Received: 29 October 2018 | Revised: 19 January 2019 | Accepted: 15 February 2019

DOI: 10.1111/ddi.12913

BIODIVERSITY RESEARCH

WILEY Diversity and Distributions

Distribution trends of European dragonflies under climate change

Tim Termaat[1,2] | Arco J. van Strien[3] | Roy H. A. van Grunsven[1] | Geert De Knijf[4] | Ulf Bjelke[5] | Klaus Burbach[6] | Klaus-Jürgen Conze[7] | Philippe Goffart[8] | David Hepper[9] | Vincent J. Kalkman[10] | Grégory Motte[8] | Marijn D. Prins[1,11] | Florent Prunier[12] | David Sparrow[13] | Gregory G. van den Top[1] | Cédric Vanappelghem[14,15] | Michael Winterholler[16] | Michiel F. WallisDeVries[1,17]

[1]De Vlinderstichting/Dutch Butterfly Conservation, Wageningen, The Netherlands

[2]Bosgroep Midden Nederland, Ede, The Netherlands

[3]Statistics Netherlands, The Hague, The Netherlands

[4]Research Institute for Nature and Forest, Brussels, Belgium

[5]Swedish Biodiversity Centre, Swedish University of Agricultural Sciences, Uppsala, Sweden

[6]AG Libellen Bayern, Marzling, Germany

[7]AK Libellen NRW, Essen, Germany

[8]Direction générale opérationnelle Agriculture, Ressources naturelles et Environnement (DGARNE), Département de l'Etude du Milieu Naturel et Agricole, Direction de la Nature et de l'Eau, Service public de Wallonie, Gembloux, Belgium

[9]British Dragonfly Society, Peterborough, UK

[10]European Invertebrate Survey—The Netherlands, Nationaal Natuurhistorisch Museum Naturalis, Leiden, The Netherlands

[11]Naturalis Biodiversity Centre, Leiden, The Netherlands

[12]AEA El Bosque Animado, Valle del Genal, Spain

[13]Cyprus Dragonfly Study Group, Pafos, Cyprus

[14]Société française d'odonatologie, Bois d'Arcy, France

[15]Unité "Evolution, Ecologie, Paléontologie", UMR CNRS 8198, Bat. SN2 Université de Lille, Villeneuve d'Ascq, France

[16]Bavarian Environment Agency, Augsburg, Germany

[17]Plant Ecology and Nature Conservation Group, Wageningen University, Wageningen, The Netherlands

Correspondence
Tim Termaat, De Vlinderstichting/Dutch Butterfly Conservation, Wageningen, The Netherlands.
Email: timtermaat@gmail.com

Editor: Alan Andersen

Abstract

Aim: 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

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
© 2019 The Authors. *Diversity and Distributions* Published by John Wiley & Sons Ltd

occurrence of dragonflies in Europe has changed in recent decades, and if these changes are in parallel with climate change.

Location: Europe.

Methods: We use data from 10 European geographical 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).

Results: 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.

Main conclusions: 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

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, Hill, Ohlemüller, Roy, & Thomas, 2011; Hickling, Roy, Hill, Fox, & Thomas, 2006; Kampichler, Van Turnhout, Devictor, & Van der Jeugd, 2012; Lindström, Green, Paulson, Smith, & Devictor, 2013; Mason et al., 2015). Species vary in their response to climate warming, due to different temperature requirements and different dispersal and colonization 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 (Franco 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, Beale, Towers, & Hewison, 2009; Clavero, Villero, & Brotons, 2011; Davey, Devictor, Jonzén, Lindström, & Smith, 2013; Devictor et al., 2012a; Jiguet et al., 2010; Roth, Plattner, & Amrhein, 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 (Dijkstra, Monaghan, & Pauls, 2014; 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 (Feest, 2013; Thomas, 2005).

Unfortunately, monitoring freshwater invertebrates comes with drawbacks. Most groups are so species-rich that collecting, sorting and identifying samples to species level require 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, Theischinger, Nipperess, Turak, & Hughes, 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 standardization, 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 (Isaac, Van Strien, August, De Zeeuw, & Roy, 2014; Van Strien, Termaat, Groenendijk, Mensing, & Kéry, 2010; Van Strien, Van Swaay, & Termaat, 2013). Moreover, Van Strien, Termaat et al. (2013) 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 geographical 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 hypothesize that (a) warm-dwelling species have more positive trends than cold-dwelling species, that, as a consequence, (b) warm-dwelling species have increased their share in regional communities and (c) that these effects increase on a south–north gradient through Europe, as the ratio of warm- and cold-dwelling species decreases with increasing latitude.



FIGURE 1 Participating European geographical regions, here considered as countries or lower administrative divisions

2 | METHODS

2.1 | Species records

We gathered dragonfly distribution records, from 1990 onwards, from the following European geographical 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 (Figure 1). The resulting data set included records of 99 species, which equals 69% of all dragonfly species recorded in Europe (Kalkman et al., 2018).

All records used in this study cover adult dragonflies only. The majority of these records are "opportunistic," that is, collected without a standardized 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 (Supporting Information Table S1). All data in each region were validated by experts to prevent false-positive records. To standardize the geographical 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.

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 colonized (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) and Van Strien, Van Swaay 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.

2.3 | Species trend analysis

2.3.1 | 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) and Van Strien, Van Swaay 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 and Kéry (2007) and Royle and 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 colonization 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 colonization 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 as 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: (a) single records of any species on one site and date without records of other species, (b) short day-lists, that is, records of two or three species made by a single observer on one site and date and (c) comprehensive day-lists, that is, 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:

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

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 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://subtrac.sara.nl). 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.

2.3.2 | 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, Plate, and Van Strien (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.

2.4 | Species Temperature Indices

We calculated the STI for each dragonfly species occurring in Europe (Boudot & Kalkman, 2015) (Supporting Information Table S2). 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 and 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 × 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 × 250 km. STIs 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).

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, Pannekoek, Verweij, Van Turnhout, & Van Strien, 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.

2.6 | Community Temperature Indices

Ultimately, we calculated a CTI for each region, as the average STI of all species in the region, weighted by species occupancies

TABLE 1 Number of species per trend class per geographical region (from north to south) and for Europe

Region	Trend period	*N* species	Increase	Stable	Decline	Uncertain	% Increase	χ^2	*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

Note. χ^2: 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.

(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).

3 | RESULTS

3.1 | Occupancy indices and trends

The number of species for which a regional trend could be calculated with sufficiently low standard errors, that is, standard errors low enough to detect a 5% or higher annual increase or decline, ranged from five for Cyprus to 79 for France (Table 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 (Supporting Information Data S1).

In 7 out of 10 regions, more species increased than decreased their occupied range (Table 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 Figure 2. Trend estimates of 12 species had too large standard errors. European indices and trends of all species are provided in Supporting Information Data S2.

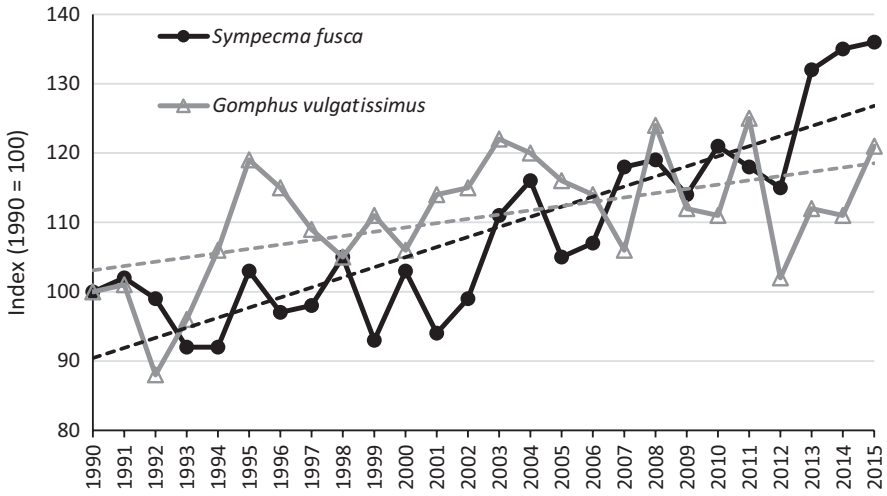


FIGURE 2 European index (1990–2015) of *Sympecma fusca* and *Gomphus vulgatissimus*. Linear regression lines (dashed lines) were aligned through the year effects to summarize overall change

3.2 | Species Temperature Indices

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) (Supporting Information Table S2).

3.3 | Multi-species Indicators

MSI of warm-dwelling species were increasing in all regions (Figure 3). Surprisingly, MSI of cold-dwelling species also increased in Sweden, Britain, the Netherlands and North Rhine-Westphalia. In Flanders,

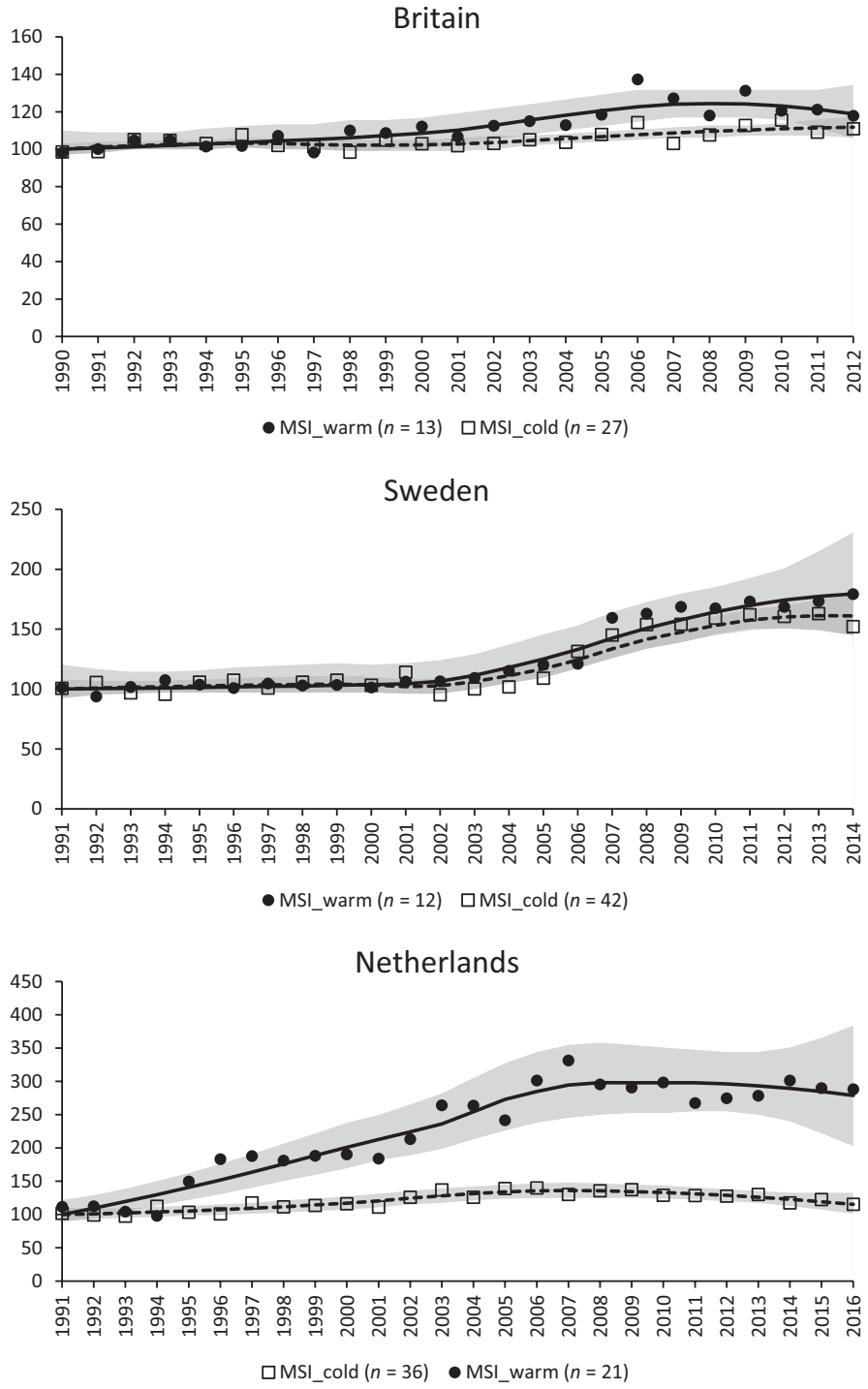


FIGURE 3 Multi-species Indicators (MSI) of warm-dwelling species (Species Temperature Index > 9.8°C) and cold-dwelling species (Species Temperature Index < 9.8°C) per geographical region (from north to south) and for Europe. The first year with data was set to 100. Smoothed trend lines were plotted through the year effects to summarize overall change. Shaded areas represent confidence intervals. Please note that *y*-axes differ

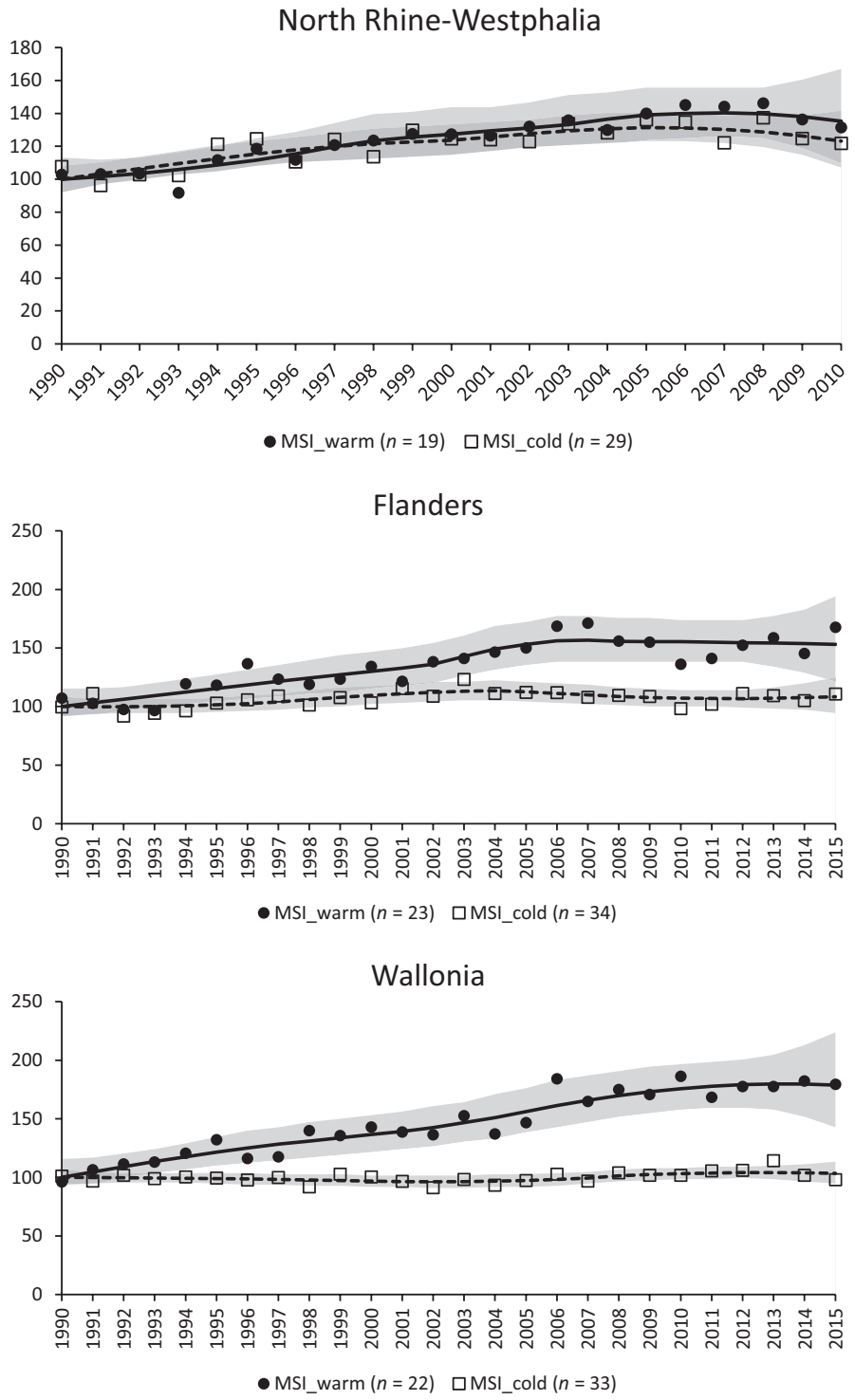


FIGURE 3 (Continued)

Wallonia and France, MSI of cold-dwelling species was stable, in Bavaria it declined, and in Andalusia, it was uncertain (Table 2). Cyprus has only one cold-dwelling species (*Enallagma cyathigerum*), which increased.

Comparing MSI trends of warm-dwelling and cold-dwelling species (Table 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.

3.4 | Community Temperature Indices

CTI increased in all regions, except Cyprus (Table 3; Supporting Information Figure S1). The most significantly increasing CTI was

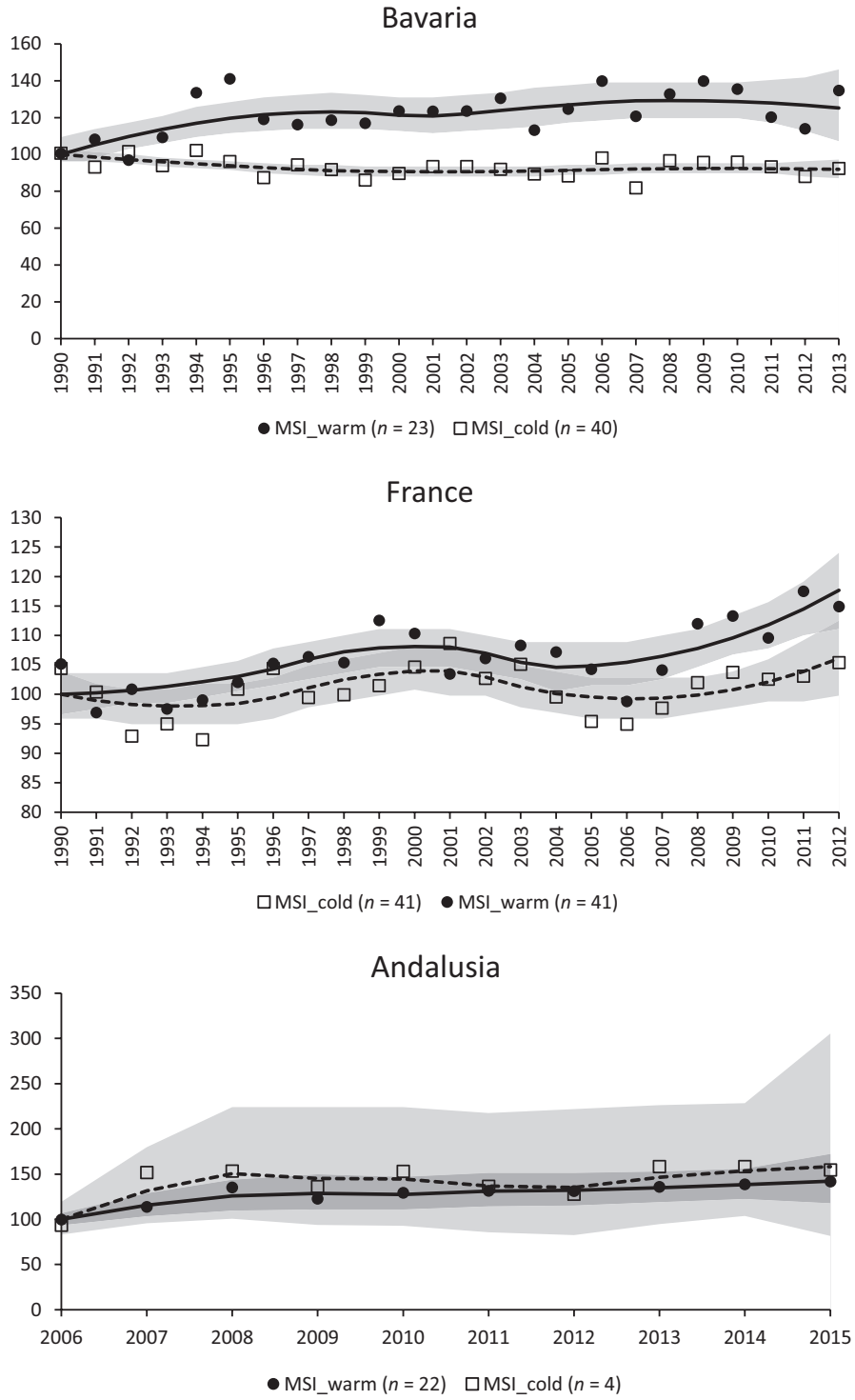


FIGURE 3 (Continued)

found for the Netherlands. The Dutch dragonfly fauna "warmed" at 9.5×10^{-3}°C year^{-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).

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

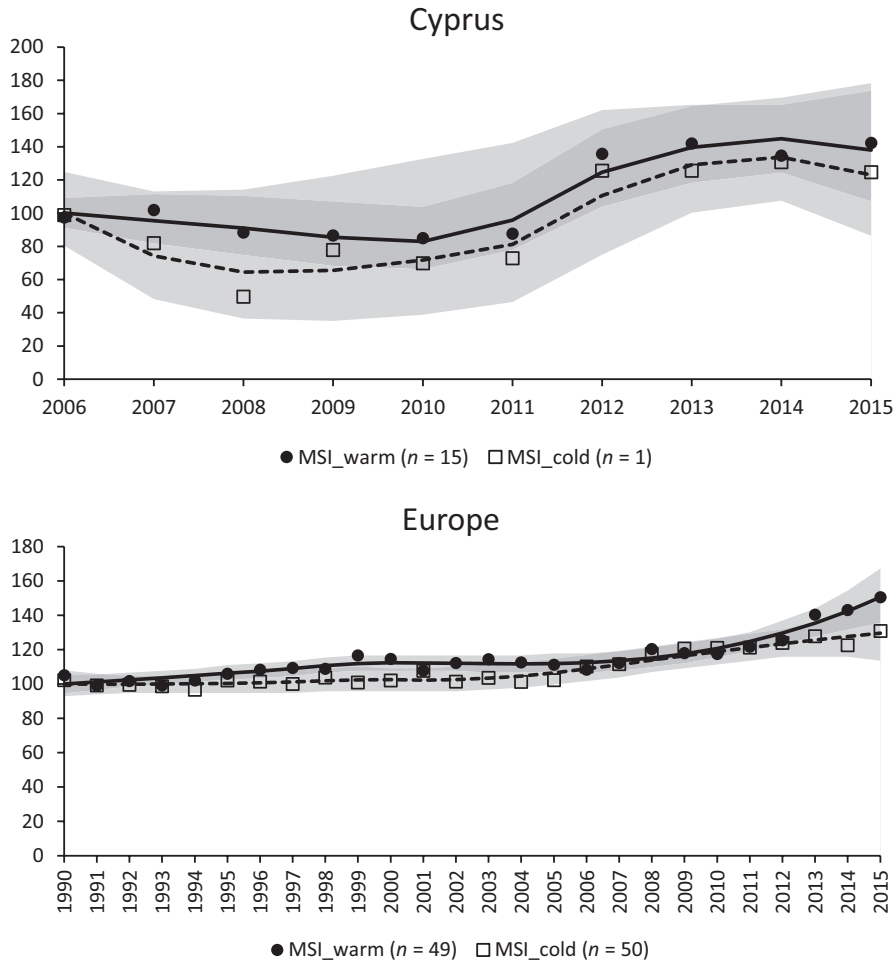


FIGURE 3 (Continued)

indicate that climate change has changed dragonfly occurrence at the community level as well.

4.1 | Testing of hypotheses

4.1.1 | Regional level

We hypothesized that (a) 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 (b) 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 year^{-1} on average, up to 9.5×10^{-3}°C year^{-1} for the Netherlands (Table 3), this "warming" of regional communities evolves more slowly than the increase in temperature itself (1.1×10^{-2}°C year^{-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," that is, 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 (c) 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

TABLE 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 geographical region (from north to south) and for Europe

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	

Note. *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.

in some of our regions than is currently available. The MSI trends of cold-dwelling and warm-dwelling species (Table 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.

4.1.2 | 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 year^{-1}

TABLE 3 Slope of Community Temperature index (CTI) per geographical region (from north to south) and for Europe

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

Note. *SE*: standard error; *p*: probability value.

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 year^{-1}, which is comparable with the increase in CTI of European butterflies (2.5×10^{-3}°C year^{-1}) and considerably greater than the increase in CTI of European birds (1.9×10^{-3}°C year^{-1}). This is in line with the well-known ability of dragonflies to quickly colonize 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.

4.2 | 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, Julliard, Couvet, & Jiguet, 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, Roy, Hill, & Thomas, 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. For example, it is likely that the reduction in 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, Van Grunsven, Plate, & Van Strien, 2015). 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 (Lindström et al., 2013; Virkkala & Lehikoinen, 2014).

4.3 | 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 recognize 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, Goffart, Kever, Motte, & Schott, 2017; Termaat et al., 2015).

Jaeschke, Bittner, Reineking, and Beierkuhnlein (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* (Supporting Information Data S1). We explain these differences by the estimations of maximum species dispersal abilities applied by Jaeschke et al. 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, Martens, & Suhling, 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 colonization. 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, 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, Thuyet, Uéda, & Watanabe, 2013; Van Dijk, Van Staalduinen, & Van der Sluijs, 2013). The relative contribution of these different environmental changes largely remains to be established.

4.4 | 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 for a standardized 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 adequately to 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 geographical coverage.

4.5 | 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 centralization of European dragonfly distribution data.

ACKNOWLEDGEMENTS

We thank all dragonfly observers who contributed to this study by making their observations available to their regional data managing organizations. Data from Sweden were obtained from the Swedish Species Observation System; this system is maintained by the Swedish Species Information Centre at Swedish University of Agricultural Sciences. Data from Britain were obtained from the British Dragonfly Society Recording Scheme. Data from the Netherlands were obtained from the Dutch National Database Flora and Fauna. Most records are currently collected through the online platforms Waarneming.nl and Telmee.nl. Data from North Rhine-Westphalia were obtained from the database managed by the Working Group Dragonflies North Rhine-Westphalia (AK Libellen NRW). Data from Bavaria were obtained from the "Datenbank Artenschutzkartierung," maintained by the Bavarian State Ministry of the Environment. Data from Flanders were obtained from the Flemish Dragonfly Society. Data from Wallonia were obtained from SPW/DGARNE/DEMNA-Working Group Gomphus and Natagora-observations. Most dragonfly records in both Flanders and Wallonia are currently collected through the online platforms Waarnemingen.be and Observations.be, which are managed by Natuurpunt and Natagora. Data from France were obtained from the database managed by the French Society of Odonatology (SfO). Data from Andalusia were obtained from the database managed by Red de Observadores de Libélulas de Andalucía (ROLA). Data from Cyprus were obtained from the database managed by the Cyprus Dragonfly Study Group; this database includes records collected through the online platform Observation.org. Vincent Devictor kindly provided the values of CTI trend slopes for birds and butterflies from his 2012 paper as based on presence–absence data. Eddie John is thanked for proofreading the text.

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.

ORCID

Tim Termaat https://orcid.org/0000-0002-5974-7294
Arco J. van Strien https://orcid.org/0000-0003-0451-073X
Roy H. A. van Grunsven https://orcid.org/0000-0001-8873-1024
Geert De Knijf https://orcid.org/0000-0002-7958-1420
Michiel F. WallisDeVries https://orcid.org/0000-0003-3808-2999

REFERENCES

Bertrand, R., Lenoir, J., Piedallu, C., Riofrío-Dillon, G., de Ruffray, P., Vidal, C., … Gégout, J.-C. (2011). Changes in plant community composition lag behind climate warming in lowland forests. *Nature*, *479*, 517–520. https://doi.org/10.1038/nature10548

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

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. https://doi.org/10.1016/j.biocon.2009.03.010

Bush, A., Theischinger, G., Nipperess, D., Turak, E., & Hughes, L. (2013). Dragonflies: Climate canaries for river management. *Diversity and Distributions*, *19*, 86–97. https://doi.org/10.1111/ddi.12007

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. https://doi.org/10.1126/science.1206432

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. M., Cumberlidge, N., Darwall, W. R. T., … Böhm, M. (2014). Global patterns of freshwater species diversity, threat and endemism. *Global Ecology and Biogeography*, *23*, 40–51. https://doi.org/10.1111/geb.12096

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

Darwall, W., Bremerich, V., De Wever, A., Dell, A. I., Freyhof, J., Gessner, M. O., … 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. https://doi.org/10.1111/1365-2656.12035

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., Herrando, S., … Jiguet, F. (2012a). Differences in the climatic debts of birds and butterflies at a continental scale. *NatureClimate Change*, *2*, 121–124.

Devictor, V., Van Swaay, C., Brereton, T., Chamberlain, D., Heliölä, J., Herrando, S., … 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*, 143–163.

Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z.-I., Knowler, D. J., Lévêque, C., … Sullivan, C. A. (2006). Freshwater biodiversity: Importance, threats, status and conservation challenges. *Biological Reviews*, *81*, 163–182. https://doi.org/10.1017/S1464793105006950

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. https://doi.org/10.1016/j.ecolind.2012.10.015

Franco, A. M. A., Hill, J. K., Kitschke, C., Collingham, Y. C., Roy, D. B., Fox, R., … 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. https://doi.org/10.1111/j.1365-2486.2006.01180.x

Gregory, R. D., Van Strien, A., Vorisek, P., Gmelig Meyling, A. W., Noble, D. G., Foppen, R. P. B., & Gibbons, D. W. (2005). Developing indicators for European birds. *Philosophical Transactions of the Royal Society B*, *360*, 269–288. https://doi.org/10.1098/rstb.2004.1602

Hassall, C. (2015). Odonata as candidate macroecological barometers for global climate change. *Freshwater Science*, *34*, 1040–1049. https://doi.org/10.1086/682210

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. https://doi.org/10.1111/j.1365-2486.2006.01116.x

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. https://doi.org/10.1111/j.1365-2486.2005.00904.x

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. https://doi.org/10.1111/2041-210X.12254

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. https://doi.org/10.1111/j.1752-4598.2012.00194.x

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. https://doi.org/10.1007/s10333-012-0317-3

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

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. https://doi.org/10.1007/s10750-017-3495-6

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. https://doi.org/10.1371/journal.pone.0035272

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. https://doi.org/10.1111/j.1600-0587.2012.07799.x

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*. San Diego, CA: Elsevier.

Mason, S. C., Palmer, G., Fox, R., Gillings, S., Hill, J. K., Thomas, C. D., & Oliver, T. H. (2015). Geographical range margins of many taxonomic groups continue to shift polewards. *Biological Journal of the Linnean Society*, *115*, 586–597. https://doi.org/10.1111/bij.12574

Menéndez, R., Megías, A. G., Hill, J. K., Braschler, B., Willis, S. G., Collingham, Y., & 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 A. Córdoba-Aquilar (Ed.), *Dragonflies and damselflies: Model organisms for ecological and evolutionary research* (pp. 79–95). Oxford, UK: Oxford University Press.
Ott, J. (2010). The big trek northwards: Recent changes in the European dragonfly fauna. In J. Settele, L. D. Penrev, T. A. Geogiev, R. Grabaum, V. Grobelink, S. Klotz, M. Kotarac, & I. Kühn (Eds.), *Atlas of biodiversity risk* (pp. 82–83). Sofia, Bulgaria: Pensoft Publishers.
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. https://doi.org/10.1038/nature01333
Rosenberg, D. M., & V. H. Resh (Eds.) (1993). *Freshwater biomonitoring and benthic macroinvertebrates*. New York, NY: Chapman & Hall.
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. https://doi.org/10.1016/j.biocon.2011.06.009
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. https://doi.org/10.1371/journal.pone.0082490
Royle, J. A., & Dorazio, R. M. (2008). *Hierarchical modeling and inference in ecology*. Amsterdam, The Netherlands: Academic Press.
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. https://doi.org/10.1016/j.ecolind.2017.05.033
Suhling, F., Martens, A., & Suhling, I. (2017). Long-distance dispersal in Odonata: Examples from arid Namibia. *Austral Ecology*, *42*, 544–552. https://doi.org/10.1111/aec.12472
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. https://doi.org/10.1086/682669
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. https://doi.org/10.1098/rstb.2004.1585
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. https://doi.org/10.1016/j.baae.2010.05.003
Van Strien, A. J., Termaat, T., Kalkman, V., Prins, M., De Knijf, G., Gourmand, A.-L., … 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. https://doi.org/10.1007/s10531-013-0436-1
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. https://doi.org/10.1111/1365-2664.12158
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. https://doi.org/10.1111/gcb.12573
Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., … Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, *416*, 389. https://doi.org/10.1038/416389a

BIOSKETCH

Tim Termaat is an ecologist at Bosgroep Midden Nederland (Forestry Owners Group): a cooperation for sustainable forest and nature management in Ede, the Netherlands. Previously, he worked at Dutch Butterfly Conservation (Wageningen, the Netherlands) on projects concerning the monitoring and conservation of dragonflies (Odonata). His main interest is understanding the occurrence of dragonflies on different scales, from local to ecozone, and the factors driving current changes.

Author contributions: T.T., G.D.K., U.B., K.B., K.-J.C., P.G., D.H., V.J.K., G.M., F.P., D.S., C.V. and M.W. contributed data for this manuscript. M.P. helped with data handling. G.v.d.T. calculated Species Temperature Indices. A.J.v.S. principally conducted statistical analyses, with input from T.T., R.H.A.v.G. and M.F.W. T.T. led the writing with significant input from R.H.A.v.G., M.F.W., A.J.v.S. and G.D.K. All authors have reviewed the manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Termaat T, van Strien AJ, van Grunsven RHA, et al. Distribution trends of European dragonflies under climate change. *Divers Distrib*. 2019;00:1–15. https://doi.org/10.1111/ddi.12913

View publication stats