was not present or at least not known to reproduce in 2001. In addition, we selected ponds where *C. hastulatum* had never been recorded for comparison (category 4; n=14). These were the closest ponds (< 2 km) to each of the ponds in category 1 and 2 with a well-known dragonfly fauna, but without records of *C. hastulatum*. Thus, category 4 consists of ponds unsuitable for *C. hastulatum*, since isolation can be ruled out as the cause for its absence.

6.2.3 DATA COLLECTION IN DIFFERENT TIME PERIODS

In order to determine how the relative importance of pressures on *C. hastulatum* has changed over time we analysed habitat information from 2001 and 2015. Data were collected on vegetation composition, vegetation structures and a selection of physical and chemical parameters regarding water quality. In 2001 this was done for the ponds of categories 1, 2, 4 and all ponds of category 3 where the species was present in 2001 (6 of 13 sites; appendix 6.1). In 2015 the same data were collected at all ponds of category 2 and category 3.

Vegetation composition was measured by means of relevés on the Tansley abundance scale (Tansley, 1946). Besides vegetation composition we quantified the cover of different vegetation structures, as vegetation structures may affect dragonfly habitat quality regardless the plant species they are composed of (e.g. Huikkonen et al., 2020; Mabry & Dettman, 2010; Raebel et al., 2012). We estimated the relative surface cover of 5 different vegetation structure classes: 'submerged vegetation' (e.g. *Sphagnum* sp., *Utricularia* sp., *Juncus bulbosus*); 'small floating leaves' (mostly *Potamogeton polygonifolius*, *P. natans* and *Hydrocharis morsus-ranae*); 'large floating leaves' (*Nymphaea alba*, *Nuphar lutea*); 'short emergent vegetation' (e.g. *Carex* sp., *Eleocharis* sp., waterlogged stands of *Molinia caerulea*); and 'tall emergent vegetation' (e.g. *Phragmites australis*, *Typha* sp., *Schoenoplectus lacustris*). Relative covers were then converted into absolute covers in m^2 using the total surface area of each pond measured from satellite images.

For water quality measurements, we collected a water sample from each pond using polyethylene bottles which were filled at approximately 10 cm below the surface of an open water patch in the water fringe vegetation. Water samples were cooled and transported to the laboratory, where pH, electrical conductivity, concentration of dissolved orthophosphate, total phosphorus, nitrate, ammonium, calcium, magnesium, potassium, sodium, iron, aluminium, chloride, bicarbonate and sulphate (2001) or total sulphur (2015) were measured. All data were standardised via z-score normalisation before statistical analysis.

During the period 2016-2021 all remaining *C. hastulatum* populations were monitored annually, to keep track of changes in population densities, water levels and vegetation covers. This gave useful additional information on recent trends and pressures. Hence, we were able to identify and compare possible threats during three periods: <2001, 2001-2015, and 2016-2021.

6.2.4 DATA ANALYSIS

The cover values of the vegetation relevés were used to weight the Ellenberg values for nitrogen and alkalinity of each recorded plant species (Ellenberg et al., 1991). These weighted Ellenberg values were then used to calculate an average value for Ellenberg Nitrogen and Ellenberg Alkalinity per ponds. Next, we applied redundancy analyses (RDA) to cluster ponds based on their vegetation composition, and to look for correlations in occurrence of *C. hastulatum* and vegetation structure, physical-chemical water quality properties, and Ellenberg Nitrogen and Alkalinity values. This was done separately for data collected in 2001 (at ponds from presence categories 1, 4 and six ponds of category 3) and for data collected in 2015 (all ponds from categories 2 and 3). In addition, we applied a redundancy analysis based on both the 2001 and the 2015 data, for all ponds which were sampled in both years (thus excluding six ponds from category 3).

We visualised the results in triplots using package 'ggbiplot' (Vu, 2011) in R (version 3.6.3; R Core Team, 2020). To test for differences between pond categories in scores on the RDA axes we used pair-wise t-test with Benjamini-Hochberg corrections to control the false discovery rate (Benjamini & Hochberg, 1995). To look for univariate differences between pond categories we applied Wilcoxon tests on all measured parameters separately, with Holm-Bonferroni corrections for pair-wise comparisons.

Analysing the data for three separate periods (1921-2000; 2001-2015; 2016-2021) enabled us to identify and compare the most prominent threats to *C. hastulatum* during these periods.

6.3 Results

6.3.1 2001 ASSESSMENT

The RDA based on the 2001 data showed that 62.8% of total variance is explained by the environmental variables and the overall model showed significant differences between pond categories ($p < 0.001$). Site scores differed on the first two RDA axes only (RDA1: $p < 0.001$; RDA2: $p = 0.020$). These axes explained 13.5% and 9.7% of total variance respectively.

A triplot based on the first two RDA axes (fig. 6.2) showed a separation of all three ponds categories. Pair-wise t-tests confirmed differences on the first axis (present-disappeared: $p = 0.032$; present-never present: $p < 0.001$; disappeared-never present: $p = 0.032$) and partly on the second axis (present-disappeared: $p = 0.010$; present-never present: $p = 0.377$; disappeared-never present: $p = 0.032$). Environmental variables which significantly contributed to these differences were small floating leaves cover ($p < 0.001$), short emergent vegetation cover ($p = 0.036$), mean Ellenberg Alkalinity ($p < 0.001$), pH ($p = 0.009$), potassium ($p = 0.004$) and nitrate ($p = 0.004$). Tall emergent vegetation cover, mean Ellenberg Nitrogen, ammonium and total phosphorus tended to differ as well ($p < 0.1$).

Visual inspection of the triplot indicates that unsuitable ponds, i.e., waterbodies where *C. hastulatum* never occurred, are characterised by a relatively low pH, high cover of submerged vegetation, low calcium concentration and high ammonium, phosphate and total phosphorus concentrations. These ponds are either too acidic or too rich in nutrients for *C. hastulatum*. The high covers of submersed vegetation in these unsuitable ponds mostly consist of *S. cuspidatum* or *J. bulbosus*, typical for acidic and ammonium-enriched conditions.

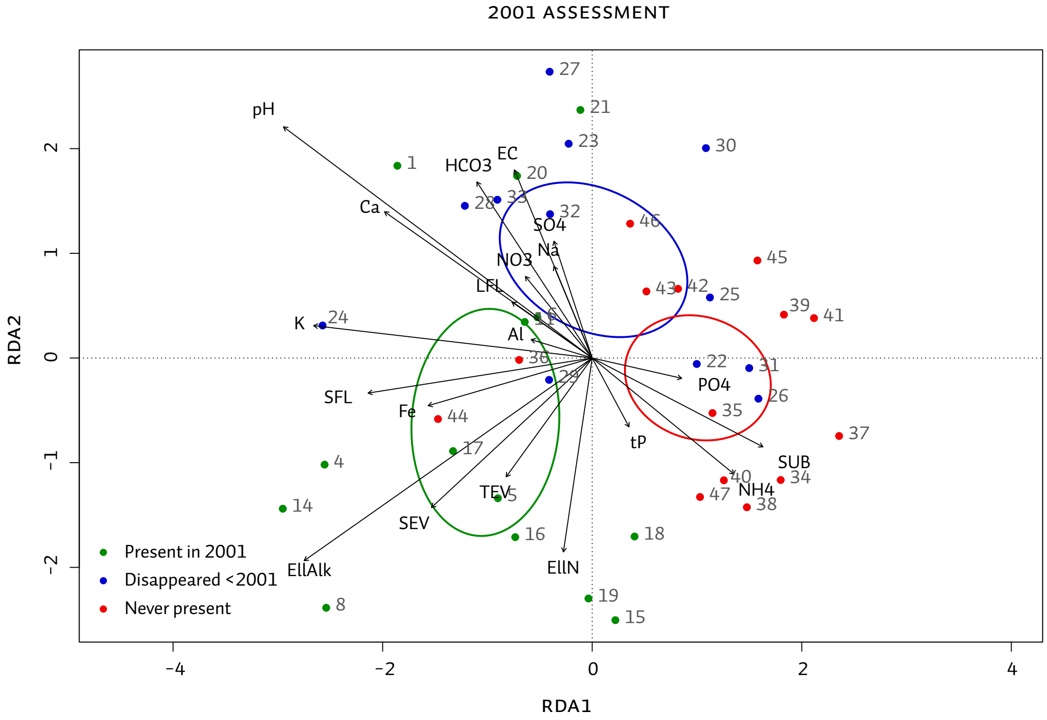
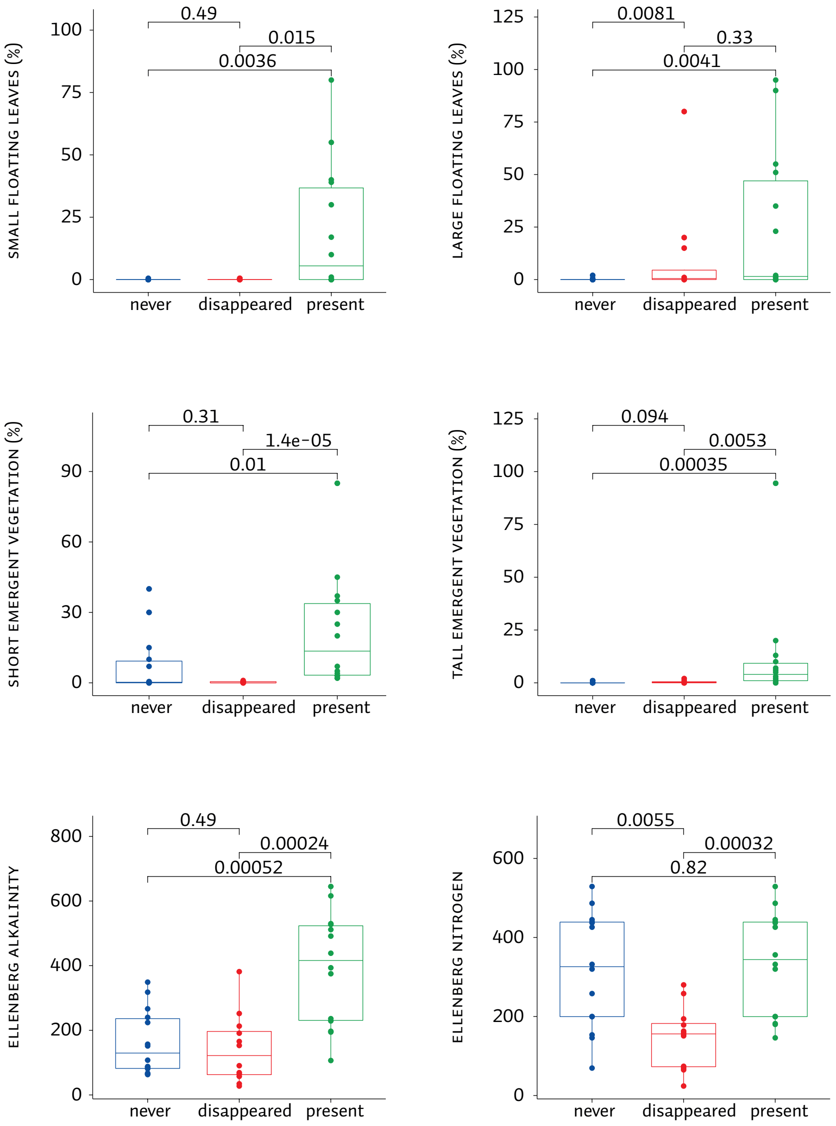


FIG. 6.2: Redundancy analysis (RDA) of the 2001 data. Numbered dots represent studied sites (see appendix 6.1 for corresponding sites) and are coloured according to presence category. Ellipses represent 95% confidence intervals. Arrows represent dissolved elements and other measured parameters: Al = aluminium, Ca = calcium, Fe = iron, HCO3 = bicarbonate, K = potassium, Na = sodium, NH4 = ammonium, NO3 = nitrate, PO4 = orthophosphate, SO4 = sulphate, SUB = submerged vegetation cover; SFL = plants with small floating leaves cover; LFL = plants with large floating leaves cover; SEV = short emergent vegetation cover; TEV = tall emergent vegetation cover; EC = electrical conductivity; EllAlk = Ellenberg Alkalinity; EllN = Ellenberg Nitrogen. Longer arrows indicate stronger correlations with first or second RDA axis.

In contrast, ponds where *C. hastulatum* still occurred in 2001 (category 2) are characterised by relatively high pH, high Ellenberg Alkalinity and Ellenberg Nitrogen, high covers of short emergent vegetation, tall emergent vegetation and small floating leaves, and high concentrations of calcium, potassium and iron (fig. 6.2). These features indicate mesotrophic and slightly buffered conditions, resulting in a mix of vegetation structures.

High pH, high covers of large floating leaves and high levels of calcium are features these ponds share with ponds where *C. hastulatum* used to be present, but disappeared before 2001 (category 1). The ponds where *C. hastulatum* had disappeared however, are further characterised by a relatively high electrical conductivity and high levels of bicarbonate, sulphate, nitrate and sodium. This indicates an influx of these compounds, either via polluted surface water or groundwater or via direct human input. Univariate testing confirmed differences in some of the mentioned variables between pond categories, but not all of them (fig. 6.3).



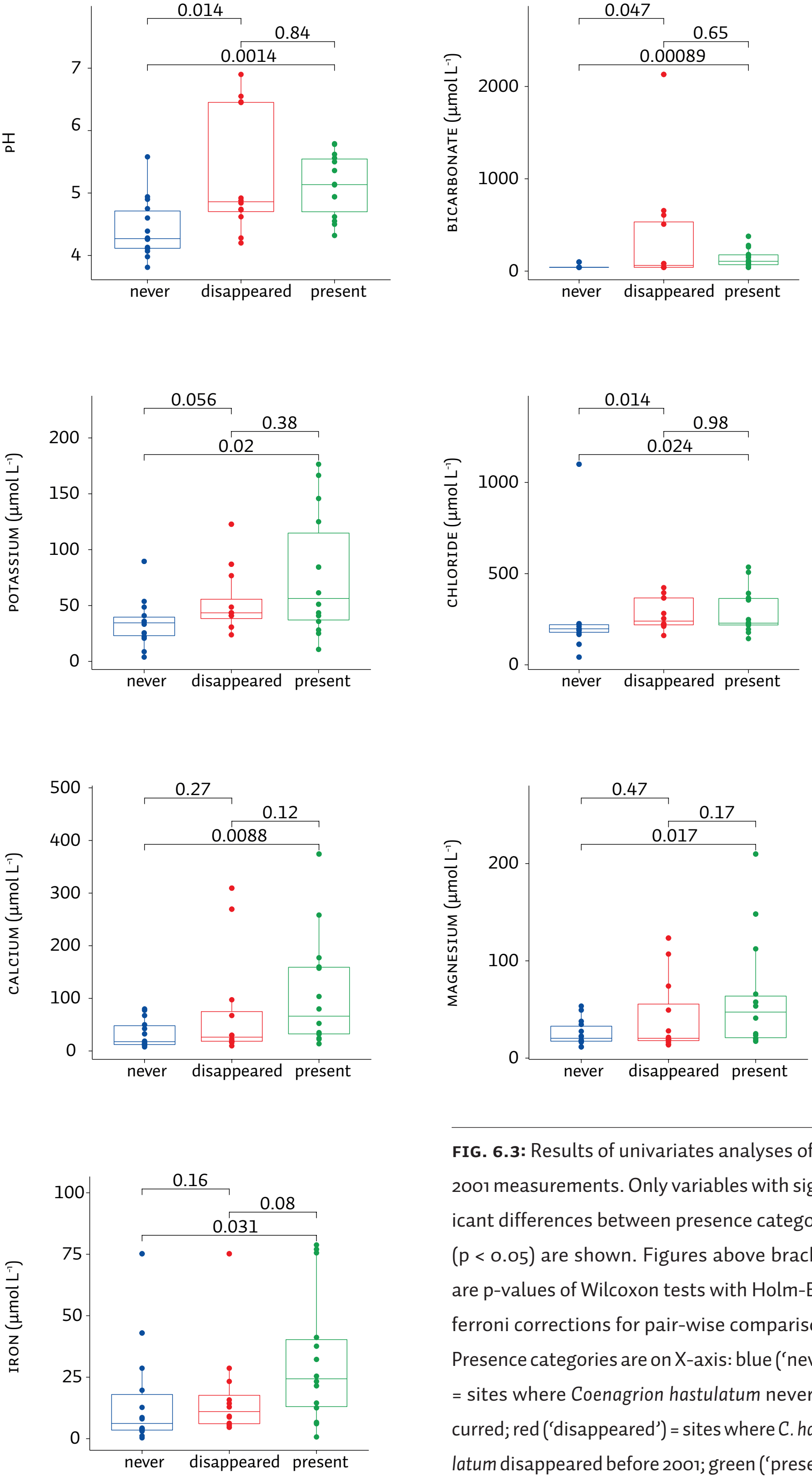


FIG. 6.3: Results of univariates analyses of the 2001 measurements. Only variables with significant differences between presence categories ($p < 0.05$) are shown. Figures above brackets are p-values of Wilcoxon tests with Holm-Bonferroni corrections for pair-wise comparisons. Presence categories are on X-axis: blue ('never') = sites where *Coenagrion hastulatum* never occurred; red ('disappeared') = sites where *C. hastulatum* disappeared before 2001; green ('present') = sites where *C. hastulatum* was present in 2001.

6.3.2 2015 ASSESSMENT

The RDA based on the 2015 data showed that 91.4% of total variance is explained by the environmental variables, but the overall model showed no significant differences between ponds where *C. hastulatum* disappeared between 2001 and 2015 (category 2) and ponds where the species was present in 2015 (category 3) (fig. 6.4). The first two RDA axes explained 21.2% and 12.4% of total variance respectively.

The RDA axes scores did not differ significantly between both categories, but specific environmental variables did differ, including small floating leaves cover (p = 0.037) and short emergent vegetation cover (p = 0.027). Large floating leaves cover tended to differ (p = 0.085). These three vegetation structures had, on average, lower covers in ponds of category 2.

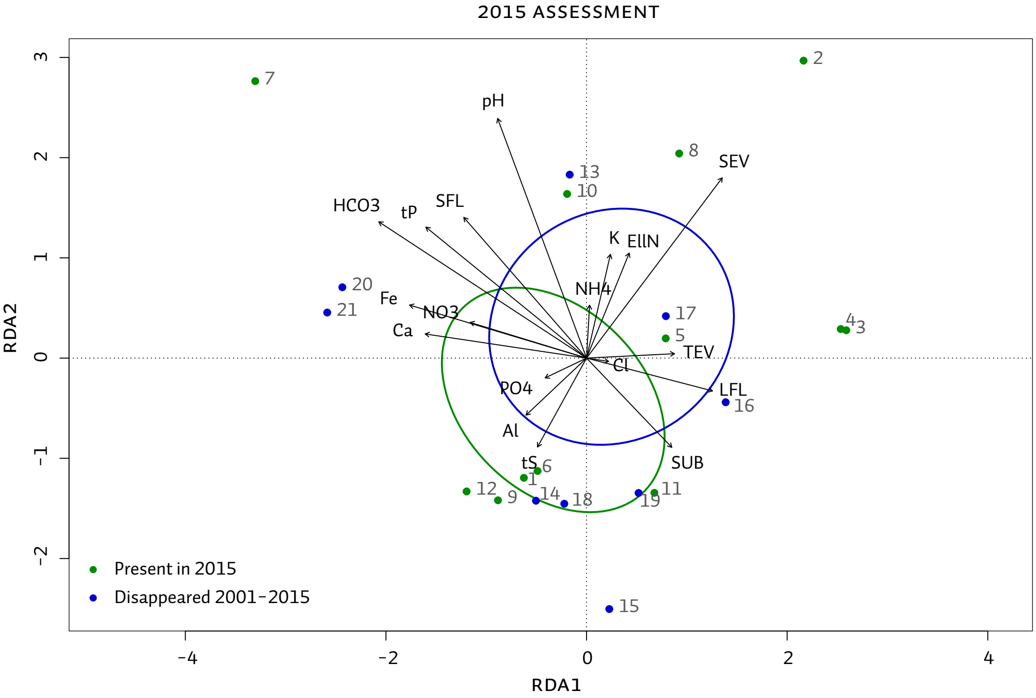


FIG. 6.4: Redundancy analysis (RDA) of the 2015 data. Numbered dots represent studied sites (see appendix 6.1 for corresponding sites) and are coloured according to presence category. Ellipses represent 95% confidence intervals. Arrows represent dissolved elements and other measured parameters: Al = aluminium, Ca = calcium, Fe = iron, HCO3 = bicarbonate, K = potassium, Cl = chloride, NH4 = ammonium, NO3 = nitrate, PO4 = orthophosphate, tP = total phosphorus, tS = total sulphur, SUB = submerged vegetation cover; SFL = plants with small floating leaves cover; LFL = plants with large floating leaves cover; SEV = short emergent vegetation cover; TEV = tall emergent vegetation cover; EllN = Ellenberg Nitrogen. Longer arrows indicate stronger correlations with first or second RDA axis.

In addition to the RDA results, univariate testing showed higher sodium ($p < 0.01$), chloride ($p < 0.01$) and manganese concentrations ($p < 0.05$) in ponds of category 2, which most likely caused the higher electrical conductivity of these ponds ($p < 0.05$) (fig. 6.5).

The triplot based on data from both 2001 and 2015 (fig. 6.6) gave some further insight on how *C. hastulatum* habitats changed during this period. Ponds where *C. hastulatum* was still present in 2015 had become more similar to ponds where the species disappeared between 2001 and 2015, mostly due to a decrease in short emergent vegetation. This suggests that these ponds, although still occupied by *C. hastulatum*, became less suitable, foreboding unfavourable prospects in the years to come.

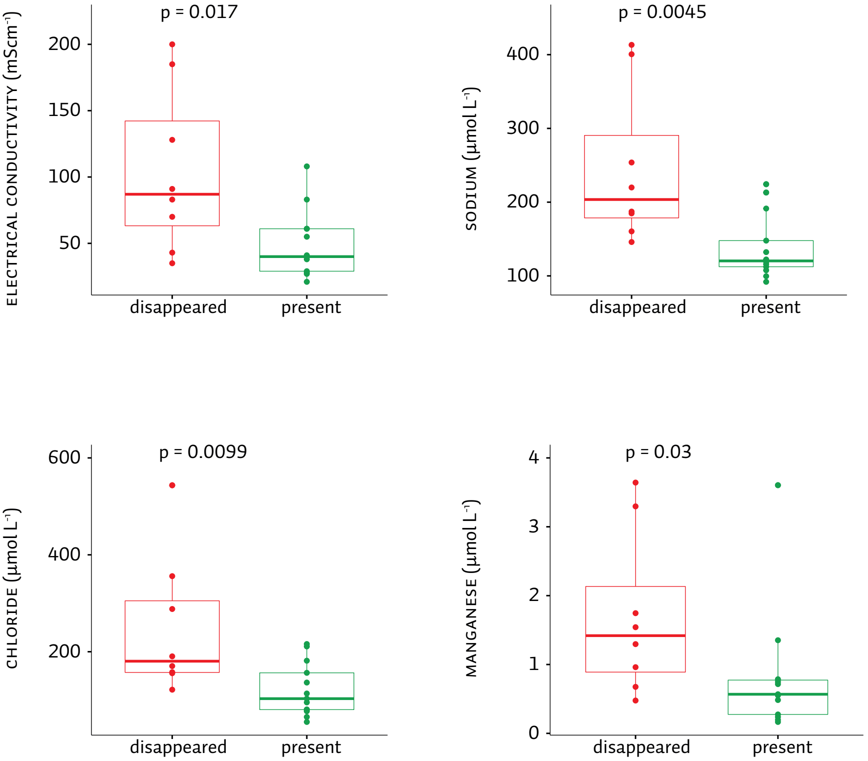


FIG. 6.5: Results of univariates analyses of the 2015 measurements. Only variables with significant differences ($p < 0.05$) are shown. Figures above brackets are p-values of Wilcoxon tests. Presence categories are on X-axis: red ('disappeared') = sites where *C. hastulatum* disappeared between 2001 and 2015; green ('present') = sites where *C. hastulatum* was present in 2015.

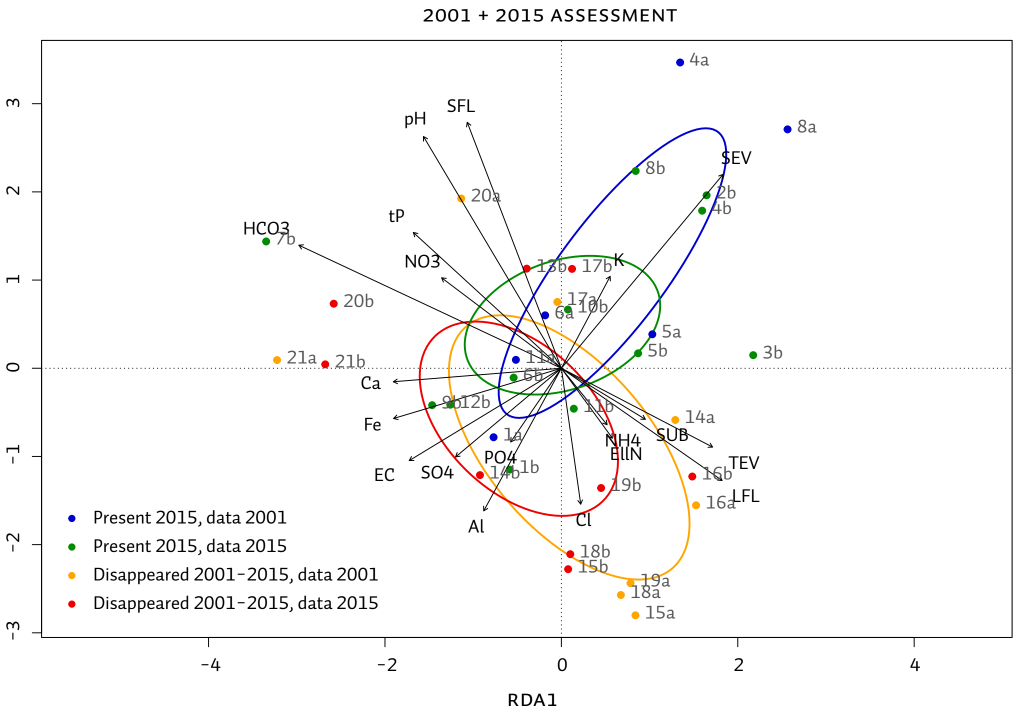


FIG. 6.6: Redundancy analysis (RDA) of both the 2001 and the 2015 data. Numbered dots represent studied sites, where 'a' = data 2001 and 'b' = data 2015 (see appendix 6.1 corresponding sites). Ellipses represent 95% confidence intervals. Arrows represent dissolved elements and other measured parameters: Al = aluminium, Ca = calcium, Fe = iron, HCO3 = bicarbonate, K = potassium, Cl = chloride, NH4 = ammonium, NO3 = nitrate, PO4 = orthophosphate, tP = total phosphorus, SO4 = sulphate, SUB = submerged vegetation cover; SFL = plants with small floating leaves cover; LFL = plants with large floating leaves cover; SEV = short emergent vegetation cover; TEV = tall emergent vegetation cover; EC = electrical conductivity, EllN = Ellenberg Nitrogen. Longer arrows indicate stronger correlations with first or second RDA axis.

6.3.3 2021 ASSESSMENT

Indeed, the conservation status of *C. hastulatum* deteriorated further in the period 2016-2021. The 12 remaining occupied ponds have been closely monitored, which gave a clear picture of changes at each pond on a year-to-year basis. Summers of 2018, 2019 and 2020 were very dry (see appendix 6.2 for meteorological records), leading to large precipitation deficits and subsequent lower groundwater levels and complete drying up of reproduction sites throughout the Dutch range of *C. hastulatum* (Brakkee et al., 2021; KNMI, 2021). These summer droughts are linked to climate change: along with the rise in temperature, which was especially steep from the 1970s onward (fig. 6.7), the frequency of summer droughts has increased as well, with 2018 being the second driest summer ever since recording started in 1901 (KNMI, 2021).

The drought of 2018 started in early spring already, leading to the complete desiccation of larval habitats of *C. hastulatum* even before the emergence of adults (fig. 6.8). As a consequence, the remaining populations of the ponds 'Beuven-Zuid', 'Brandtorenven', 'Hoenderboom', 'Peelloop', 'Vogelsven' and 'Vressels Bos, groot ven' disappeared in 2018-2019. No observations of *C. hastulatum* have been made at these ponds after 2018 or 2019. The population at pond 'Korenburgerveen, Brandsloot' met the same fate, although at this pond *C. hastulatum* numbers had clearly dropped before 2018 already and the species could not be confirmed in 2017. If it was still (marginally) present in 2018, the 2018-2020 drought likely gave the final blow.

One positive event can be mentioned from period 2016-2021 as well, as a small population was established in a nature restoration area close to pond 'Vressels Bos, groot ven'. This nature restoration area concerns a former arable field from which the nutrient-rich topsoil was removed in 2002 to establish nutrient poor conditions. The ground level lowering resulted in a permanently wet area with groundwater fed pools. In 2015 the vegetation succession in these pools had sufficiently progressed to enable colonisation by *C. hastulatum*. The newly established population survived the drought of 2018-2020 due to the ground level lowering and specific hydrological situation.

Anno 2021 only 5 occupied ponds remained: 'Haaksbergerveen, Stobbenveen', 'Klein Hasselsven', 'Klokketorenven', 'Ronde Vlaas' and the new site near 'Vressels Bos, groot ven'.

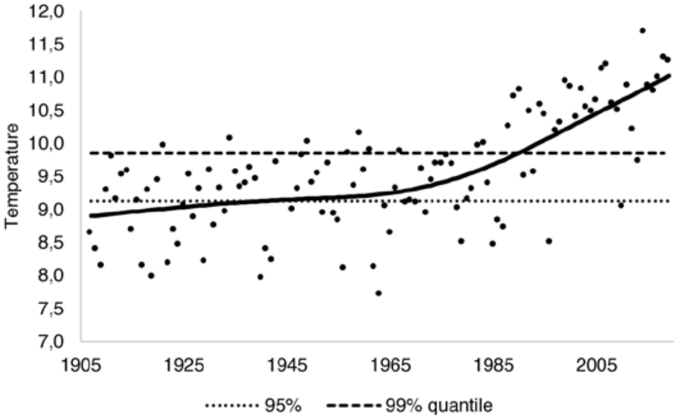


FIG. 6.7: Mean annual temperature (°C) recorded at 5 weather stations of Royal Netherlands Meteorological Institute (KNMI), 1907-2019 with the 95% and 99% quantile of the occurrence of *C. hastulatum*.

FIG. 6.8: Moorland pool 'Beuven-Zuid' on May 25th 2015 (l) and May 25th 2019 (r). Extreme drought during spring and summer of 2018 led to complete desiccation of emergent beds of *Carex lasiocarpa* and *C. rostrata*. Prior to desiccation, this site harboured the largest remaining population of *Coenagrion hastulatum* in the Netherlands, with hundreds of adults during the peak of the flight season. In 2020 none could be found.

6.4 Discussion

6.4.1 DATA CONSIDERATIONS

This exploratory study is based on a rather limited number of sites, especially concerning the number of sites still occupied by *C. hastulatum* in 2015. This limits the power of our analyses. However, since we included *all* known ponds where *C. hastulatum* once reproduced we made the best assessment possible. Given the alarming conservation status of *C. hastulatum* in the Netherlands, we believe that it is opportune to see what can be learnt from these analyses, in order to optimise conservation efforts.

6.4.2 2001 ASSESSMENT

Analyses of the 2001 data showed that ponds (once) occupied by *C. hastulatum* are at least periodically fed by slightly buffered, mineral-rich groundwater. This may consist of regional groundwater, but in many cases ponds with *C. hastulatum* have local aquifers that are disconnected from the regional groundwater table (Ketelaar, 2001; Termaat & Van Kleef, 2016). In both cases however, groundwater influence is essential for habitat suitability since it enhances buffer capacity and helps stabilise the water level. In turn, these abiotic conditions enable the growth of a diverse and richly structured aquatic and riparian vegetation, typically consisting of a combination of plants with small floating leaves (mainly *Potamogeton sp.*, *Hydrocharis morsus-ranae*), plants with large floating leaves (*Nymphaea alba* and *Nuphar lutea*), beds of short emergent vegetation in shallow water (mainly *Carex rostrata*, *C. lasiocarpa*, *Eleocharis sp.*) and fringes of tall emergent vegetation at the borders (*Phragmites australis*, *Schoenoplectus lacustris*, *Typha sp.*). It is plausible that a combination of these groundwater dependent vegetation structures provides necessary shelter and sufficient prey for *C. hastulatum* larvae (but see Dinning et al., 2022, who found a negative association with high densities of emergent and floating vegetation in Scotland). The historical absence of *C. hastulatum* from strictly rainwater fed ponds is likely driven by the lack of suitable vegetation structures, although increased stability of water level and water temperature in groundwater fed ponds may be directly beneficial to *C. hastulatum* as well.

Besides groundwater influence, the historical anthropogenic use of ponds with *C. hastulatum* has led to comparable mesotrophic, lightly buffered conditions. In the 19th century and first half of the 20th century the ponds 'Belversven', 'Groot Goorven' and 'Groot Malpieven' were fed by moderately enriched brook water, which led to suitable gradients in trophic level, pH and subsequent vegetation structures (Termaat, 2006). Also, the influx of drifting sand, the washing of sheep and duck trapping in ponds are mentioned as historical sources of mild enrichment and buffering (Van Dam et al., 1988). Later, the mesotrophic, lightly buffered conditions were lost in many ponds, because they became too eutrophic. This eutrophication can have different causes, including the inlet of enriched surface water (pond 'Belversven'), fertilisation for the benefit of fish farming or (later) recreational fishing (ponds 'Belversven', 'Groot Malpieven' and 'Groot Goorven'), or the establishment of large breeding colonies of Black-headed gull (*Chroicocephalus ridibundus*), whose droppings led to a considerable nutrient input (ponds 'Groot Malpieven' and 'Pikmeeuwwater') (Ketelaar, 2001). In other cases, ponds acidified as brooks were disconnected, the influx of drifting sand stopped, or because the washing of sheep and trapping of ducks were no longer common practise.

From the 1960s onward, another development strongly affected the water quality of Dutch ponds. Rising emissions of sulphur dioxide, ammonia and nitrogen oxides, originating from industries, agriculture and traffic, caused a strongly elevated acid load in ponds via atmospheric deposition of acidifying sulphur and nitrogen compounds. These depositions peaked in the 1960s and 1970s (sulphur dioxide) and 1980s (ammonia and nitrogen oxides) (CBS et al., 2019) and are well-known bottlenecks in Dutch moorland pools, shallow oligo-mesotrophic lakes and peat bogs (Roelofs, 1983; Van Dam & Kooijman-van Blokland, 1978; Van Dobben et al., 2014).

All of the developments mentioned above led to either acidification or eutrophication and alkalinisation of ponds where *C. hastulatum* disappeared before 2001. Additionally, one population disappeared just before 2001 as a result of a well-intended pond restoration measure. During winter 1999-2000 pond 'Kluizerweg, ven langs' was 'restored' by removing all accumulated organic sediment from the bottom, together with all vegetation in the pond (Ketelaar, 2001). As the occurrence of *C. hastulatum* at this ponds was not known to the local site manager, the complete larval habitat of the species was accidentally excavated.

Overall, the 2001 assessment indicates that habitat suitability of *C. hastulatum* is mediated by some degree of acid buffering, by medium levels of nutrient input and by relatively stable water levels, resulting in a rich combination of vegetation structures. Historically, the source of nutrients and base cations may either have been natural, via contact with (local) groundwater or influx of drifting sand, or anthropogenic. Later, after large-scale deterioration of stream water quality in the Netherlands, the inlet of polluted water led to eutrophication of *C. hastulatum* habitats and subsequent disappearance of its populations. When water inlet was terminated, (local) groundwater was left as the most important source for buffering in ponds with remaining populations. Acidification by elevated sulphur dioxide, ammonia and nitrogen dioxides then led to the loss of another share of *C. hastulatum* populations before 2001. Other historical populations have disappeared due to external input of nutrients, or accidental habitat destruction.

6.4.3 2015 ASSESSMENT

In accordance with the 2001 assessment the additional loss of *C. hastulatum* populations between 2001 and 2015 is associated with low coverage of emergent and floating vegetation, leading to lower availability of typically well-vegetated larval habitats. Underlying causes for the decline of *Carex* sp. and *Potamogeton* sp. (the mesotraphent plant species which most often build these essential vegetation structures) could not be clearly demonstrated, due to the small sample size (n=9).

Deposition of nitrogen and especially sulphur depositions have decreased in recent decades, resulting in a recovery towards higher pH values and other improvements in pond water chemistry (Van Kleef et al., 2010). However, ponds in nutrient-poor landscapes still cope with their detrimental effects (Brouwer et al., 2018). Moreover, recent nitrogen deposition in the Netherlands remains very high (24.7 kg N ha-1 yr-1 in 2019) and still exceeds the critical load for oligotrophic and mesotrophic standing waters by a factor 2-5 (Bobbink & Roelofs, 1995; CBS et al., 2022). Under these unfavourable conditions, the buffering effect of groundwater, either from a regional or local origin, remains essential to prevent acidification of these waters. Unfortunately however, regional groundwater levels have dropped significantly throughout most of the Dutch range of *C. hastulatum* (CBS et al., 2020a), as a result of groundwater extraction for drinking water production, agricultural irrigation and industrial purposes. Local aquifers, which are characteristic for many ponds with *C. hastulatum*, have shrunk as well, due to increased interception and evaporation by coniferous tree plantations and more frequent droughts. The decrease in (local) groundwater influence led to a decrease in acid buffering and water level stabilisation, probably to a decrease of floating and emergent vegetation, and ultimately to the loss of *C. hastulatum* populations.

Besides acidification, eutrophication of ponds remained a threat after 2000. Higher temperatures, due to climate warming, and less severe acidification have led to faster mineralisation of accumulated organic matter in ponds (Van Dam & Mertens, 2019; Van Kleef et al., 2010). This has led to increased phosphate mobilisation, a process known as 'internal eutrophication' (Smolders et al., 2006).

Just like during the period before 2001, some *C. hastulatum* populations were lost between 2001 and 2015 as a direct result of harmful habitat management rather than environmental pressures.
Pond 'Achtereind, ven bij' was intentionally drained by means of two small ditches, which were dug between the pond and a nearby stream. This caused desiccation of the shallow pond edges, leading to strong oxidation of organic matter and a decrease in the surface area of water-logged *C. rostrata* fringes.
Pond 'Grevenschutven, NO-baai' concerns a small, shallow, mesotrophic bay of a much larger, eutrophic fish farming pond. The water levels in the pond are actively

managed by adjusting the inlet and outlet of surface water from a nearby stream. During winter 2009-2010 the water levels were lowered to a point where the shallow bay completely dried up. This unavoidably led to the loss of the *C. hastulatum* population.
Site 'Buurserzand, afvoersloot' concerns a ditch with dense stands of *P. polygonifolius*, which harboured the *C. hastulatum* larvae. During winter 1999-2000 the ditch was completely 'cleaned' by the local water board to enhance drainage of an upstream agricultural area. All aquatic vegetation was removed at once. The *C. hastulatum* population was unable to recover.
Lastly, although speculative, the disappearance of *C. hastulatum* from pond 'Karperven' may have been caused by the presence of exotic fish species. In terms of vegetation structures the pond seems still suitable, but both Pumpkinseed (*Lepomis gibbosus*) and Eastern mudminnow (*Umbra pygmaea*) are known to occur, the latter in high densities. Both exotic fish species prey on small invertebrates, including damselfly larvae.

On the positive side, pond 'Klokkentorenven' was successfully restored in 2012, when the population was on the brink of extinction. Ditches in the surrounding of the site were closed and coniferous forest in the infiltration zone was removed to elevate and stabilise the local groundwater table. In addition, the banks were set free of trees, scrubs and accumulated organic matter to enable expansion of the riparian vegetation. In 2014 the number of recorded *C. hastulatum* adults had already risen again and in 2015 it was even higher than it had been since 2000.

6.4.4 2021 ASSESSMENT

All 7 populations that were lost after 2015 disappeared with certainty, or in the case of pond 'Korenburgerveen, Brandsloot' most likely, due to the summer droughts of 2018-2020. The larval habitats at these ponds dried up completely or almost completely. Other remaining populations may well have suffered from these droughts as well. Even if larval habitats did not dry up completely, rising water temperatures elevate metabolic demand for oxygen by Odonata larvae and cause a reduction in the oxygen saturation of the water, at least during the night when oxygen is respired but not produced (Harrison et al., 2018; Verberk & Bilton, 2013). This combination might have been fatal for *C. hastulatum* larvae or might have reduced their ability to compete with co-occurring species that prefer higher temperatures, such as *Coenagrion puella* or *Ceriagrion tenellum*.

Remarkably, the populations at both sites where rewetting measures were recently carried out – pond 'Klokkentorenven' and the recently colonised site near 'Vressels Bos, grote ven'– survived the 2018-2020 droughts. Nonetheless, the recorded numbers at these sites were very low in 2021, with a maximum of 5 and 4 counted damselflies on a single day respectively.

While the mean annual temperature in the Netherlands has always been above average for the entire European range of C. *hastulatum* (Termaat et al., 2019), it has exceeded its 99% quantile from the 1980s onward (fig. 6.7). This is a strong indication that climate change has indeed rendered the Netherlands largely unsuitable for the species. However, climate change being the cause for the loss of populations after 2015 does not imply that acidification or internal eutrophication are no longer deteriorating the quality of C. *hastulatum* habitats. It rather means that the populations of C. *hastulatum* most exposed to these threats had already been lost, or that the negative impact of climate change has become the predominant threat.

6.4.5 TEMPORAL CHANGE IN CAUSES OF DECLINE

This study shows that the most prominent threats for a species may change over time and that with each new threat an additional set of populations may be lost. In the period 1921-2000, eutrophication and acidification through changes in the anthropogenic use of C. *hastulatum* reproduction sites, followed by acidification through atmospheric sulphur and nitrogen deposition, were the most prominent causes for loss of C. *hastulatum* populations. In the period 2001-2015, the causes were more versatile. Nitrogen deposition remained a pressure as it still exceeded the critical deposition value for oligotrophic and mesotrophic water bodies. Eutrophication shifted from a mainly external to mainly internal process, as decreased acidification and increased water temperatures led to faster decomposition of organic matter in ponds. In addition, several populations were lost in this period due to harmful habitat management. After 2015, dry summer spells, which are linked to climatic changes in temperature and precipitation, were the main cause for the loss of additional C. *hastulatum* populations.

Thus, in the course of time, different pressures have repeatedly claimed more and more C. *hastulatum* populations. In 2021 merely 5 of the initial 33 known populations in the Netherlands remained.

6.4.6 CHANGING PRESSURES REQUIRE CHANGING MEASURES

The notion that different threats become prominent over time implies that conservation strategies should be evaluated and adjusted regularly in order to focus on threats that are the most pressing. Our study may serve as an example, as we identified three periods with different threats based on assessments in 2001, 2015 and 2021. Prior to 2001, avoiding external (anthropogenic) nutrient input, avoiding drainage of ponds, restoring local groundwater levels and reducing sulphur dioxide, ammonia and nitrogen dioxides emissions would have contributed most to the conservation of C. *hastulatum*. In the period 2001-2015, further reduction of atmospheric nitrogen deposition would have been most effective, as well as more careful habitat management. From 2015 until today, C. *hastulatum* habitats should first be made more resilient to the impact of rising temperatures and summer droughts. This requires a landscape-ecological approach to restore the hydrology of nutrient-poor ponds which are fed by regional or local groundwater. In the meanwhile, further reduction of nitrogen emissions is still urgent, but acidification and eutrophication have been overtaken by desiccation and warming as most acute threats to the last remaining populations.

In this example, threats to *C. hastulatum* not only changed over time, but became more demanding to oppose as well. After all, avoiding direct habitat destruction through drainage or fertilisation of a pond is much easier to accomplish than solving the larger-scaled problems that came next, such as eutrophication and acidification via sulphur and nitrogen emissions. Subsequently, counteracting the most recent threat, climate change, is even harder. This means that conserving the last remaining *C. hastulatum* populations is more challenging than it would have been to conserve populations that disappeared earlier, even when the increased negative effects of habitat fragmentation and isolation of remaining populations are not taken into account.

6.4.7 PERSPECTIVE

Lately, some authors have expressed cautious optimism about recent developments in Dutch moorland pools and shallow oligo-mesotrophic lakes. Brouwer et al. (2018) conclude that a long decline of biodiversity and environmental quality of such water bodies switched into a gradual recovery, as a reaction to a strong decrease in sulphur deposition and a modest decrease in nitrogen deposition in the last decades. This gradual recovery has indeed been documented for various species groups, including dragonflies (Termaat et al., 2015). In the meantime, however, climate change has become a dominant threat for the biodiversity of ponds characterised by oligotrophic and mesotrophic conditions and rather stable water levels. As these ponds mainly occur in areas of higher latitudes and altitudes, the characteristic insect species that prefer these water bodies generally also prefer cool conditions, such as *C. hastulatum*. Therefore, many of these species are likely to be sensitive to climate warming.

Climate change has already been shown to be a prominent explanation for recent dragonfly trends at European level (Termaat et al. 2019). We expect this is to become more and more evident at national level in the Netherlands as well. While populations may have lingered for some time under suboptimal climatic conditions, a phenomena often referred to as 'extinction debt' (Hanski & Ovaskainen, 2002), the first losses are now becoming apparent. Besides *C. hastulatum*, other species which prefer cool conditions such as *C. lunulatum*, *Aeshna juncea*, *Leucorrhinia rubicunda* and *Sympetrum danae* (Termaat et al., 2019) are recently showing strong declines in the Netherlands as well (Van Grunsven et al., 2020). More species are likely to follow, as the rising of water temperatures will continue and summer droughts are predicted to occur more frequently in years to come. Since local or even national measures will not turn the tide of climate change, it is urgent to carry out measures that lie within the sphere of influence of policy makers and nature conservation managers. Restoration of groundwater systems and rewetting measures are first priorities. Whether these measures will save *C. hastulatum* for the Netherlands is unknown, but they are essential to reduce a further loss of pond biodiversity.

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References

Benjamini Y., & Hochberg Y. (1995). Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal statistical society: series B (Methodological)* 57: 289-300.

Bobbink R. & Roelofs J.G.M. (1995). Nitrogen critical loads for natural and semi-natural ecosystems: the empirical approach. *Water, Air, & Soil Pollution* 85: 2413-2418.

Boudot J.P. & Kalkman V.J. (editors) (2015). *Atlas of the European dragonflies and damselflies*. KNNV Publishing, Zeist.

Brakkee E., Van Huijgevoort M. & Bartholomeus R.P. (2021). Spatiotemporal development of the 2018–2019 groundwater drought in the Netherlands: a data-based approach. *Hydrology and Earth System Sciences Discussions* 2021: 1-26.

Bried J., Ries L., Smith B., Patten M., Abbott M., ... & White, E. (2020). Towards global volunteer monitoring of odonate abundance. *Bioscience* 70: 914-923.

Brouwer E., Van Dam H., Van Tooren B.F., Hanhart K. & Van Erve F.J.H. (2018). Vennen in Midden-Brabant: er is weer leven na de dood. *De Levende Natuur* 119: 91-94.

CBS, PBL, RIVM & WUR (2019). *Verzurende depositie, 1990-2017* (indicator 0184, version 18, 5 June 2019). www.clo.nl. https://www.clo.nl/indicatoren/nl0184-verzurende-depositie. Accessed 20 July 2022.

CBS, PBL, RIVM & WUR (2020a). *Geschiktheid grondwaterstand verdrogingsgevoelige landnatuur, 2018* (indicator 1594, version 03, 23 June 2020). https://www.clo.nl/indicatoren/nl1594-kwaliteit-grondwaterafhankelijke-ecosystemen. Accessed 20 July 2022.

CBS, PBL, RIVM & WUR (2020b). *Temperatuur in Nederland en mondiaal, 1907 - 2019* (indicator 0226, version 14, 21 April 2020). https://www.clo.nl/indicatoren/nl0226-temperatuur-mondiaal-en-in-nederland. Accessed 20 July 2022.

CBS, PBL, RIVM & WUR (2022). *Stikstofdepositie, 1990-2020* (indicator 0189, version 19, 8 June 2022). https://www.clo.nl/indicatoren/nl0189-stikstofdepositie. Accessed 20 July 2022.

Corbet P.S. (1999). *Dragonflies: Behaviour and ecology of Odonata*. Harley Books, Colchester

Daguet C.A., French GC & Taylor P (2008). The Odonata Red Data List for Great Britain. Species Status 11:1-34. Joint Nature Conservation Committee, Peterborough.

De Knijf G., Wils C. & Maes D. (2021). *IUCN Rode Lijst van de libellen (Odonata) in Vlaanderen*. Rapporten van het Instituut voor Natuur- en Bosonderzoek 2021(59). Instituut voor Natuur- en Bosonderzoek, Brussel.

Dinning J., Stockan J.A., Fielding D.A. & Young M.R. (2022). Habitat suitability for *Coenagrion hastulatum* (Charpentier)(Northern Damselfly) in North-east Scotland. *Journal of the British Dragonfly Society* 38: 47-64.

Di Marco M., Chapman S., Althor G., Kearney S., Besancon C., … & Watson J.E. (2017). Changing trends and persisting biases in three decades of conservation science. *Global Ecology and Conservation* 10: 32-42.

Ellenberg H., Weber H.E., Dull R., Wirth V., Werner W. & Paulisen D. (1991). Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica*, Band 18. Verlag Erich Goltze KG, Göttingen

Fox R., Harrower C.A., Bell J.R., Shortall C.R., Middlebrook I. & Wilson R.J. (2019). Insect population trends and the IUCN Red List process. *Journal of Insect Conservation* 23: 269-278.

Hallmann C.A., Sorg M., Jongejans E., Siepel H., Hofland N., … & De Kroon H. (2017). More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS ONE* 12 e0185809.

Hanski I. & Ovaskainen O. (2002). Extinction debt at extinction threshold. *Conservation Biology* 16: 666-673.

Harrison J.F., Greenlee K. & Verberk W.C.E.P. (2018). Functional Hypoxia in Insects: Definition, Assessment, and Consequences for Physiology, Ecology and Evolution. *Annual Review of Entomology* 63: 303-325.

Huikkonen I.M., Helle I. & Elo M. (2020). Heterogenic aquatic vegetation promotes abundance and species richness of Odonata (Insecta) in constructed agricultural wetlands. *Insect Conservation and Diversity* 13: 374-383.

Jansen A. & Grootjans A. (editors) (2019). *Hoogvenen*. Noordboek, Gorredijk.

Kalkman V.J., Boudot J.P., Bernard R., Conze K.J., De Knijf G., … &. Sahlén G. (2010). *European Red List of Dragonflies*. Publications Office of the European Union, Luxembourg.

Kalkman V.J., Boudot J.P., Bernard R., De Knijf G., Suhling F. & Termaat T. (2018). Diversity and conservation of European dragonflies and damselflies (Odonata). *Hydrobiologia* 811: 269-282.

Ketelaar R. (2001). *De speerwaterjuffer in Nederland: verspreiding, ecologie en bescherming*. *De Vlinderstichting*. Rapport VS2001.032, Wageningen.

KNMI Royal Netherlands Meteorological Institute (2022). *Drought Monitor.* https://www.knmi.nl/nederland-nu/klimatologie/droogtemonitor. Accessed 20 July 2022.

Mabry C. & Dettman C. (2010). Odonata richness and abundance in relation to vegetation structure in restored and native wetlands of the Prairie Pothole Region, USA. Ecological Restoration 28: 475-484.

Motte G., Dufrêne M., Mayon N., Goffart P., Barbier Y., … & Vandevyvre X. (2021). Liste rouge 2021 des Libellules de Wallonie. *Naturalistes Belges*: 102.

Nederlandse Vereniging voor Libellenstudie (2002). *De Nederlandse libellen (Odonata).* Nederlandse Fauna 4. Nationaal Natuurhistorisch Museum Naturalis, KNNV Uitgeverij, and European Invertebrate Survey-Nederland, Leiden.

Ott J., Conze K.J., Günther A., Lohr M., Mauersberger R., … & Suhling F. (2015). *Rote Liste der Libellen Deutschlands 2015*. Libellula, Supplement 14, Atlas der Libellen Deutschlands, GdO e.V.

R Core Team (2013). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.R-project.org/.

Raebel E.M., Merckx T., Feber R.E., Riordan P., MacDonald D.W. & Thompson D.J. (2012). Identifying high-quality pond habitats for Odonata in lowland England: implications for agri-environment schemes. *Insect Conservation and Diversity* 5: 422-432.

Roelofs J.G.M. (1983). Impact of acidification and eutrophication on macrophytes communities in soft waters in the Netherlands. I. Field observations. *Aquatic Botany* 17: 139-155.

Schowalter T.D., Pandey M., Presley S.J., Willig M.R. & Zimmerman J.K. (2021). Arthropods are not declining but are responsive to disturbance in the Luquillo Experimental Forest, Puerto Rico. *Proceedings of the National Academy of Sciences of the United States of America* 118.

Smolders A.J.P., Lamers L.P.M., Lucassen E.C.H.E.T., Van der Velde G. & Roelofs J.G.M. (2006). Internal eutrophication: how it works and what to do about it—a review. *Chemical Ecology* 22: 93-111.

Tansley, A.G. (1946). *Introduction to plant ecology*. Allen & Unwin, Londen.

Termaat T. (2006). *Op de bres voor de speerwaterjuffer: beschermingsplan voor de speerwaterjuffer in Noord-Brabant*. Provincie Noord-Brabant, 's-Hertogenbosch.

Termaat T. & Kalkman V.J. (2012). Basisrapport Rode Lijst Libellen volgens Nederlandse en IUCN-criteria. *Brachytron* 14: 75-186.

Termaat T. & Van Kleef H. (2016). Als een speer aan de slag. *Vlinders* 29: 12-14.

Termaat T., Van Grunsven R.H.A., Plate C.L. & Van Strien A.J. (2015). Strong recovery of dragonflies in recent decades in The Netherlands. *Freshwater Science* 34: 1094-1104.

Termaat T., Van Strien A.J., Van Grunsven R.H.A., De Knijf G., Bjelke U., … & WallisDeVries M.F. (2019). Distribution trends of European dragonflies under climate change. *Diversity and Distributions* 25: 936-950.

Van Dam H. & Kooijman-van Blokland H. (1978). Man-made changes in some Dutch moorland pools, as reflected by historical and recent data about diatoms and macrophytes. *Internationale Revue der gesamten Hydrobiologie* 63: 587-607.

Van Dam H. & Mertens A. (2019). *Monitoring recovery of acidification and effects of climate change in shallow soft water lakes in The Netherlands: Temperature, hydrology, chemistry, diatoms*. Herman van Dam Adviseur Water en Natuur, report AWN 1702, Amsterdam.

Van Dam H., Van Geel B., Van der Wijk A., Geelen J.F.M., Van der Heijden R. & Dickman M.D. (1988). Palaeolimnological and documented evidence for alkalization and acidification of two moorland pools (The Netherlands). *Review of Palaeobotany and Palynology* 55: 273-316.

Van Dobben H.F., Bobbink R., Bal D. & Van Hinsberg A. (2014). *Overview of critical loads for nitrogen deposition of Natura 2000 habitat types occurring in The Netherlands (No. 2488)*. Alterra, Wageningen-UR, Wageningen.

Van Grunsven R., Bos G. & Poot M. (2020). Strong changes in Dutch dragonfly fauna. *Agrion* 24: 134-138.

Van Kleef H.H., Brouwer E., Van Leuven R.S., Van Dam H., De Vries-Brock A., ... & Esselink H. (2010). Effects of reduced nitrogen and sulphur deposition on the water chemistry of moorland pools. *Environmental Pollution* 158(8): 2679-2685.

Van Klink R., Bowler D.E., Gongalsky K.B., Swengel A.B., Gentile A. & Chase J.M. (2020). Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. *Science* 368: 417-420.

Van Strien A.J., Van Swaay C.A.M. & Termaat T. (2013). Opportunistic citizen science data of animal species produce reliable estimates of distribution trends if analysed with occupancy models. *Journal of Applied Ecology* 50: 1450-1458.

Verberk W.C.E.P. & Bilton D.T. (2013). Respiratory control in aquatic insects dictates their vulnerability to global warming. *Biology Letters* 9: 20130473.

Vu V.Q. (2011). ggbiplot: *Biplot for Principal Components using ggplot2. R package version 0.55*. Available at: http://github.com/vqv/ggbiplot.

Wagner D.L., Fox R., Salcido D.M. & Dyer L.A. (2021). A window to the world of global insect declines: Moth biodiversity trends are complex and heterogeneous. *Proceedings of the National Academy of Sciences of the United States of America* 118.

Warren M.S., Maes D., Van Swaay C.A.M., Goffart P., Van Dyck H., ... & Ellis S. (2021). The decline of butterflies in Europe: Problems, significance, and possible solutions. *Proceedings of the National Academy of Sciences of the United States of America* 118.

Appendix 6.1

Study sites (ponds), with location, presence category and years of sampling.

Site no.	Site name	Long	Lat	Presence category	Sampled 2001	Sampled 2015	Presence
1	Korenburgerveen, Brandsloot	6.659633	51.98830	3	X	X	present in 2015
2	Beuven-Zuid	5.642952	51.39358	3		X	present in 2015
3	Brandtorenven	5.552417	51.38924	3		X	present in 2015
4	Hoenderboom	5.638622	51.38999	3	X	X	present in 2015
5	Klein Hasselsven	5.517765	51.32906	3	X	X	present in 2015
6	Klokketorenven	5.241581	51.55107	3	X	X	present in 2015
7	Peelloop	5.655894	51.39534	3		X	present in 2015
8	Ronde Vlaas	5.520700	51.35153	3	X	X	present in 2015
9	Vogelsven	5.509729	51.54211	3		X	present in 2015
10	Vressels Bos, groot ven	5.502546	51.55200	3		X	present in 2015
11	Haaksbergerveen, Stobbenveen	6.790451	52.12075	3	X	X	present in 2015
12	Haaksbergerveen, ZW-hoek Oost	6.777285	52.12001	3		X	present in 2015
13	Meddosche Veen, vlonderpad	6.665481	51.98914	3		X	present in 2015
14	Meddosche Veen, kern	6.659709	51.99100	2	X	X	disappeared between 2001 and 2015
15	Achtereind, ven bij	5.490608	51.37493	2	X	X	disappeared between 2001 and 2015
16	Grevenschutven, NO-baai	5.515019	51.37311	2	X	X	disappeared between 2001 and 2015
17	Karperven	5.505054	51.40728	2	X	X	disappeared between 2001 and 2015
18	Molenven	5.446029	51.33092	2	X	X	disappeared between 2001 and 2015
19	Vressels Bos, laagte N-zijde	5.505432	51.55290	2	X	X	disappeared between 2001 and 2015
20	Buurserzand, afvoersloot	6.773855	52.15061	2	X	X	disappeared between 2001 and 2015
21	Harrevelder Schans	6.776748	52.14968	2	X	X	disappeared between 2001 and 2015
22	Kluizerweg, ven langs	5.516386	51.34884	1	X		disappeared prior to 2001
23	Italiaanse Meren	6.782986	51.92847	1	X		disappeared prior to 2001
24	Nonnenven	6.771108	51.92052	1	X		disappeared prior to 2001

Site no.	Site name	Long	Lat	Presence category	Sampled 2001	Sampled 2015	Presence
25	Uiversnest	5.795942	51.79044	1	X		disappeared prior to 2001
26	Pikmeeuwenwater	6.168120	51.51978	1	X		disappeared prior to 2001
27	Belversven	5.244403	51.57085	1	X		disappeared prior to 2001
28	Groot Goorven	5.204041	51.56450	1	X		disappeared prior to 2001
29	Groot Malpieven	5.451749	51.31743	1	X		disappeared prior to 2001
30	Meeuwven	5.499265	51.39111	1	X		disappeared prior to 2001
31	Peetersven	5.466179	51.36686	1	X		disappeared prior to 2001
32	Wolfsputten	5.219865	51.57531	1	X		disappeared prior to 2001
33	Bestmenerven	6.444467	52.49468	1	X		disappeared prior to 2001
34	Harrevelder Schans, ven W van	6.772338	52.14883	4	X		never present
35	Wooldsche Veen	6.748873	51.9064	4	X		never present
36	Bierven	5.513538	51.35693	4	X		never present
37	Brugven	5.470416	51.32821	4	X		never present
38	Dorven	5.500521	51.3183	4	X		never present
39	Grevenschutven, ven N van	5.510730	51.38031	4	X		never present
40	Kranenmeer, ven O van	5.641610	51.41066	4	X		never present
41	Laagveld Noord	5.494830	51.33808	4	X		never present
42	Lammervennen	5.211276	51.55822	4	X		never present
43	Raadven	5.467626	51.37315	4	X		never present
44	Rietven	5.509380	51.41267	4	X		never present
45	Buursermeertje	6.798773	52.15302	4	X		never present
46	Buurserveld	6.806506	52.16641	4	X		never present
47	Haaksbergerveen West	6.762854	52.12557	4	X		never present

Appendix 6.2

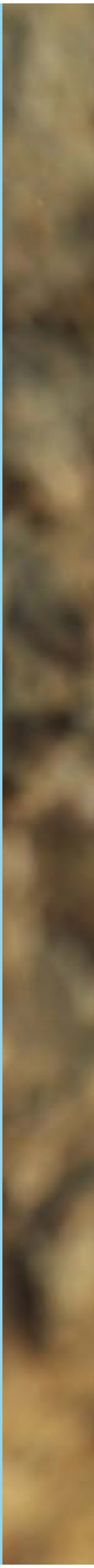
Weather data from two weather stations in the range of *Coenagrion hastulatum* in the Netherlands in the period 2000-2021 (source: Royal Netherlands Meteorological Institute (KNMI)).
Weather station ‘Twenthe’ is situated near the eastern (former) populations, weather station ‘Eindhoven’ is situated near de southern (former) populations. Mean temperature and precipitation sum are calculated over the complete years. Precipitation deficit is calculated as the cumulative difference between the measured amount of precipitation and the reference eva-potranspiration in the period April-September.

	Wheather station ‘Twenthe’ (east)	**Wheather station ‘Eindhoven’ (south)**				
Year	**Mean temperature (°C)**	**Precipitation sum (mm)**	**Precipitation deficit (mm)**	**Mean temperature (°C)**	**Precipitation sum (mm)**	**Precipitation deficit (mm)**
2000	10.6	8520	221	11.0	8393	641
2001	9.9	8362	368	10.5	9092	201
2002	10.3	7809	1057	11.0	8025	1437
2003	10.0	6188	1797	10.8	6779	1917
2004	9.9	8547	101	10.4	8172	285
2005	10.1	7987	278	10.8	7000	1237
2006	10.8	7222	1516	11.3	7251	1698
2007	10.7	9165	144	11.2	8457	499
2008	10.1	7311	1746	10.6	7105	980
2009	10.1	7807	1663	10.6	7319	2428
2010	8.5	7956	85	9.4	7557	1323
2011	10.4	6488	886	11.3	7304	1233
2012	9.8	7610	724	10.5	8493	115
2013	9.4	7571	886	10.1	7032	1505
2014	11.3	7926	10	11.8	8116	-190
2015	10.5	8770	673	11.1	6855	1994
2016	10.2	7160	1478	10.9	8366	669
2017	10.5	8535	584	11.2	7204	1729
2018	11.2	6102	3093	11.8	6302	3196
2019	11.0	7744	2573	11.5	7075	2812
2020	11.3	6871	2840	12.0	6835	3117
2021	10.1	-	1044	10.6	8217	666

Boyeria cretensis is endemic to the island of Crete (Greece), where it lives in streams that are at risk of desiccation.

CHAPTER 7

Synthesis



Methods for dragonfly monitoring

In the search for suitable methods to adequately monitor biodiversity, occupancy models have gained much attention in the last 20 years (Bailey et al., 2014; Kéry et al., 2010; MacKenzie et al., 2002, 2005; Van Strien et al., 2013). Since they may be helpful to derive robust trend information from opportunistic records rather than records collected via standardised field protocols, occupancy models make it possible to obtain trend information for more taxonomic groups than was previously possible. Dragonflies are among those taxonomic groups and represent the first aquatic taxa to be included. Chapter 2 of this thesis shows that occupancy models can successfully be used to derive reliable trend estimates from opportunistic data, mostly collected by voluntary dragonfly recorders ('citizen scientists'). By comparing occupancy probabilities based on opportunistic records with occupancy probabilities based on standardised collected records (the 'golden standard'), it is shown that the occupancy trends are indeed unbiased. This was later confirmed by Isaac et al. (2014) who tested the performance of 11 different statistical methods used in literature to infer trend estimations from opportunistic data. Each of these methods differed in the way they deal with various forms of variation in recorder activity. Their results showed that an occupancy-detection model with components to address uneven spatial coverage and sampling effort, which is very similar to the occupancy model used in chapters 2-5 of this thesis, outperformed all other methods. It had the most optimal combination of low Type I error rate and a relatively high power to detect trends. It is therefore the most appropriate method to analyse opportunistic (dragonfly) data for monitoring purposes.

Although the opportunistic records required for occupancy modelling do not have to meet specific criteria other than observation date and locality, the total dataset must meet some conditions in order to be able to apply the occupancy model successfully. First of all, sufficient repeated visits with comprehensive lists of recorded species are necessary to calculate detection histories, which are vital to infer detection probabilities for each species-year combination. This means that records of common, 'uninteresting' species and rarer, 'interesting' species are equally important. Dragonfly recorders should therefore be encouraged to report *all* dragonfly species during their field work and to make repeated visits to sites. Secondly, occupancy models assume that records are collected within a period of 'closure'. This means that, for a given year, a site must stay either occupied or not, but must not become permanently abandoned or colonised during the period of survey. As dragonflies are very mobile and may cover large distances during their adult lifetime this criterium cannot be fully met. However, it is shown in chapter 2 that using the boundaries of the species main flight season serves as an adequate proxy for a period of closure.

Using opportunistic data and occupancy modelling resulted in trends with sufficiently low standard errors for 56 of the 62 dragonfly species that reproduced in the Netherlands in 1991-2013 (chapter 4). This is 11 species more than the number of species for which the standardised Dutch Dragonfly Monitoring Scheme (DDMS) yielded robust trend estimates. Since these 11 species include 8 species listed on the Dutch Red List (Termaat & Kalkman, 2012), the occupancy trends have an important added value from a conservation point of view. However, it must be stressed that trends in occupancy represent trends in species *distribution*, while trends based on standardised counts reflect trends in species *abundance*. While these two variables are clearly linked they represent two fundamentally different aspects of the population dynamics and therefore provide different information on species occurrence. Comparing occupancy and abundance indices (chapter 4) showed that the latter are usually more sensitive, so that significant increases or declines become apparent earlier. This might be expected, as the number of individuals of a species at occupied sites is likely to increase for some time before new sites are colonised, or decrease before sites become abandoned. However, less frequently, opposite occupancy and abundance trends may occur, thus providing complementary information. A positive occupancy trend in combination with a negative abundance trend likely reflects frequent colonisation resulting in small populations, while the number of individuals in existing large populations is declining. This seems to be the case for *Calopteryx virgo* in the Netherlands (fig. 7.1). On the other hand, the reverse combination of trends can reflect a shrinking distribution while the remaining populations are doing well.

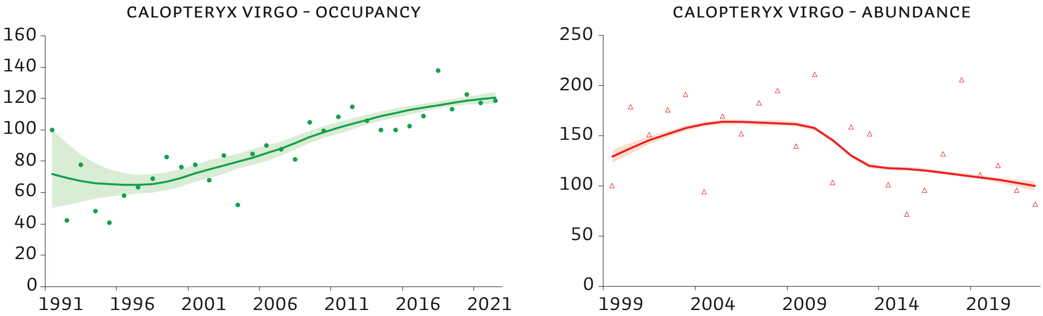


FIG. 7.1: Indices of *Calopetryx virgo* in the Netherlands. Left: occupancy index (distribution; 1991 was set to 100), right: abundance index, based on standardised counts (1999 was set to 100). Smoothed trend lines were plotted through the year effects to summarise overall change. Shaded areas represent 95% confidence intervals. While more sites continue to be colonised by this species, the number of individuals counted along fixed transects of the Dutch Dragonfly Monitoring scheme is dropping.

In addition, occupancy modelling is not suitable for very rare species or species with a very low detection probability, as these models do not perform well with a very limited number of sites with records. In the Netherlands, this was the case for three Red-listed species: *Stylurus (Gomphus) flavipes*, *Ophiogomphus cecilia* and *Leucorrhinia albifrons*. Occupancy trends for these species were uncertain, but the latter two species are counted along fixed monitoring transects of DDMS, yielding reliable abundance trends. *S. flavipes* is a notoriously hard to monitor species, because mature adults are seldom seen (Turnhout, 2020). For this species, monitoring may be based on counting exuviae (larval skins; Hardersen & Toni, 2019), although this is more time consuming and requires enough trained and dedicated recorders. This method has recently been adopted by DDMS and will hopefully result in reliable trend information in the future.

In conclusion, abundance monitoring based on standardised counts and distribution monitoring based opportunistic data analysed with occupancy models are complementary methods, which both have their own merits. The choice for which one to use depends on data availability and on the aspects of population dynamics being studied.

Monitoring distribution via occupancy modelling is a promising option for countries which do not have standardised monitoring schemes, but do have large data sets of opportunistic dragonfly records. Currently this is the case for the majority of European countries (Boudot & Kalkman, 2015; Bried et al., 2020), although no thorough evaluation has been made of which of these data sets suffice (quantitatively and qualitatively) to successfully calculate the detection histories needed for occupancy modelling. Since the publication of the paper in Chapter 5 (Termaat et al., 2019) dragonfly distribution trends based on occupancy modelling have been assessed for the Netherlands (Van Swaay et al., 2023), the United Kingdom (Outhwaite et al., 2020), Germany (Bowler et al., 2021) and Flanders (calculated in the context of the European Red List update; De Knijf et al., 2023), but this should be feasible for many more countries.

Dragonfly trends and their causes on different spatial scales

Chapters 4 and 5 paint a rather positive picture of the development of dragonflies populations in general. Both at national level (the Netherlands; period 1991-2013; Chapter 4) and continental level (Europe; period 1990-2015; Chapter 5) the number of species with positive distributions trends exceeds the number of species with negative trends. This conclusion may come as a surprise, given the worrying messages about declining insect populations (Hallman et al., 2017; Wagner, 2020) and the poor conservation status of freshwater habitats (Reid et al., 2019; WWF, 2020). But zooming in on different groups of dragonfly species, their trends on different spatial scales, and more recent developments (> 2015) yields a more differentiated picture.

EUROPEAN LEVEL

At European level, many dragonfly species have increased in distribution in the period 1990-2015 and none of the species studied in Chapter 5 declined. Warm-adapted species (i.e. species with STI > 9.8 oC, see Chapter 5) have clearly profited from climate warming, while cold-adapted species (STI < 9.8) either benefited from climate warming in northern Europe as well, or have profited from other changes in their habitats which compensated for the potential negative effects of climate warming. In any case, however, warm-adapted species increased stronger than cold-adapted species, leading to a larger share of warm-adapted species at community level. Furthermore, although dragonflies are highly mobile insects, the pace in which dragonfly communities ‘warmed up’ in the period 1990-2015 lagged behind the increase in mean annual temperature itself. Dragonfly communities in Europe thus accumulated a ‘climatic debt’, which means that a backlash on cold-adapted species was to be expected later. And indeed this backlash has recently become abundantly clear from the analysis underlying the recently presented European Red List (De Knijf et al., 2023). 21 of the 51 cold-adapted species are Red-listed (Near Threatened, Vulnerable, Endangered, or Critically Endangered), 20 of which due to a decline in distribution, calculated over the period 2010-2020. In the previous version of the European Red List (Kalkman et al., 2010), only 6 cold-adapted species were listed in any of the these categories. Although the methods used for trend assessment were not identical, the deteriorating conservation status of cold-adapted species seems real and recent, supporting the climatic debt assumption. The debt is now being paid.

It should be stressed that climate change does not only affect dragonflies through rising water temperatures. Desiccation of larval habitats due to more frequent or prolonged summer droughts is a relevant harmful consequence of climate change as well. Warm-adapted species of lentic habitats (standing waters) are generally better adapted to a temporary lack of water than cold-adapted species of lentic habitats. But this difference does not apply to species of lotic habitats (running waters). Desiccation of streams and smaller rivers is an increasing problem in southern Europe in particular, which means that some warm-adapted species (or at least species with a high STI) of running waters are at risk too. Unfortunately, most species endemic to Europe belong to this group. Species such as *Coenagrion intermedium, Pyrrhosoma elisabethae, Boyeria cretensis, Onychogomphus cazuma* and *Cordulegaster helladica* are restricted to such small ranges that they may easily go globally extinct if ongoing climate change leads to more frequent desiccation of streams and rivers in the Mediterranean region. None of these species are protected by the European Habitats Directive, which adds to the risk that their habitats are drained, be it accidentally or as a result of the rise in demand for fresh water for human consumption or agricultural irrigation (Kalkman et al., 2018; Tang & Visconti, 2020; European Environmental Agency, 2021).

In central and northern Europe it is cold-adapted species of lentic habitats that raise the most concern, rather than species from lotic habitats. However, when interpreting negative trends of cold-adapted species the complication arises that these species are also often restricted to oligotrophic and mesotrophic habitats, such as moorland pools, bogs, peatlands and fens. These habitats are particularly susceptible to human-induced eutrophication and acidification, especially in northwestern Europe where nitrogen deposition is highest and declines of cold-adapted species are steepest. In order to distinguish between the effects of environmental pollution and climate change, it is necessary to zoom in on these pressures on a smaller spatial scale, as has been done in chapters 4 and 5 for the Netherlands.

NATIONAL AND LOCAL LEVEL: THE NETHERLANDS

The dragonfly fauna of the Netherlands has undergone dramatic changes during the 20th and beginning of the 21st century. Since the early 20th century, possibly even before, species of running waters have been negatively impacted by organic pollution of streams and rivers with wastewater and sewage. The levels of pollution further increased in the 1940s and 1950s, due to human population growth, further industrialisation and a growing agricultural sector. Species of oligo-mesotrophic habitats declined in the first half of the 20th century, due to intensified land use and alterations of surface water and groundwater systems. Later, many of these species declined further due to the detrimental effects of atmospheric deposition of sulphur dioxide (SO_2), ammonia (NH_3) and nitrogen oxides (NO_x), mainly caused by industries, agriculture and traffic.

The tide turned in the period 1960-1980. Sulphur dioxide emissions dropped significantly as power plants switched from coal to gas for power generation and metal and petrochemical industries adjusted their production processes. To a lesser ex-

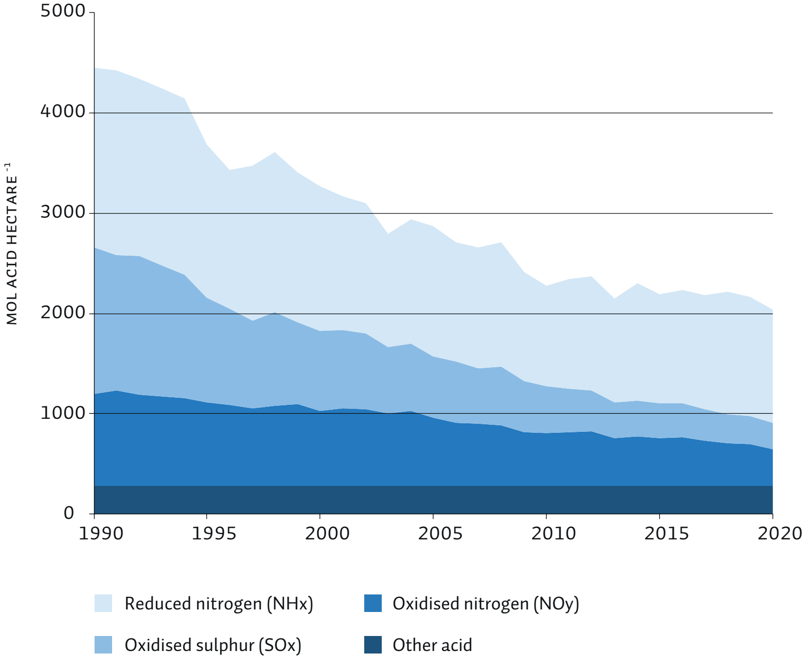


FIG. 7.2: Trend in the deposition of different acidifying compounds in the Netherlands in 1990-2020. Source: CBS et al., 2023c.

tent, nitrogen emissions dropped too, as a result of stricter agricultural legislation (especially regarding manure production and management) and the application of catalytic converters in cars (CBS et al., 2023c; fig. 7.2). Organic pollution of streams and rivers was reduced as well, thanks to the same stricter agricultural regulations and as a result of improved waste water treatment (CBS et al., 2016). At the same time, an increasing number of habitat restoration projects were carried out in moorland pools, bog remnants, fens, coastal dune ponds and streams (Jansen et al., 2010).

As a result of the combination of these efforts the quality of dragonfly habitats of both standing and running waters improved considerably, even though the vast majority of waterbodies in the Netherlands still does not meet the quality standards of the European Water Framework Directive (CBS et al., 2022). The improvements led to (at least partial) recovery of the dragonfly fauna of all main habitat types after 1990. This recovery could be accurately documented thanks to the large number of dragonfly records collected by voluntary observers and the start of the Dutch Dragonfly Monitoring Scheme in 1998.

Among the species with positive trends after 1990 are multiple species of oligo-mesotrophic habitats such as *Lestes dryas*, *Cordulia aenea*, *Somatochlora flavomaculata*, *Leucorrhinia dubia*, *L. pectoralis* (fig. 7.3) and *L. rubicunda*. Truly spectacular was the rediscovery of 6 critical species of oligo-mesotrophic habitats, after decades of absence from the Netherlands: *Sympecma paedisca*, *Coenagrion armatum*, *Somatochlora arctica*, *Leucorrhinia albifrons*, *Leucorrhinia caudalis* and, most recently, *Nehalennia speciosa*. While *C. armatum* and *N. speciosa* are still restricted to a single, possibly overlooked location the other 4 species increased in distribution since their rediscoveries.

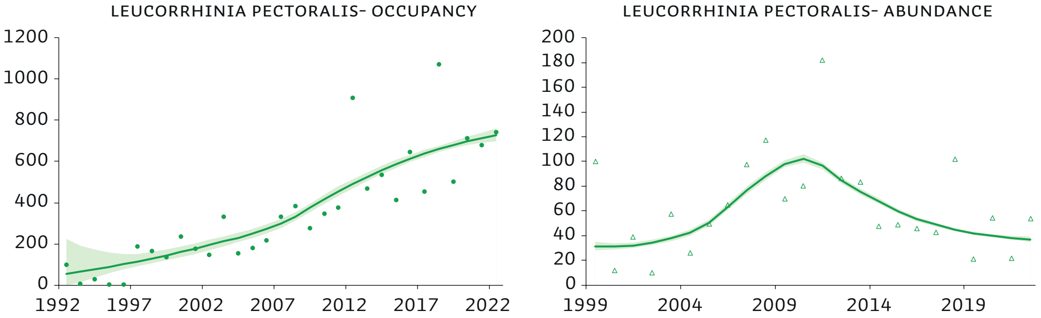


FIG. 7.3: Indices of *Leucorrhinia pectoralis* in the Netherlands. Left: occupancy index (distribution; 1992 was set to 100), right: abundance index, based on standardised counts (1999 was set to 100). Smoothed trend lines were plotted through the year effects to summarise overall change. Shaded areas represent 95% confidence intervals. The decline in abundance after 2010 is likely caused by increased competition from *Leucorrhinia caudalis*, which re-established in the Netherlands from that year. Both species occur at the same sites in lowland marshes (fens), where the abundance of *L. pectoralis* is highest. In terms of distribution, however, *L. pectoralis* is still increasing, especially outside the lowland marshes.

Coenagrion hastulatum, arguably the species most sensitive to acidification and eutrophication, never recovered though, although habitat restoration measures may have slowed down its demise.
Species of lotic habitats showed at least similar positive developments with the return of *Onychogomphus forcipatus*, *Ophiogompus cecilia* and *Stylurus* (*Gomphus*) *flavipes*, and positive trends of the scarce *Calopteryx virgo*, *Gomphus vulgatissimus* and several more common species of running waters.

The revival of the dragonfly fauna of oligo-mesotrophic habitats is remarkable, since nitrogen deposition remained well above the known critical load of nitrogen-sensitive Natura 2000 habitats and their underlying vegetation communities

(Van Dobben et al., 2012). Most terrestrial species bound to these habitats, including plants, birds and butterflies, have not shown comparable signs of recovery. However, nitrogen pathways in aquatic ecosystems differ from those in terrestrial ecosystems. In Dutch moorland pools, inorganic nitrogen mainly occurs in the form of ammonium (NH_4^+), which has an acidifying effect. In the period 1978-2018 Van Dam (2023) measured a much stronger decline in ammonium concentration in Dutch moorland pools than the decline in atmospheric nitrogen deposition. This may explain why dragonflies and other moorland pool organisms (Brouwer et al., 2018) responded, on average, more positively to a moderate reduction in nitrogen deposition than terrestrial species in the surrounding forest and heath ecosystems (CBS et al., 2023a, b).

In the meantime, the effects of climate warming on the Dutch dragonfly fauna became more and more noticeable as well. Positive effects on warm-adapted species already became evident as early as the mid-1990s, when rare or previously absent warm-adapted species like *Sympecma fusca*, *Lestes barbarus*, *Erythromma lindenii*, *Crocothemis erythraea* and *Sympetrum fonscolombii* rapidly colonised large parts of the country and more common warm-adapted species such as *Coenagrion puella*, *Erythromma viridulum*, *Anax imperator* and *Sympetrum striolatum* became omnipresent. Later, more species from southern Europe joined the chorus: *Coenagrion scitulum*, *Aeshna affinis*, *Anax parthenope*, *Orthetrum brunneum* and *Sympetrum meridionale* now all reproduce on multiple locations in the Netherlands. *Anax ephippiger* was first recorded as a vagrant in 1995, but influxes of this species now occur in most years and the species reproduced successfully in the Netherlands in 2019 (Hoppenbrouwers, 2022).

Negative effects of climate change on cold-adapted species took more time to become clearly measurable. These species were either able to cope with rising temperatures for some time, or the negative effects of rising temperatures were temporarily masked by the aforementioned improvements in oligo-mesotrophic habitats, or both.
As described in Chapter 6, this time lag was not found for the very critical *Coenagrion hastulatum*, which never recovered from the loss of populations due to land use changes, human-induced acidification and eutrophication, and harmful habitat management. The most recent loss of *C. hastulatum* populations, however, was caused by the complete desiccation of larval habitats during dry summers, which occur more frequently due to climate change. It shows that the relative importance of pressures can shift over time and that, at least for some species, targeted ecological research is needed to fully understand what caused its decline, and which conservation measures might (still) be effective.

Two other cold-adapted species of moorland pools and bogs, *Coenagrion lunulatum* and *Aeshna juncea*, started to decline in distribution from approximately 2005 and were newcomers to the Dutch Red List of 2012 (Termaat & Kalkman, 2012). The pace in which these two species, which used to be fairly common, are disappearing from the Netherlands is astonishing. In less than 20 years the number of sites they occupied is decimated. These species are likely affected by the same pressures as *C. hastulatum*, but may be a little less susceptible to sulphur- and nitrogen-induced acidification. Climate change now pushes them over the brink.

Even more recently, most other cold-adapted species started to decline too. As these species include previously very abundant, nitrophilous species such as *Lestes sponsa*, *Enallagma cyathigerum* and *Sympetrum danae*, climate warming is likely to be the culprit, rather than other environmental issues such as nitrogen deposition. This is further supported by the fact that negative trends of cold-adapted species are now reported from other European regions as well, where nitrogen deposition is much lower, e.g. in southern Sweden. Also, *warm*-adapted species bound to oligo-mesotrophic habitats, such as *Lestes barbarus*, *Lestes virens* and *Ceriagrion tenellum* are increasing in the Netherlands, instead of declining.

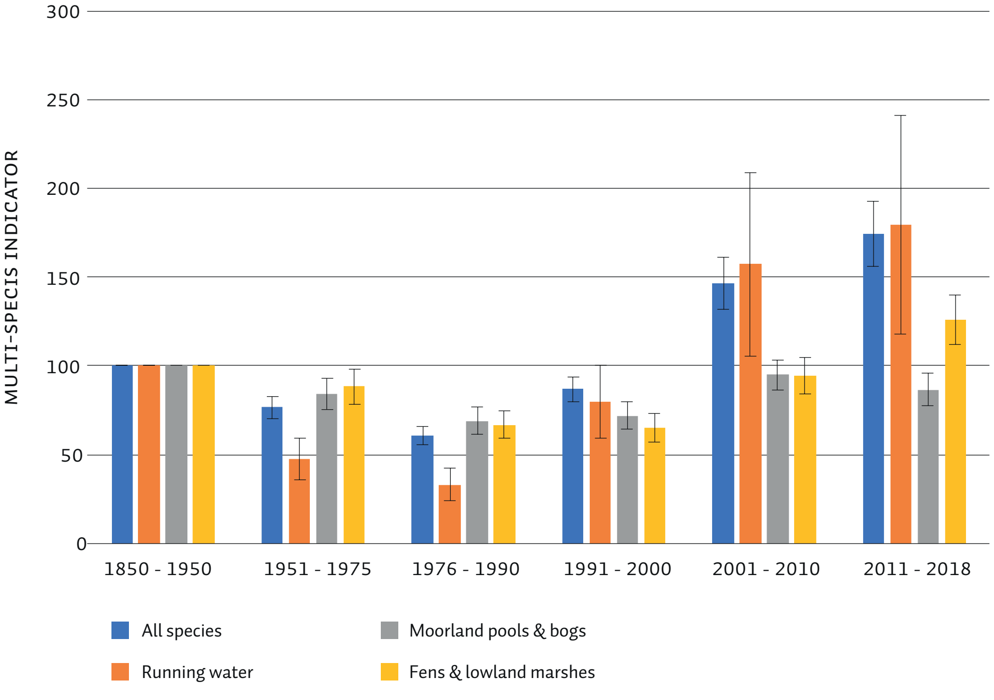


FIG. 7.4: Long-term Multi-species Indicators of dragonflies in the Netherlands. Species are categorised by habitat preferences. Trend in the deposition of different acidifying compounds in the Netherlands in 1990-2020. Source: Van Strien & Van Grunsven (2023).

A recent analysis of long-term dragonfly trends in the Netherlands by Van Strien & Van Grunsven (2023) showed that species of moorland pools and bogs almost (but not fully) recovered their range in the period 2001-2010 compared to their historic range in the period 1850-1950, but have declined again in the period 2011-2018 (fig. 7.4). This, too, supports the conclusion that species of oligo-mesotrophic habitats initially recovered due to environmental improvements, but are now under pressure of climate change.

In short, dragonflies in the Netherlands reacted negatively to environmental problems in the 20th century, but most species quickly recovered as these problems decreased. However, climate change now has a dominant effect, both positive on warm-adapted species and negative on cold-adapted species. Thus, key factors driving trends at species level and at community level changed over time.

As the climate still continues to change, so will the dragonfly fauna. On the one hand, the most critical cold-adapted species such as *Coenagrion hastulatum*, *C. lunulatum* and *Aeshna juncea*, *A. subarctica* and *Somatochlora arctica* are likely to disappear from the Netherlands, or will become restricted to the most intact oligo-mesotrophic systems with stable water levels. Local bottlenecks, such as harmful management of moorland pools and bogs, can accelerate the decline of these species, as we have seen in *C. hastulatum*. On the other hand, more warm-adapted species are likely to extend their ranges from southern Europe into the Netherlands. This especially applies to warm-adapted species of lentic habitats, such as *Orthetrum albistylum* (De Knijf, 2019) and *Trithemis kirbyi* (De Knijf, 2022), which already reached Belgium. Warm-adapted species of lotic habitats seem to have slower north-bound range expansions, with the notable exception or *Boyeria irene*, which developed a strong population in northern Germany (Clausnitzer et al., 2010).

Conclusions, implications and future prospects

This thesis shows that it is feasible to monitor dragonflies at different spatial scales in Europe, based on opportunistic records analysed with occupancy models. The resulting occupancy indices and associated trends provide insight in the predominant drivers of change in dragonfly communities. However, to identify species-specific threats at regional or local level, targeted ecological research may be essential to formulate effective conservation measures. It is then important to discriminate between former and current threats, as their relevance may shift over time. These findings have implications for the protection of dragonflies, they give rise to further research and increase the chance of establishing dragonflies as an additional European biodiversity indicator group.

IMPLICATIONS FOR DRAGONFLY CONSERVATION

The recovery of the Dutch dragonfly fauna after 1990 proved that national environmental policies in combination with local habitat restoration efforts can be very effective to improve the conservation status of dragonflies and their freshwater habitats. These measures were often prompted by European regulations, most notably the Habitats Directive (https://environment.ec.europa.eu/topics/nature-and-biodiversity/habitats-directive_en) and the European Water Framework Directive (https://water.europa.eu/freshwater/europe-freshwater/water-framework-directive). These regulations were implemented in national legislation and gave rise to subsidy programmes for nature restoration, such as the European LIFE programme (https://cinea.ec.europa.eu/programmes/life_en) and the Dutch EGM programme (Van Ommering & Hendriks, 2004). Currently however, global climate change is the dominant driver of change in dragonfly occurrence throughout Europe, including the decline of cold-adapted species (De Knijf et al., 2023). As key pressures on cold-adapted species shifted from local and national level to global level they became increasingly difficult to oppose. This is a contemporary dilemma in nature conservation: if key pressures lie without the sphere of influence of local nature managers and national policy makers, what is their remaining action perspective?

Schippers et al. (2021) review various options for the conservation of biodiversity in communities that are changing under climate change. A relevant recommendation for any species, including dragonflies, is to increase ecosystem resilience by increasing habitat patch sizes and maintaining landscape heterogeneity. However, the most useful suggestion might be to simply accept that some species will inevitably go locally extinct and to evaluate species survival at a global rather than local scale.

As climate warming proceeds, dragonflies will continue to shift their range where possible. Species with very low STI cannot shift their range to even cooler regions and may become at risk. This may be expected for *Coenagrion johanssoni* and *Somatochlora sahlbergi*, and for the alpine populations of *C. hastulatum*, *C. hylas*, *A. caerulea*, *A. subarctica* and *S. alpestris*. In other cases, there is some room for range expansion of cold-adapted species in Scandinavia, the Baltic States and northern Russia, were oligo-mesotrophic habitats are abundant. However, it is then increasingly important that these habitats *remain* abundant and unaffected. As climate warming will become an increasing pressure in the foreseeable future in northern Europe as well, oligo-mesotrophic ecosystems should be consolidated where possible without delay, even if their species communities are currently stable. To achieve that, halting human exploitation of these ecosystems and consolidating both surface and groundwater levels are first priorities.

Perhaps even more pressing is the protection of watersheds in southern and southeastern Europe, as multiple dragonfly species of lotic habitats are at risk due to desiccation of streams in rivers, including some European endemics with very small ranges (De Knijf et al., 2023). However, the desiccation of these habitats is not only caused by the direct effects of climate warming, but also to a large extend by increased anthropogenic water extraction. Failing to limit these extractions could easily lead to global extinction of range restricted lotic dragonfly species.

Acting upon the large-scale threats of climate change on the biodiversity of freshwater habitats in general and dragonflies in particular requires a decisive European nature conservation policy, with more emphasis on oligo-mesotrophic ecosystems, groundwater retention and range-restricted species.

RECOMMENDATIONS FOR FURTHER RESEARCH ON THE IMPACT OF CLIMATE WARMING

It has become clear that cold-adapted dragonfly species are declining in Europe due to climate change. However, little is known about the precise mechanisms underlying this decline. It is suggested that the respiratory performance of larvae of cold-adapted species is more hindered by increasing water temperature than that of warm-adapted species. With increasing temperature the metabolism of aquatic ectotherms accelerates, leading to increased oxygen demand which may exceed the bioavailability of oxygen (Verberk & Bilton, 2013). With a given temperature rise, larvae of cold-adapted dragonfly species may show a stronger increase in oxygen demand than those of warm-adapted species and may therefore sooner experience (sub)lethal effects of hypoxia. This hypothesis remains to be tested in laboratory trials.

Another hypothesis is that larvae of cold-adapted dragonfly species suffer from intraguild competition shifts, now that warm-adapted species have established or expanded in virtually all dragonfly habitats. As warm-adapted species tend to have higher egg or larval development rates under warm conditions than cold-adapted species, the first group may quickly gain a competitive advantage, leading to increased intraguild predation of the second group. Hogreve & Suhling (2022) showed under laboratory conditions that these mechanisms may well explain the diverging trends of the syntopic sibling species *Sympetrum striolatum* (increasing, STI = 10.8 oC) and *S. vulgatum* (declining, STI = 7.8 oC) in Germany. Their hypothesis can be further tested by relating annual weather data to the occupancy estimates of both species in subsequent years. Another interesting species in this respect is the warm-adapted *Anax imperator.* This species, which is one of Europe's largest dragonflies, used to be rather rare in central European moorland pools and bogs, which were mainly occupied by cold-adapted dragonfly species. Nowadays however, *A. imperator* has increased to such extent that most permanent standing waters are occupied. In moorland pools and bogs, which are usually fishless, *A. imperator* is now an apex predator hunting dragonfly larvae and other macrofauna alike. It is quite conceivable that this has an impact on the original dragonfly fauna in these habitats. This hypothesis can be tested in mesocosm experiments by measuring the survival rate of larvae of cold-adapted dragonfly species (e.g., *Aeshna juncea*), with and without the presence of *A. imperator* larvae.

TOWARDS DRAGONFLIES AS EUROPEAN FRESHWATER BIODIVERSITY INDICATORS

The results in Chapter 5 prove that it is feasible to monitor dragonflies at European level, by combining regional occupancy indices into supra-national indices with sound trend estimates.

Furthermore, chapters 4, 5 and 6 of this thesis have shown that dragonflies react to environmental change almost instantly, both positively and negatively, and therefore inform on the *current* state of freshwater ecosystems. This is highly relevant as key pressures on freshwater ecosystems may change rather quickly over time, as shown in Chapter 6. The fast reaction of dragonflies is mediated by their short life cycle. Longer-lived species such as vertebrates and perennial plants may linger at former suitable sites long after the quality of their habitat has deteriorated. Dragonflies on the contrary show immediate declines in abundance after habitat deterioration, followed by declines in distribution shortly after. On the other hand, their strong flight ability enables dragonflies to reach and (re)colonise restored or newly created suitable habitats faster than most other taxonomic groups. As habitat fragmentation plays a limited role for dragonflies, they readily inform on local aspects of habitat quality, with very little delay caused by dispersion limitations. For these reasons, dragonfly trends have an 'early signalling' function and may be used as predictors of the future trends of other freshwater organisms that respond less rapidly.

Thus, dragonflies would indeed be a valuable addition to the existing European biodiversity monitoring programme. As freshwater insects, they fill an important gap in the current coverage of ecosystems and taxonomic groups (see Chapter 1), they react quickly and sensitively to environmental change, and they are popular with citizen scientists (see Chapter 1), resulting in extensive data availability throughout Europe. Since the paper of chapter 5 was published, more countries have professionalised their database, making it possible to include more countries in a European monitoring scheme than were included in the study of Chapter 5. Furthermore, a (semi-)professional network of European dragonfly researchers has emerged, which has been organising a biennial conference since 2010 (the European Congresses on Odonatology (EECO)) and facilitates collaboration on projects such as distribution atlases, IUCN Red List assessments and various scientific studies. This facilitates the cooperation between countries that is necessary to start up a European monitoring programme for Odonata.

Now the time is truly ripe to start a European dragonfly monitoring programme, by compiling readily available distribution data from more countries and repeating data analysis on a regular basis.
The European Butterfly Monitoring Scheme (eBMS) may serve as an example, even though it uses standardised counts instead of opportunistic distribution records (https://butterfly-monitoring.net/). eBMS is managed by Butterfly Conservation Europe (BCE), a partnership organisation in which 39 European countries are currently represented at present (https://www.vlinderstichting.nl/butterfly-conservation-europe/). eBMS yields indices for many European butterfly species, which are combined into several policy relevant multi-species indicators (Van Swaay et al., 2020). One of these indicators, the European grassland butterfly indicator, is adopted by European Environment Agency (EEA), as one of the tools to assess the state of biodiversity at European level (Van Swaay et al., 2019; https://biodiversity.europa.eu/track/streamlined-european-biodiversity-indicators).
The addition of a comparable indicator based on dragonflies as representatives of freshwater biodiversity would narrow the gap in the current indicator set. It would be wise if the EEA were to prioritise this addition.

In order to effectively build and manage a European dragonfly monitoring programme, it is advisable to start a partnership organisation similar to BCE. Such an organisation should coordinate the monitoring programme itself, but it may also use its results to send out clear, evidence-based messages on dragonfly trends and conservation to policymakers and the general public. After all, as *Guardians of the watershed* (Clausnitzer & Jödicke, 2008), dragonflies reflect how sustainably we treat our freshwater ecosystems. As these ecosystems are vital for both biodiversity and human welfare (Albert et al., 2021) we have a moral obligation to monitor them closely and to take protective measures when necessary.

References

Albert J.S., Destouni G., Duke-Sylvester S.M., Magurran A.E., Oberdorff T., ... & Ripple W.J. (2021). Scientists' warning to humanity on the freshwater biodiversity crisis. *Ambio* 50: 85-94.

Bailey L.L., MacKenzie D.I. & Nichols J.D. (2014). Advances and applications of occupancy models. *Methods in Ecology and Evolution* 5: 1269-1279.

Bried J., Ries L., Smith B., Patten M., Abbott J., ... & White E. (2020). Towards global volunteer monitoring of odonate abundance. *BioScience* 70: 914-923.

Boudot J.P. & Kalkman V.J. (editors) (2015). *Atlas of the European dragonflies and damselflies*. Zeist, The Netherlands: KNNV Publishing.

Bowler D.E., Eichenberg D., Conze K.J., Suhling F., Baumann, ... & Bonn A. (2021). Winners and losers over 35 years of dragonfly and damselfly distributional change in Germany. *Diversity and Distributions* 27: 1353-1366.

CBS, PBL, RIVM, WUR (2016). *Vermesting in grote rivieren, 1970-2014* (indicator 0249, version 10 , 13 april 2016). https://www.clo.nl/indicatoren/nl0249-vermesting-in-grote-rivieren. Centraal Bureau voor de Statistiek (CBS), Den Haag; PBL Planbureau voor de Leefomgeving, Den Haag; RIVM Rijksinstituut voor Volksgezondheid en Milieu, Bilthoven; en Wageningen University and Research, Wageningen.

CBS, PBL, RIVM, WUR (2022). *Waterkwaliteit KRW, 2022* (indicator 1438, version 09 , 18 augustus 2022). https://www.clo.nl/indicatoren/nl1438-kwaliteit-oppervlaktewater-krw. Centraal Bureau voor de Statistiek (CBS), Den Haag; PBL Planbureau voor de Leefomgeving, Den Haag; RIVM Rijksinstituut voor Volksgezondheid en Milieu, Bilthoven; en Wageningen University and Research, Wageningen.

CBS, PBL, RIVM, WUR (2023a). *Fauna van bos, 1990-2021* (indicator 1162, version 20 , 10 maart 2023). https://www.clo.nl/indicatoren/nl1162-fauna-van-het-bos. Centraal Bureau voor de Statistiek (CBS), Den Haag; PBL Planbureau voor de Leefomgeving, Den Haag; RIVM Rijksinstituut voor Volksgezondheid en Milieu, Bilthoven; en Wageningen University and Research, Wageningen.

CBS, PBL, RIVM, WUR (2023b). *Fauna van de heide, 1990-2021* (indicator 1134, version 19 , 24 maart 2023). https://www.clo.nl/indicatoren/nl1134-fauna-van-de-heide. Centraal Bureau voor de Statistiek (CBS), Den Haag; PBL Planbureau voor de Leefomgeving, Den Haag; RIVM Rijksinstituut voor Volksgezondheid en Milieu, Bilthoven; en Wageningen University and Research, Wageningen.

CBS, PBL, RIVM, WUR (2023c). *Verzurende depositie, 1990-2020* (indicator 0184, version 19 , 28 februari 2023). https://www.clo.nl/indicatoren/nl0184-verzurende-depositie. Centraal Bureau voor de Statistiek (CBS), Den Haag; PBL Planbureau voor de Leefomgeving, Den Haag; RIVM Rijksinstituut voor Volksgezondheid en Milieu, Bilthoven; en Wageningen University and Research, Wageningen.

Clausnitzer, H. J., Hengst, R., Krieger, C., & Thomes, A. (2010). *Boyeria irene* in Niedersachsen (Odonata: Aeshnidae). *Libellula* 29: 155-168.

Clausnitzer V. & Jödicke R. (editors) (2004). Guardians of the Watershed. Global Status of Dragonflies: Critical Species, Threat and Conservation. *International Journal of Odonatology* 7: 163-188.

De Knijf G. (2019). Eerste voortplantingsbewijs van de Witpuntoeverlibel (*Orthetrum albistylum*) in België. *Brachytron* 20: 55-62.

De Knijf G. (2022). Eerste waarnemingen van de Oranje zonnewijzer (*Trithemis kirbyi*) in België. *Brachytron* 23: 28-32.

De Knijf G., Billqvist M., van Grunsven R., Prunier F. & Vinko D. (2023). *A new Red List of the dragonflies and damselflies of Europe*. Congress presentation. International Congress on Odonatology 2023 (ICO 2023), 25-30 June 2023, Paphos, Cyprus.

European Environmental Agency (2021). *Water resources across Europe — confronting water stress: an updated assessment*. EEA Report No 12/2021. Copenhagen, Denmark.

Hallmann C.A., Sorg M., Jongejans E., Siepel H., Hofland N., … & de Kroon H. (2017). More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PloS one* 12: e0185809.

Hardersen S. & Toni I. (2019). Proposal for a time-based standard sampling method for the monitoring of *Gomphus flavipes* (Charpentier, 1825) and *Ophiogomphus cecilia* (Fourcroy, 1785)(Odonata: Gomphidae). *Fragmenta entomologica* 51: 55-62.

Hogreve J. & Suhling F. (2022). Development of two common dragonfly species with diverging occupancy trends. *Journal of Insect Conservation* 26: 571-581.

Hoppenbrouwers P. (2022). Ei-afzet en voortplanting van de Zadellibel (*Anax ephippiger*) in de regio Nijmegen in 2019. *Brachytron*, 23: 22-27.

Isaac N.J., van Strien A.J., August T.A., de Zeeuw M.P. & Roy D.B. (2014). Extracting robust trends in species' distributions from unstructured opportunistic data: a comparison of methods. *BioRXiv*: 006999.

Jansen A.J.M., Bekker R.M., Bobbink R., Bouwman J.H., Loeb R., … & Wallis de Vries M. (2010). *De effectiviteit van de regeling Effectgerichte Maatregelen (EGM) voor Rode-lijstsoorten*. Report DKI nr. 2010/dk137-O. Directie Kennis en Innovatie, Ministerie van Landbouw, Natuur en Voedselkwaliteit, Ede, the Netherlands.

Kalkman V.J., Boudot J.P., Bernard R., De Knijf G., Suhling F., & Termaat, T. (2018). Diversity and conservation of European dragonflies and damselflies (Odonata). *Hydrobiologia*, 811: 269-282.

Kalkman V.J., Boudot J.P., Bernard R., Conze K.J., De Knijf G., … & Sahlén G. (2010). *European Red List of Dragonflies*. Publications Office of the European Union, Luxembourg.

Kéry M., Royle J.A., Schmid H., Schaub M., Volet B., … & Zbinden N. (2010). Site-occupancy distribution modeling to correct population-trend estimates derived from opportunistic observations. *Conservation Biology* 24: 1388-1397.

MacKenzie D., Nichols J., Lachman G., Droege S., Royle J. & Langtimm C. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83: 2248-2255.

MacKenzie D.I., Nichols J.D., Royle J.A., Pollack K.H., Bailey L.L. & Hines J.E. (2005). *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*. Academic Press, San Diego, California, USA.

Outhwaite C.L., Gregory R.D., Chandler R.E., Collen B. & Isaac N.J. (2020). Complex long-term biodiversity change among invertebrates, bryophytes and lichens. *Nature Ecology & Evolution* 4: 384-392.

Reid A.J., Carlson A.K., Creed I.F., Eliason E.J., Gell P.A., … & Cooke S. J. (2019). Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biological Reviews* 94: 849-873.

Schippers P., Abarca E.L., Verboom J., Wamelink G.W., Vos C.C., … & Cobben M. M. (2021). Biodiversity conservation in climate change driven transient communities. *Biodiversity and Conservation* 30: 2885-2906.

Tang D.H.Y. & Visconti P. (2020). Biases of Odonata in Habitats Directive: Trends, trend drivers, and conservation status of European threatened Odonata. *Insect Conservation and Diversity* 14: 1-14.

Termaat T. & Kalkman V.J. (2012). *Basisrapport Rode Lijst Libellen 2011 volgens Nederlandse en IUCN-criteria. Brachytron* 14: 75-187.

Termaat T., van Strien A.J., van Grunsven R.H.A., De Knijf G., Bjelke U., … & WallisDeVries M.F. (2019). Distribution trends of European dragonflies under climate change. *Diversity and Distributions* 25: 936-950.

Turnhout S. (2020). *Following the River Clubtail around: how Games and Grids transform networks of biodiversity recording and policy*. PhD thesis. Radboud University, Nijmegen, the Netherlands.

Van Dam H. (2023). The Role of Hydromorphology in the Partial Recovery of Chemistry in Acidified and Warmed Dutch Moorland Pools. *Water, Air, & Soil Pollution* 234: 10.

Van Dobben H.F., Bobbink R., Bal D. & van Hinsberg A. (2012). *Overzicht van kritische depositiewaarden voor stikstof, toegepast op habitattypen en leefgebieden van Natura 2000*. Alterra-rapport 1654. Alterra, Wageningen, the Netherlands.

Van Klink R., Bowler D.E., Gongalsky K.B., Swengel A.B., Gentile A. & Chase J.M. (2020). Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. *Science* 368: 417-420.

Van Ommering G. & Hendriks R.J.J. (2014). *Handleiding Subsidie Effectgerichte Maatregelen 2005:*

Overlevingsplan Bos en Natuur, Regeling effectgerichte maatregelen in bossen en natuurterreinen. Report EC-LNV nr. 2004/326-O. Expertisecentrum LNV, Ministerie van Landbouw, Natuur en Voedselkwaliteit, Ede, the Netherlands.

Van Strien A.J., & van Grunsven R.H. (2023). In the past 100 years dragonflies declined and recovered by habitat restoration and climate change. *Biological Conservation* 277: 109865.

Van Strien, A.J., van Swaay C.A.M. & Termaat T. (2013). Opportunistic citizen science data of animal species produce reliable estimates of distribution trends if analysed with occupancy models. *Journal of Applied Ecology* 50: 1450-1458.

Van Swaay C.A.M., Dennis E.B., Schmucki R., Sevilleja C.G., Balalaikins M., … & Roy D.B. (2019). *The EU Butterfly Indicator for Grassland species: 1990-2017: Technical Report.* Butterfly Conservation Europe & ABLE/eBMS (https://butterfly-monitoring.net/).

Verberk W.C. & Bilton D.T. (2013). Respiratory control in aquatic insects dictates their vulnerability to global warming. *Biology Letters* 9: 20130473.

Wagner D.L. (2020). Insect declines in the Anthropocene. *Annual Review of Entomology* 65: 457-480.

WWF (2020). *Living Planet Report 2020 - Bending the curve of biodiversity loss.* Almond R.E.A., Grooten M. & Petersen T. (editors). WWF, Gland, Switzerland.

Nehalennia speciosa is a critical species of densely vegetated bog fringes. It was rediscovered in the Netherlands in 2015 after 60 years of absence. Picture taken in Overijssel, 2022.

SUMMARY

Monitoring biodiversity is necessary to keep track of the progress towards conservation targets and to measure the success of conservation strategies. However, adequate biodiversity monitoring programmes are not easy to achieve. They require enough data on species occurrence over a longer period of time, and a scientifically sound method for data analysis to derive robust, unbiased trend information. Monitoring programmes that meet these requirements are scarce and often cover only a small geographic area. In Europe, only two species groups currently are covered by monitoring programmes that have resulted in pan-European biodiversity indicators: birds and butterflies. Evidently, these two species groups do not sufficiently represent total biodiversity.

Dragonflies (Odonata, including damselflies) may be a suitable additional indicator group. They are likely sensitive to other aspects of ecosystem quality than birds and butterflies and due to their strong dispersal capacities they may quickly respond to environmental change. The number of amateur naturalists watching dragonflies has greatly increased in recent decades, leading to a sharp rise in available distribution records throughout Europe. The majority of these records, however, are ‘opportunistic’, that is, collected without a standardised field protocol and without a design ensuring the geographical representativeness of sampled sites. Using these records requires a new method for data analysis that successfully corrects for unequal observation efforts. The aim of the research covered in this thesis is to find and test such a method, and use it to derive trends in the distribution of dragonflies at different spatial scales in Europe. Subsequently, it examines how the obtained trends can be explained and which consequences this has for dragonfly conservation.

CHAPTER 2 of this thesis explores if occupancy models (also known as site-occupancy models) may be helpful to reduce biases in estimating trends based on opportunistic data, caused by temporal variation of observation effort and by incomplete reporting of sightings. Occupancy models estimate the probability of sites to be occupied while taking into account imperfect detection of a species, via the deduction of ‘detection histories’ from replicated visits. Such models were applied to three opportunistic datasets of dragonfly species (1999–2007) in the Netherlands: (1) one-species records, (2) short species day-lists and (3) comprehensive species day-lists. The resulting trend estimates were compared to trend estimates based on presence-absence records collected at fixed monitoring transects, via the standardised field protocol of the Dutch Dragonfly Monitoring Scheme (the ‘golden standard’). In addition, conventional logistic regression analyses were applied to test if occupancy models performed better. Occupancy trends based on comprehensive species day-lists in combination with occupancy models were similar to those based on standardly collected data, while trends based on single-species records and short day-lists were too imprecise. Application of logistic regression models led to less realistic trend estimates than application of occupancy models. Thus, analysing comprehensive day-lists of opportunistic records with occupancy models can be a suitable and feasible alternative for dragonfly monitoring based on standardised observations.

The monitoring method described in Chapter 2 can of course be used in other countries than the Netherlands as well, provided that these countries have sufficiently large datasets of opportunistic dragonfly records. However, to infer dragonfly trends on an supranational scale, a method is needed to combine trends from different countries while taking into account the unequal geographical occupation of surveyed sites. **CHAPTER 3** describes a pilot study for the Banded demoiselle (*Calopteryx splendens*). Opportunistic distribution records were collected from five countries (Ireland, Great Britain, the Netherlands, Belgium and France), covering the period 1990–2008. Occupancy trends were first estimated for each country separately. Then the countries were weighted according to the number of sites surveyed and the range of the species per country. These weights were then applied during the aggregation of the national trends into a supranational trend. This showed that the distribution of *C. splendens* increased significantly in the five countries combined. The pilot demonstrated that supranational occupancy trends can be successfully calculated, which opens new perspectives for international monitoring of biodiversity.

CHAPTER 4 investigates how the dragonfly fauna of the Netherlands has developed in the period 1991-2013, using both standardised monitoring data on abundance and opportunistic data on distribution. Trends of dragonfly species from different habitat types are compared, as are trends of species with southern vs. northern distributions in Europe. Many species had declined prior to 1990, due to environmental pollution and habitat loss. Since the 1980s, stricter environmental regulations and habitat restoration projects led to improvements in freshwater habitats and many dragonfly species were able to quickly recover, leading to more positive conservation statuses. Species of running waters benefitted more than species of standing waters, and southern species had more positive trends than northern species, suggesting that climate change has contributed to the recovery. These outcomes support the suitability of dragonflies as indicators of freshwater habitat condition. However, dragonflies recovered more strongly in the Netherlands than many other aquatic or terrestrial insects (e.g. stoneflies, caddisflies, mayflies, butterflies, moths), likely because of their higher dispersal abilities or different habitat requirements.

Following the method for supranational trend assessment in Chapter 3 and the explanations for the Dutch dragonfly trends found in Chapter 4, **CHAPTER 5** explores how the occurrence of dragonflies has changed at a European level, in the period 1990-2015. Based on distribution data from 10 European geographic regions, occupancy indices were calculated for 99 (69%) of the European species. 55 of them increased in distribution at European level, 32 species remained stable, and none declined. Trends for 12 species were uncertain. To determine whether the changes found in dragonfly communities are driven by climate warming, Species Temperature Indices (STI) were calculated. STI is a simple measure of a species' preferred temperature regime, expressed as the mean annual temperature in the species' European range. Based on these STI, all species were categorised as either being cold-dwelling or warm-dwelling and Multi-species Indicators (MSI) were compiled. MSI of cold-dwelling and warm-dwelling species differed in some of the regions, but increased at a similar rate at European level. Furthermore, Community Temperature Indices (CTI) were calculated, as the average STI of all species in a region, weighted by species occupancies. CTI increased in all regions, except Cyprus. The European CTI increased slightly, but lagged behind the increase in temperature itself. This implies that dragonflies have accumulated a 'climate debt', meaning that problems for cold-dwelling species can still be expected after 2015. Dragonflies proved to be a suitable species group for monitoring changes in communities, both at regional and continental level.

For effective species conservation it is not only important to notice early that a species is declining, but also to properly understand the causes of its decline. Furthermore, as insects may respond rapidly to environmental changes, it is necessary to discriminate between former and current threats and to focus conservation efforts on the latter. **CHAPTER 6** describes a study on the habitat requirements of the Spearhead Bluet (*Coenagrion hastulatum*), an endangered species in the Netherlands, and investigates what has caused the progressive loss of its populations during the 20th and beginning of 21st century. Historically, habitat loss and changes in anthropogenic use of moorland pools and bogs were the most prominent causes. In the second half of the 20th century, strongly elevated atmospheric deposition of sulphur and nitrogen compounds, leading to acidification and eutrophication, was the main culprit. Sites where *C. hastulatum* disappeared between 2001 and 2015 had lower cover of essential vegetation structures. This suggests that they never fully recovered, despite the strong reduction in sulphur and moderate reduction in nitrogen deposition since the 1980s. Most recently, more populations have been lost as a direct result of prolonged droughts, a consequence of climate change. Thus, the most relevant pressures have indeed changed over time. Restoration of groundwater systems and rewetting measures are now first priorities for the conservation of *C. hastulatum* and other cold-adapted species of moorland pools and bogs.

CHAPTER 7 contains an overall synthesis. It draws general conclusions, addresses implications for dragonfly conservation and discusses future prospects.

At national level in the Netherlands, dragonflies reacted negatively to environmental problems in the 20th century, but most species quickly recovered as these problems were overcome or mitigated. However, climate change now has a dominant effect, both positive on warm-adapted species and negative on cold-adapted species. This is also true at a European level: the ‘climatic debt’ that dragonfly communities accumulated is now being paid, as many cold-adapted species have started to decline and will be listed as threatened on the updated IUCN Red List of European Odonata. Conservation efforts should prioritise the protection of oligo-mesotrophic freshwater habitats in northern Europe as areas of refuge for cold-adapted species. Halting human exploitation of these ecosystems and consolidating surface and groundwater levels are the most important measures. Protection of watersheds in southern and southeastern Europe is also pressing, as multiple dragonfly species in those regions are at risk due to desiccation of streams and rivers, including some range-restricted European endemics.

This thesis supports the suitability of dragonflies as biodiversity indicators. Since dragonflies react to environmental change almost instantly, both positively and negatively, they inform us on the current condition of freshwater ecosystems. Due to their strong dispersal ability, habitat fragmentation plays a limited role. Dragonfly trends therefore have an 'early signalling' function and may be used as predictors of the future trends of other freshwater organisms that respond less rapidly.

Furthermore, this thesis proves that it is feasible to start a European dragonfly monitoring programme right away, by compiling distribution data that are already available in many countries, and analysing those data with occupancy models. The resulting species indices and trends could form the basis of a freshwater biodiversity indicator, narrowing the gap in the availability of indicators currently employed by the European Environmental Agency.

The fens and lowland marshes of the Netherlands are important for the European conservation status of *Aeshna viridis*.

SAMENVATTING

Monitoring van biodiversiteit is noodzakelijk om te kunnen volgen in hoeverre instandhoudingsdoelstellingen worden gehaald en om het succes van beschermingsstrategieën te meten. Adequate monitoringprogramma's voor biodiversiteit zijn echter niet eenvoudig te realiseren. Ze moeten gebaseerd zijn op voldoende gegevens over het voorkomen van soorten over een langere periode en er moet een wetenschappelijk verantwoorde methode voor data-analyse beschikbaar zijn om robuuste, betrouwbare trendinformatie te verkrijgen. Monitoringprogramma's die aan deze eisen voldoen zijn schaars en bestrijken vaak maar een klein geografisch gebied. In Europa lopen er momenteel slechts voor twee soortengroepen monitoringprogramma's die hebben geresulteerd in pan-Europese biodiversiteitsindicatoren: vogels en dagvlinders. Het is duidelijk dat deze twee soortengroepen de totale biodiversiteit niet afdoende vertegenwoordigen.

Libellen (Odonata, inclusief waterjuffers) kunnen een geschikte aanvullende indicatorgroep zijn. Ze zijn waarschijnlijk gevoelig voor andere kwaliteitsaspecten van ecosystemen dan vogels en dagvlinders en kunnen vanwege hun sterke verspreidingsvermogen snel reageren op veranderingen in hun omgeving. Het aantal natuurwaarnemers dat naar libellen kijkt is de afgelopen decennia flink toegenomen, waardoor het aantal beschikbare libellenwaarnemingen in heel Europa sterk is gestegen. De meeste van deze waarnemingen zijn echter 'opportunistisch', dat wil zeggen dat ze verzameld zijn zonder een gestandaardiseerd waarnemingsprotocol en zonder een onderzoeksopzet die de geografische representativiteit van bezochte locaties garandeert. Het gebruik van opportunistische data vereist daarom een nieuwe analysemethode, waarmee gecorrigeerd kan worden voor ongelijke waarnemingsinspanning. Het doel van dit promotieonderzoek is om zo'n analysemethode te vinden, te testen en toe te passen bij het bepalen van trends in de verspreiding van libellen, op verschillende schaalniveaus in Europa. Vervolgens is onderzocht hoe de vastgestelde trends verklaard kunnen worden en welke consequenties dit heeft voor libellenbescherming.

HOOFDSTUK 2 van dit proefschrift onderzoekt of occupancy-modellen (ook wel site-occupancy-modellen genoemd) gebruikt kunnen worden om de kans te verkleinen dat systematische vertekening optreedt bij het schatten van trends op basis van opportunistische data, als gevolg van temporele variatie in warnemingsinspanning en onvolledige rapportage van waarnemingen. Occupancy-modellen schatten de waarschijnlijkheid van locatiebezetting, rekening houdend met een onvolmaakte detectie van een soort, door 'detectiegeschiedenissen' af te leiden uit herhaalde bezoeken. Deze modellen werden toegepast op drie datasets van opportunistische libellenwaarnemingen (1999-2007) in Nederland: (1) waarnemingen van één soort, (2) korte daglijsten van soorten en (3) uitgebreide daglijsten van soorten. De resulterende trendschattingen werden vergeleken met trendschattingen op basis van aan- en afwezigheidswaarnemingen die werden verzameld langs vaste telroutes, via het gestandaardiseerde veldprotocol van het Landelijk Meetnet Libellen (de 'gouden standaard'). Daarnaast werden conventionele logistische regressieanalyses toegepast om te testen of occupancy-modellen beter presteerden. Occupancy-trends op basis van uitgebreide daglijsten in combinatie met occupancy-modellen waren vergelijkbaar met trends op basis van gestandaardiseerd verzamelde gegeven. Trends op basis van waarnemingen van één soort en korte daglijsten bleken te onnauwkeurig te zijn. Het toepassen van logistische regressiemodellen leidde tot minder realistische trendschattingen dan het toepassen van occupacy-modellen. Het analyseren van uitgebreide daglijsten van opportunistische waarnemingen met occupancy-modellen kan dus een geschikt en haalbaar alternatief zijn voor libellenmonitoring op basis van gestandaardiseerde waarnemingen.

Uiteraard kan de in Hoofdstuk 2 beschreven monitoringmethode ook in andere landen dan Nederland worden toegepast, mits deze landen beschikken over voldoende grote datasets van opportunistische libellenwaarnemingen. Om libellentrends op internationale schaal te kunnen berekenen is echter een methode nodig om trends uit verschillende landen te combineren, rekening houdend met de ongelijke geografische bezetting van de onderzochte locaties. **HOOFDSTUK 3** beschrijft een pilotstudie voor de weidebeekjuffer (*Calopteryx splendens*). Uit vijf landen (Ierland, Groot-Brittannië, Nederland, België en Frankrijk) werden opportunistische waarnemingen verzameld, uit de periode 1990-2008. De occupancy-trends werden eerst voor elk land afzonderlijk geschat. Vervolgens werden de landen gewogen op basis van het aantal onderzochte locaties en het verspreidingsgebied van de soort per land. Deze gewichten zijn vervolgens toegepast bij de aggregatie van de landelijke trends tot een supranationale trend. Hieruit bleek dat de verspreiding van *C. splendens* sterk toenam in de vijf landen samen. De pilot toonde aan dat het mogelijk is om supranationale occupancy-trends te berekenen, wat nieuwe perspectieven biedt voor monitoring van biodiversiteit op internationale schaal.

HOOFDSTUK 4 onderzoekt hoe de libellenfauna van Nederland zich heeft ontwikkeld in de periode 1991-2013, waarbij zowel gebruik wordt gemaakt van gestandaardiseerde monitoringdata (abundantie van soorten) als van opportunistische data (verspreiding van soorten). Trends van libellensoorten van verschillende habitattypen worden vergeleken, alsook trends van soorten met een zuidelijk vs. noordelijk verspreidingsgebied in Europa. Veel soorten waren vóór 1990 afgenomen als gevolg van milieuvervuiling en verlies van leefgebied. Sinds de jaren 1980 hebben strengere milieuregels en natuurherstelprojecten geleid tot verbeteringen in zoetwaterhabitats en konden veel libellensoorten zich snel herstellen, wat leidde tot een positievere staat van instandhouding. Soorten van stromend water lieten sterker herstel zien dan soorten van stilstaand water. Zuidelijke soorten vertoonden meer positieve trends dan noordelijke soorten, wat suggereert dat klimaatverandering heeft bijgedragen aan het herstel. Deze uitkomsten ondersteunen de geschiktheid van libellen als indicatoren van de toestand van zoetwaterhabitats. Libellen herstelden zich in Nederland echter sterker dan veel andere aquatische en terrestrische insecten (bijvoorbeeld steenvliegen, kokerjuffers, eendagsvliegen, dagvlinders, nachtvlinders), waarschijnlijk vanwege hun grotere verspreidingsvermogen of andere habitateisen.

In navolging van de methode voor het bepalen van supranationale trends in Hoofdstuk 3 en de verklaringen voor de trends van libellen in Nederland in Hoofdstuk 4, wordt in **HOOFDSTUK 5** onderzocht hoe het voorkomen van libellen op Europese schaal is veranderd in de periode 1990-2015. Op basis van verspreidingsgegevens van 10 Europese geografische regio's werden occupancy-indexen berekend voor 99 (69%) van de Europese soorten. 55 van hen namen toe in verspreiding op Europees niveau, 32 soorten bleven stabiel en geen enkele ging achteruit. Van 12 soorten was de trend onzeker. Om te bepalen of de gevonden veranderingen in libellengemeenschappen worden veroorzaakt door klimaatopwarming, werden Species Temperature Indices (STI) berekend. STI is een eenvoudige maat voor de temperatuurvoorkeur van een soort, gedefinieerd als de gemiddelde jaartemperatuur in het Europese verspreidingsgebied van die soort. Op basis van deze STI werden alle soorten gecategoriseerd als koelte- of warmteminnend en werden Multi-species Indicators (MSI) samengesteld. De MSI van koelte- en warmteminnende soorten verschilden in sommige regio's, maar namen op Europese schaal in een vergelijkbaar tempo toe. Verder werden Community Temperature Indices (CTI) berekend, als de gemiddelde STI van alle soorten in een regio, gewogen naar de occupancy per soort. CTI steeg in alle regio's, behalve op Cyprus. De Europese CTI steeg licht, maar bleef achter bij de toename van de temperatuur zelf. Dit betekent dat libellen een 'klimaatschuld' hebben opgebouwd, waardoor problemen voor koelteminnende soorten nog verwacht kunnen worden na 2015. Libellen bleken een geschikte soortgroep te zijn om veranderingen in soortgemeenschappen te monitoren, zowel op regionale als continentale schaal.

Voor effectieve soortenbescherming is het niet alleen belangrijk om vroegtijdig op te merken dat een soort achteruitgaat, maar ook om de oorzaken van die achteruitgang goed te begrijpen. Bovendien is het noodzakelijk om onderscheid te maken tussen voormalige en actuele bedreigingen, aangezien insecten snel kunnen reageren op veranderingen in het milieu. Beschermingsmaatregelen moeten geconcentreerd worden op actuele bedreigingen. **HOOFDSTUK 6** beschrijft een onderzoek naar de habitatvereisten van de speerwaterjuffer (*Coenagrion hastulatum*), een bedreigde soort in Nederland, en onderzoekt wat de oorzaak is van het voortdurende verlies van populaties gedurende de 20e en begin van de 21e eeuw. Aanvankelijk waren habitatvernietiging en veranderingen in het menselijk gebruik van vennen en hoogvenen de voornaamste oorzaken. In de tweede helft van de 20e eeuw werden de sterk verhoogde atmosferische deposities van zwavel- en stikstofverbindingen de belangrijkste boosdoeners. Deze leidden tot verzuring en eutrofiëring van leefgebieden. Locaties waar *C. hastulatum* tussen 2001 en 2015 verdween hadden een lagere bedekking van belangrijke vegetatiestructuren. Dit suggereert dat deze locaties zich nooit volledig hebben hersteld, ondanks de sterke afname van zwaveldepositie en de gematigde afname van stikstofdepositie sinds de jaren tachtig van vorige eeuw. Recent zijn nog meer populaties verloren gegaan als een direct gevolg van langdurige droogteperioden, een gevolg van klimaatverandering. De meest relevante drukfactoren zijn dus inderdaad in de loop van de tijd veranderd. Herstel van grondwatersystemen en vernattingsmaatregelen zijn nu de eerste prioriteiten voor het behoud van *C. hastulatum* en andere koelteminnende soorten van vennen en hoogvenen.

HOOFDSTUK 7 bevat een overkoepelende synthese. Hierin worden algemene conclusies getrokken, implicaties voor libellenbescherming benoemd en toekomstperspectieven besproken.

Op nationaal niveau in Nederland hebben libellen negatief gereageerd op milieuproblemen in de 20e eeuw, maar de meeste soorten herstelden zich snel toen deze problemen verdwenen of afnamen. Klimaatverandering heeft nu echter een dominant effect, zowel positief op warmteminnende soorten als negatief op koelteminnende soorten. Dit geldt ook op Europees niveau: de 'klimaatschuld' die libellengemeenschappen hebben opgebouwd wordt nu betaald, aangezien veel koelteminnende soorten beginnen af te nemen en als bedreigd op de nieuwe IUCN Rode Lijst van Europese libellen komen te staan. Libellenbescherming moet prioriteit geven aan het behoud van oligo-mesotrofe zoetwaterhabitats in Noord-Europa, zodat deze als toevluchtsoorden kunnen dienen voor koelteminnende soorten. Het stopzetten van de exploitatie van deze ecosystemen en het stabiliseren van oppervlakte- en grondwaterstanden zijn de belangrijkste maatregelen. Nog dringender wellicht, is de bescherming van stroomgebieden in Zuid- en Zuidoost-Europa, waar meerdere libellensoorten gevaar lopen door uitdroging van beken en rivieren, waaronder enkele soorten die alleen in Europa voorkomen en een klein verspreidingsgebied hebben.

Dit proefschrift ondersteunt de geschiktheid van libellen als indicatoren voor biodiversiteit. Omdat libellen snel reageren op veranderingen in het milieu, zowel positief als negatief, informeren ze ons over de actuele toestand van zoetwaterecosystemen. Vanwege hun sterke verspreidingsvermogen speelt versnippering van leefgebieden een relatief beperkte rol. Libellentrends hebben daarom een 'vroege signaleringsfunctie' en kunnen worden gebruikt als voorspellers van toekomstige trends van andere zoetwaterorganismen die minder snel reageren.

Bovendien bewijst dit proefschrift dat het haalbaar is om direct een Europees libellenmeetnet te starten, door verspreidingsgegevens te verzamelen die al in veel landen beschikbaar zijn en die gegevens te analyseren met occupancy-modellen. De indexen en trends die daarmee verkregen worden kunnen de basis vormen voor een biodiversiteitsindicator van zoete wateren, waardoor het hiaat in de indicatoren die momenteel door het European Environmental Agency worden gebruikt kleiner wordt.

With a Species Temperature Index (STI) of 18.3 °C, *Trithemis arteriosa* is the most warm-adapted dragonfly species in Europe.

DANKWOORD

Volgens het promotiereglement van Wageningen University is het schrijven van een proefschrift bedoeld als ‘proeve van bekwaamheid tot het zelfstandig beoefenen van de wetenschap’. Ik heb dat altijd een merkwaardige bepaling gevonden, want wetenschap is in de regel teamwerk en zelden promoveert iemand zonder hulp of medewerking van anderen. Ik in elk geval niet!

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Het Landelijk Meetnet Libellen, dat door De Vlinderstichting wordt gecoördineerd en door het CBS bij de les wordt gehouden, is een belangrijke pijler geweest voor mijn onderzoek. Aan het libellenmeetnet werkten veel oud-collega's mee, waarvan ik Dick Groenendijk, Jaap Bouwman, Kim Huskens, Victor Mensing, Menno Venema, Marijn Prins, José Kok, Gerdien Groenendijk en Kars Veling in het bijzonder wil bedanken. En Chris van Swaay, die met 'zijn' vlindermeetnet ver voor de troepen vooruit liep en mijn onderzoek met raad en daad heeft gesteund. Met het CBS was het altijd fijn en constructief samenwerken. Naast Arco ben ik vooral ook Calijn Plate hier bijzonder dankbaar voor. Het Landelijk Meetnet Libellen zou niet bestaan zonder de vele vrijwillige libellenwaarnemers die Nederland tot het best onderzochte libellenland ter wereld hebben gemaakt.

Mijn interesse in libellen, de veldbiologie en de natuur in het algemeen vindt zijn oorsprong in mijn tienerjaren bij de Nederlandse Jeugdbond voor Natuurstudie (NJN). Ik voel me schatplichtig aan het zooitje ongeregeld dat me destijds op sleeptouw heeft genomen. En aan Marcel Wasscher, nestor van de Nederlandse libellenstudie, die op het legendarische libellenkamp in 1995 (mijn eerste NJN-zomerkamp) ervoor heeft gezorgd dat het hek voor goed van de dam was. Tekenend is het feit dat op datzelfde kamp nog twee deelnemers waren die inmiddels een proefschrift over een libellenonderwerp hebben geschreven, alsook mijn copromotor.

De fascinatie voor biodiversiteit is na de NJN een belangrijke drijfveer gebleven, ook tijdens mijn studie, mijn werk en dit promotieonderzoek. En gedeelde pret is dubbele pret. Roy, Albert, Antoine en Dick, bedankt voor jullie vriendschap! Onze gezamenlijke zoektochten naar leuke soorten – van Texel tot Zuid-Limburg en van Andalusië tot Finland – ze zijn me veel waard.

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CURRICULUM VITAE

Tim Termaat was born on 18 August 1980 in IJsselstein, the Netherlands. Shortly after he moved to Boxtel, where he grew up. After finishing his VWO diploma at the Jacob-Roeland Lyceum in 1998 he studied Biology at Wageningen University. He specialised in Ecosystem Biology and Entomology. He graduated in 2003 (MSc), after an internship on Entomology at the University of California, Riverside (USA) and an internship on Nature management at Elings Landscape Architectures in Oisterwijk (the Netherlands).

Tim continued working at Elings until 2005, when he was hired at Dutch Butterfly Conservation (De Vlinderstichting) in Wageningen. Here, he worked as an ecologist, dragonfly expert and project manager, mostly on projects on dragonfly conservation and monitoring. The research in this PhD thesis is largely based on work carried out at Dutch Butterfly Conservation. In 2017 Tim switched to 'Bosgroep

Midden Nederland' in Ede, where he worked as an ecologist on landscape ecological projects. In 2022 he started his present position at State Forestry Service (Staatsbosbeheer) as a senior ecologist. Here, he contributes to the management, restoration and development of nature reserves in the province of Gelderland. From 2012 to present Tim has been secretary of the Brook valleys Expert Team of the OBN Knowledge Network for Nature Restoration and Management.

Tim currently lives in Renkum, with his wife Maartje and their children Matthijs, Lieke and Niels. After leaving Dutch Butterfly Conservation in 2017, he finished this PhD thesis in his spare time.

For more information please visit about.me/timtermaat.

List of publications

PUBLICATIONS IN PEER-REVIEWED JOURNALS

Kalkman V.J., Boudot J.P., Bernard R., De Knijf G., Suhling F. & Termaat T. (2018). Diversity and conservation of European dragonflies and damselflies (Odonata). *Hydrobiologia* 811: 269-282.

Termaat T., van Grunsven R.H.A., Plate C.L. & van Strien A.J. (2015). Strong recovery of dragonflies in recent decades in The Netherlands. *Freshwater Science* 34: 1094-1104.

Termaat T., Ketelaar R., van Kleef H.H., Verberk W.C.E.P., van Grunsven R.H.A. & WallisDeVries M.F. (*submitted*). Spearhead blues: How threats to the damselfly *Coenagrion hastulatum* changed over time.

Termaat T., van Strien A.J., van Grunsven R.H., De Knijf G., Bjelke U., … & WallisDeVries M.F. (2019). Distribution trends of European dragonflies under climate change. *Diversity and Distributions* 25: 936-950.

Van Strien A.J., van Swaay C.A.M. & Termaat T. (2013). Opportunistic citizen science data of animal species produce reliable estimates of distribution trends if analysed with occupancy models. *Journal of Applied Ecology* 50: 1450-1458.

Van Strien A.J., Termaat T., Groenendijk D., Mensing V. & Kéry M. (2010). Site-occupancy models may offer new opportunities for dragonfly monitoring based on daily species lists. *Basic and Applied Ecology* 11: 495-503.

Van Strien A.J., Termaat T., Kalkman V.J., Prins M., De Knijf G., … & Vanreusel W. (2013). Occupancy modelling as a new approach to assess supranational trends using opportunistic data: a pilot study for the damselfly *Calopteryx splendens*. *Biodiversity and Conservation* 22: 673-686.

BOOKS

Brochard C., Groenendijk D., van der Ploeg E. & Termaat T. (2012). *Fotogids Larvenhuidjes van Libellen*. KNNV Uitgeverij, Zeist.

SELECTION OF OTHER ARTICLES AND BOOK CHAPTERS

Bouwman J.H., Kalkman V.J., Abbing G., de Boer E.P., Geraeds R.P.G., … & Termaat T. (2008). Een actualisatie van de verspreiding van de Nederlandse libellen. *Brachytron* 11: 103-198.

De Knijf G. & Termaat T. (2010). Statut et distribution de *Sympetrum meridionale* (Selys, 1841) dans le nord ouest de l'Europe, en particulier en Belgique et aux Pays-Bas (Odonata, Anisoptera: Libellulidae). *Martinia* 26: 81-82.

De Knijf G., Termaat T. & Ott J. (2015). Conservation of European dragonflies and damselflies. *In*: Boudot J.P. & Kalkman V.J. (editors) (2015). *Atlas of the European dragonflies and damselflies*. KNNV Publishing, Zeist.

Kalkman V. & Termaat T. (2014). Wat vertellen de SNL-insecten ons? Dagvlinders, libellen en sprinkhanen geven een gemengd beeld. *Vakblad Natuur, Bos, Landschap* 11: 10-13.

Kranenbarg B., van Vliet T., Termaat T. & Ketelaar R. (2010). Index van bijna 40 jaar publicaties van de Nederlandse Vereniging voor Libellenstudie en voorlopers. *Brachytron* 13: 65-96.

Termaat T. (1999). Ontdekking van een populatie van *Coenagrion mercuriale* (Charpentier, 1840) nabij Virton. *Gomphus* 15: 29-30.

Termaat T. (2000). Een overzicht van de nieuwe vindplaatsen van de Rivierrombout (*Gomphus flavipes*) in Nederland in 1999. *Brachytron* 4: 13-17.

Termaat T. & De Knijf G. (2010). De Zuidelijke heidelibel (*Sympetrum meridionale*) in België en Nederland: herkenning, verspreiding en status in Noordwest-Europa. *Brachytron* 13: 4-17.

Termaat T. & Kalkman V.J. (2012). Basisrapport Rode Lijst Libellen volgens Nederlandse en IUCN-criteria. *Brachytron* 14: 75-186.

Termaat T., Kalkman V.J. & Bouwman J.H. (2010). Changes in the range of dragonflies in the Netherlands and the possible role of temperature change. *In*: Ott J. (editor). Monitoring climatic change with dragonflies. *BioRisk* 5: 155-173. Pensoft, Sofia.

Van Grunsven R.H.A. & Termaat T. (2010). Waarneming van een jonge Paardenbijter (*Aeshna mixta*) op een ongebruikelijke plaats. *Brachytron* 13: 44-46.

Vliegenthart A. & Termaat T. (2001). De mercuurwaterjuffer (*Coenagrion mercuriale*) in Nederland? *Brachytron* 5: 3-7.

SELECTION OF REPORTS

Bouwman J.H. & Termaat T. (2008). *Libellen in terreinen van het Limburgs Landschap*. Rapport VS2008.27, De Vlinderstichting, Wageningen.

Bouwman J., Groenendijk D., Termaat T. & Plate C. (2009). *Dutch Dragonfly Monitoring Scheme, a manual*. Report VS2009.15, Dutch Butterfly Conservation, Wageningen & CBS Statistics Netherlands, Den Haag.

De Vries H.H., Bremer P., de Bruijn B., Koks B., Kragten S., Rossenaar A.J., Termaat T., Thissen J. & Zollinger R. (2008). *Uitwerking leefgebiedenbenadering Flevoland voor soorten*. Rapport VS2008.38, De Vlinderstichting, Wageningen.

De Vries H.H., Stip A., Soldaat L., Huskens K. & Termaat T. (2015). *Ontwerp Agrarisch meetnet libellen*. Rapport VS2015.14, De Vlinderstichting, Wageningen.

De Vries H. & Termaat T. (2013). *Trendanalyse groene glazenmaker*. Rapport VS2013.01, De Vlinderstichting, Wageningen.

Groenendijk D., Termaat T. & de Vries H. (2006). *Libellen in de oostrand van Flevoland: actuele situatie, potenties en maatregelen*. Rapport VS2005.30, De Vlinderstichting, Wageningen.

Jansen A.J.M., Kieskamp A.A.M., Termaat T., Versluijs R., Westerhof P. & Bulten G.H. (2020). *Landschapsecologische systeemanalyse Wrange - Slangenburg*. Coöperatie Bosgroep Midden Nederland u.a., Ede & Stichting Bargerveen, Nijmegen.

Ketelaar R., Plate C., Bouwman J., Termaat T. & Groenendijk D. (2008). *Manual Dutch Dragonfly Monitoring Scheme* (translation and revision). Dutch Butterfly Conservation, Wageningen & CBS Statistics Netherlands, Voorburg.

Kieskamp A.A.M., Smeenge H. & Termaat T. (2022). *Gulbroek: landschapsecologische systeemanalyse*. Coöperatie Bosgroep Midden Nederland u.a., Ede.

Struijk R.P.J.H., Zollinger R. & Termaat T. (2010). *Oases van biodiversiteit: beheer, aanleg en analyse van soortenrijke stilstaande kleine wateren in Nederland*. Rapport 2008.095, Stichting RAVON, Nijmegen.

Termaat T. (2006). *De gewone bronlibel in het stroomgebied van Aa en Maas en de Dommel*. Rapport VS2006.11, De Vlinderstichting, Wageningen.

Termaat T. (2006). *Op de bres voor de speerwaterjuffer: beschermingsplan voor de speerwaterjuffer in Noord-Brabant*. Provincie Noord-Brabant, 's-Hertogenbosch.

Termaat T. (2006). *Status en habitat van de gevlekte witsnuitlibel in Noord-Brabant*. Rapport VS2006.38, De Vlinderstichting, Wageningen.

Termaat T. (2007). *Actieplan kleine ijsvogelvlinder Gelderland*. Rapport VS2007.37, De Vlinderstichting, Wageningen.

Termaat T. (2007). *Quickscan libellen voor zes Brabantse vennen*. Rapport VS2007.28, De Vlinderstichting, Wageningen.

Termaat T. (2008). *De Kleine ijsvogelvlinder* (Limenitis camilla)*: beschermingsplan voor de Kleine ijsvogelvlinder in Noord-Brabant*. Provincie Noord-Brabant, 's-Hertogenbosch.

Termaat T. (2008). *Libellen van zeventien beken op en rond de Veluwe: nulmeting*. Rapport VS2008.01, De Vlinderstichting, Wageningen.

Termaat T. (2009). *Begrazing Esperloop: onderzoek naar de effecten voor de gewone bronlibel*. Rapport VS2009.35, De Vlinderstichting, Wageningen.

Termaat T. (2010). *Krabbenscheer in de Krimpenerwaard: resultaten van het herintroductieproject en tips voor natuurvriendelijk slootonderhoud*. Rapport VS2010.29, De Vlinderstichting, Wageningen.

Termaat T. (2013). *Test kansenkaart rivierrombout: onderzoek naar een alternatieve inventarisatiemethode*. Rapport VS2013.06, De Vlinderstichting, Wageningen.

Termaat T., Bouwman J.H., Groenendijk D. & Wallis de Vries M.F. (2007). *Goed beheer voor bedreigde vliegers in Overijssel.* Rapport VS2006.39, De Vlinderstichting, Wageningen.

Termaat T. & Groenendijk D. (2005). *De gewone bronlibel op de Esperloop: beschermingsplan en gebiedsvisie*. Rapport VS2004.59, De Vlinderstichting, Wageningen.

Termaat T. & Groenendijk D. (2006). *Witsnuitlibellen in de Groote en Deurnese Peel: onderzoek naar oorzaken van het verspreidingspatroon*. Rapport VS2006.19, De Vlinderstichting, Wageningen.

Termaat, T., Huskens K. & van Strien A.J. (2015). *Libellen geteld: Jaarverslag 2014*. Rapport VS2015.006, De Vlinderstichting, Wageningen.

Termaat T. & Kalkman V.J. (2011). *Basisrapport Rode Lijst Libellen volgens Nederlandse en IUCN-criteria*. Rapport VS2011.015, De Vlinderstichting, Wageningen.

Termaat T., Smeenge H., Kieskamp A., Wijhe P., Thielemans J. & Bulten G. (2022). *Leemputten bij Staverden en Verbrande Bos: Landschapsecologische systeemanalyse en maatregelenplan*. Coöperatie Bosgroep Midden Nederland u.a., Ede.

Termaat T. , van Kleef H. & van Grunsven R.H.A. (2017). *Als een speer aan de slag voor de speerwaterjuffer*. Rapport VS2017.033, De Vlinderstichting, Wageningen.

Termaat T., Veling K. & Vliegenthart A. (2010). *Soortbeschermingsplan bruine eikenpage Noord-Brabant*. De Vlinderstichting, Wageningen.

Termaat T., Veling K., Vliegenthart A. (2010). *Soortbeschermingsplan bruine eikenpage Noord-Brabant, Gebiedsuitwerking*. De Vlinderstichting, Wageningen.

Van Duinhoven G., Termaat T., Stortelder A., van de Weerd R. & Runhaar H. (2016). *Van stroomgoot tot beekdallandschap: kansen voor herstel en ontwikkeling van beekdallandschappen*. OBN Deskundigenteam Beekdallandschap. OBN/VBNE, Driebergen.

Van Swaay C.A.M., Groenendijk D., Termaat T. & Plate C.L. (2010). *Vlinders en libellen geteld: jaarverslag 2009*. Rapport VS2010.01, De Vlinderstichting, Wageningen.

Van Swaay C.A.M., Huigens T., Termaat T. & Plate C.L. (2014). *Vlinders en libellen geteld: jaarverslag 2013*. Rapport VS2014.05, De Vlinderstichting, Wageningen.

Van Swaay C.A.M., Termaat T., Kok J., Huskens K. & Poot M. (2016). *Vlinders en libellen geteld: jaarverslag 2015*. Rapport VS2016.01, De Vlinderstichting, Wageningen.

Van Swaay C.A.M., Termaat T. & Plate C.L. (2011). *Handleiding Landelijke Meetnetten Vlinders en Libellen*. Rapport VS2011.01, De Vlinderstichting, Wageningen & Centraal Bureau voor Statistiek (CBS), Den Haag.

Van Swaay C.A.M., Termaat T. & Plate C.L. (2011). *Vlinders en libellen geteld: jaarverslag 2010*. Rapport VS2011.04, De Vlinderstichting, Wageningen.

Van Swaay C.A.M., Veling K., Termaat T., Huskens K. & Plate, C.L. (2013). *Vlinders en libellen geteld. Jaarverslag 2012*. Rapport VS2013.003, De Vlinderstichting, Wageningen.

Van Swaay C.A.M., Veling K., Termaat T. & Plate C.L. (2012). *Vlinders en libellen geteld: jaarverslag 2011*. Rapport VS2012.05, De Vlinderstichting, Wageningen.

Wallis de Vries M.F., Termaat T. & Venema M. (2006). *Voorspelling van de vliegtijden van libellen*. Rapport VS2006.32, De Vlinderstichting, Wageningen.

Wallis de Vries M., Wynhoff I., Zollinger R., Brouwer E., van der Burg R., van Duinen G.-J., Frigge P. & Termaat T. (2013). *Van appelrussula tot zompsprinkhaan: leefgebiedsplan bedreigde soorten van de Brabantse Zandgronden*. Provincie Noord-Brabant, ’s-Hertogenbosch.

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