

# Southern dragonflies expanding in Wallonia (south Belgium): a consequence of global warming?

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## Abstract

The occurrence of seven southern Odonata species has been watched in Wallonia over the last two decades (from 1981 to 2000). They have clearly expanded in the meantime and this pattern is still highly significant when the data are corrected for the increase of sampling efforts. Moreover, reproduction evidences have been collected recently (from 1993 onwards) for all these species and several settled and have now resident populations in Wallonia. In a second step, all present regular and irregular resident species of Wallonia were looked for change in range size and observation rate per visit between two six years periods of a survey and monitoring scheme, from 1989 to 2000. Analysis was achieved on grid cells visited at the right time at both periods, a procedure designed to neutralize the spatio-temporal heterogeneity of sampling. The comparison of results in relation to the distribution types of species and their habitat preferences show a significant global trend toward an increase for southern species during the investigated time interval, contrasting with other groups of species. If there is a tendency to rise for species preferring eutrophic still waters, this proves to be clearly due to the southern species sub-group, the other dragonflies of this habitat type showing a stable or even decreasing trend. Three distinct hypotheses are examined and discussed as possible explanations of the expansion pattern of southern species: (1) global warming, (2) change in aquatic habitats, especially eutrophication, and (3) intrinsic population dynamics. The rise of temperatures appears to be the main factor explaining the observed expansions.

## Keywords

Odonata, range shift, climate change, aquatic habitat change, eutrophication, Belgium

## Introduction

Climate has proved to change rapidly during the last century, with the rising of global temperatures, and this warming has proved already to bring about significant impacts on earth's life (Hughes 2000; Walther et al. 2002; Parmesan and Yohe 2003; Root et al. 2003).

One of the main expected responses of organisms to changing climate is to shift their geographical range poleward. Insects are likely to be particularly sensible to climate change and there have been actually many publications showing evidences of poleward range shifts in insects, especially butterflies (Parmesan et al. 1999; Hill et al. 1999, 2001, 2002; Warren et al. 2001; Ryrholm 2003), but also other groups like syrphids (Reemer et al. 2003). For dragonflies, reports of range shifts are plentiful in Europe as well as in America (Ott 2000 and 2001; Parr 2003) or Japan (Aoki 1997) but quantitative studies are still rare (De Knijf et al. 2003; Hickling et al. 2005).

To be properly appreciated, range shifts have to be looked at large scale, a continent scale ideally, in order to monitor as well southern as northern boundaries of species geographical distributions (Parmesan et al. 1999; Parmesan and Galbraith 2004). This can be watched also in latitudinally extended countries like in Great Britain (Hill 1999, 2002; Warren et al. 2001) or Sweden (Ryrholm 2003). However, range shifts have been also inferred from abundance changes of warm- vs cold-adapted species within local communities which have proved to contribute also to a 'coherent fingerprint' of climate change impacts if examining overall patterns (Parmesan and Yohe 2003). The present study takes place between these two extremes, as it refers to a rather small region (Wallonia area = 16844 km<sup>2</sup>) extending over about 180 km (1°20') in latitudinal height, lying around the middle of western Europe. I used the data gathered during two decades about Odonata by the *Gomphus* Working Group in the perspective of distribution atlases and population monitoring.

A range/abundance shift observed for a single species in the direction predicted by climate change may suggest its influence but, alone, doesn't demonstrate it. Indeed, other causes can lead to the same result and several species may potentially move in diverse, even opposite, directions, in a particular region of the world. Therefore, it is needed to search for overall trends deduced from many species and address different alternative hypotheses and their predictions, before to conclude that climate change is the main driving force (Parmesan and Yohe 2003; Parmesan and Galbraith 2004). Apart from climate change, two other main causes can be *a priori* put forward to explain range or abundance shifts in Odonata, as those in most organisms (Warren et al. 2001; Parmesan and Yohe 2003): (1) habitat or land-use change and (2) intrinsic population dynamics, driven by (eventually unknown) species-specific factors. Eutrophication appears to be an important process which induced profound and widespread modifications in aquatic habitats. It is particularly the case in industrialised regions during the XXth century due to discharge of domestic sewage and excessive use of manure in modern agriculture (Jefferies and Maron 1997). It is regarded also as one of the main threat for many Odonata species in north-western Europe (Corbet 1999; Kalkman et al. 2002). This phenomenon could have favoured southern dragonflies, as

it is known that southern species are more linked to eutrophic waters while northern ones thrive preferably in oligotrophic ones (Corbet 1999).

In this paper, I firstly gave a synthetic view of the apparent status change of seven southern species during the last two decades in Wallonia, addressing the question of the confounding effect of recording increase. Then, I measured trends in occurrence for 59 regular and occasional breeding species between two periods from 1989 to 2000, with a method minimizing the impact of spatio-temporal variation of sampling efforts. Finally, I compared these trends in relation to the distribution types of species and their habitat preferences, in order to evaluate the potential roles of global warming, water habitat modification (eutrophication) and intrinsic population dynamics on the observed frequency changes.

## Material and methods

### Dragonfly data

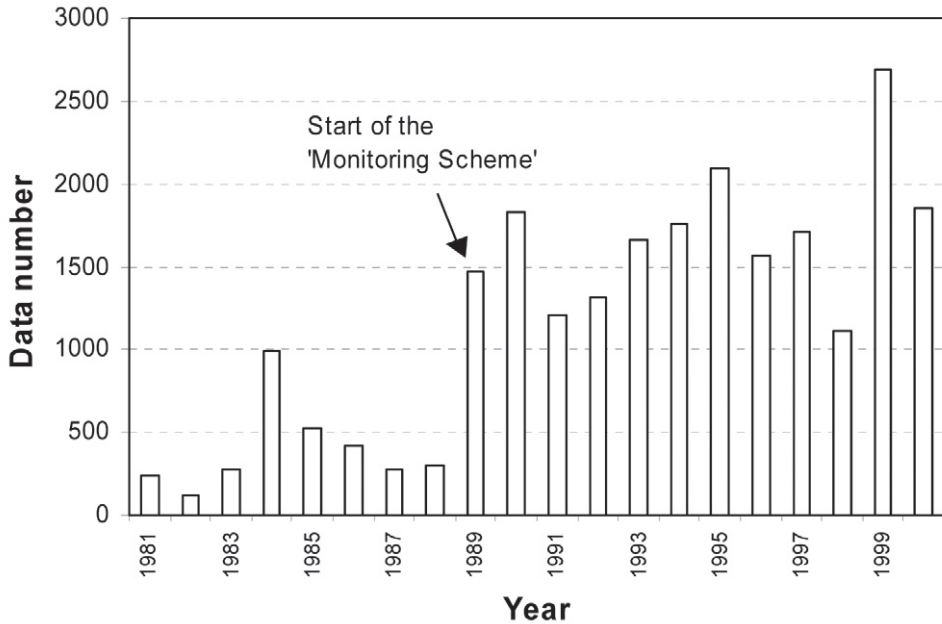
Biogeographical information about Odonata has been regularly recorded since at least the beginning of the eighties in Belgium, thanks to the *Gomphus* Working Group, formed in 1982. Volunteers have been stimulated to collect field observation data with the aim to produce comprehensive atlases (Michiels et al. 1986; Goffart et al. 2006). As a matter of fact, there has been a clear increase of dragonfly watching during the next two decades. In Wallonia, an important step has been the start, in 1989, of the so called «monitoring scheme », which is more a continued survey (Goffart 2006): on average, around 1700 individual records (unique combination of one species - place - date) were gathered every year from 1989 to 2000, against around 400 between 1981 and 1988 (Fig. 1). The records of rare and difficult species were submitted to a ratification process, based on field descriptions, photographs or voucher specimens. Since all the species identified on a particular place were generally mentioned on the data sheets, the relative frequency of the species in the data set are thought to be close to that in the field.

Conversely, the data available for the period before 1981 are more scattered and originated mainly from insect collections or literature, sources generating biased frequencies, with typically, an overestimation of rare species. Therefore, they were not considered here for comparison and quantitative analysis with subsequent data.

In all, since the beginning of the search for dragonflies, during the XIXth Century, 66 species have been listed in Wallonia, from which 61 have been recorded from 1981 to 2000.

### Trend analysis

Variations of recording efforts over time and space are a general problem with biological atlas data (Dennis et al. 1999). So, there is a need to counter these sampling biases when



**Figure 1.** Temporal pattern of data gathered by the Gomphus Working Group during the last two decades.

quantifying change in range size, spatial frequency or abundance (Telfer et al. 2002). Here, an adapted procedure was developed, combining elements from earlier methods (Stroot and Depierreux 1986; Telfer et al. 2002; Warren et al. 2001; Thomas et al. 2004) and new ones.

First, only the more numerous data collected since the start of the Monitoring Scheme were used for the analysis (from 1989 to 2000). Second, I divided this period into two periods of six years (called p1 & p2) for subsequent comparisons. Then, I selected the grid cells (of 1 km square) which were sampled at both periods during the main flight period of each species. On that selection, i.e. a sub-sample of the original data, I calculated the differences in (1) the number of grid cells of 1 km square with observation (UTM1) and (2) the observation rate per visit (OBS), which were converted in percentage change (from the first period). The variable UTM1 evaluate the range size and spatial occupancy, when the parameter OBS add to these a component dealing with species persistence and abundance within individual grid cells. Finally I applied goodness of fit tests (G-test with William's correction – Sokal and Rohlf 1995; H0: ratio of 1:1 between p1 and p2) comparing both different variables for each species. These data selection and analysis processes have been conducted with SAS System (SAS Institute Inc. 1999).

### Comparisons among species

Groups of species were distinguished according to (1) their general distribution in Europe and (2) their main habitat type preference, with the aim to compare their global

trends and to separate the potential influence of climate versus habitat changes on the changing frequency of our dragonfly fauna.

For these purposes, species were classified into five “distribution type” categories, according to the relative position of the centroid of their European distribution area (as given by d’Aguilar and Dommanget 1998 and Bos and Wasscher 1998) towards Wallonia: southern species ( $n = 15$ ), mid-European spp. ( $n = 34$ ), northern spp. ( $n = 7$ ), eastern spp. ( $n = 2$ ), montane spp. ( $n = 1$ ) (see appendix for individual species’ attributions). Similarly, they were classified into five “main habitat type” categories: eutrophic still waters species ( $n = 18$ ), mesotrophic still waters spp. ( $n = 17$ ), oligotrophic still waters spp. ( $n = 5$ ), rheophilic spp. ( $n = 9$ ), ubiquist spp. (still and running waters) ( $n = 10$ ) (see appendix).

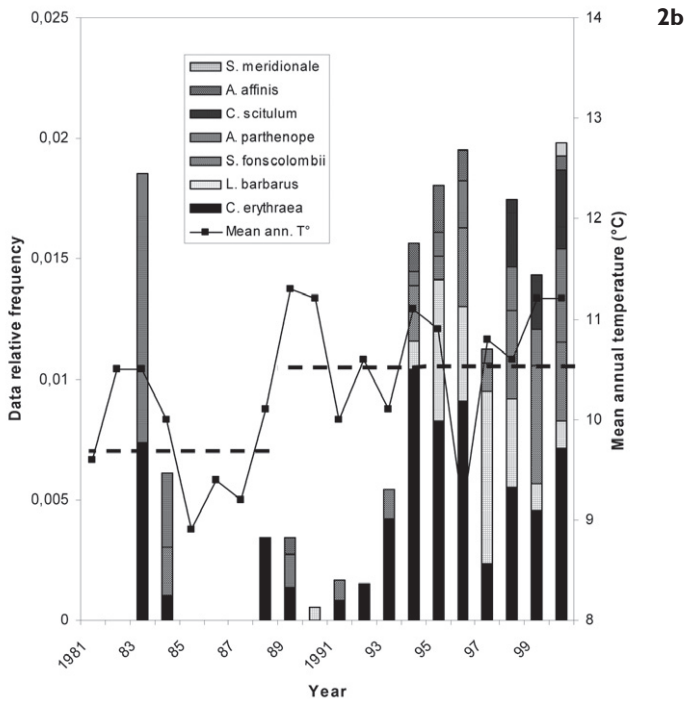
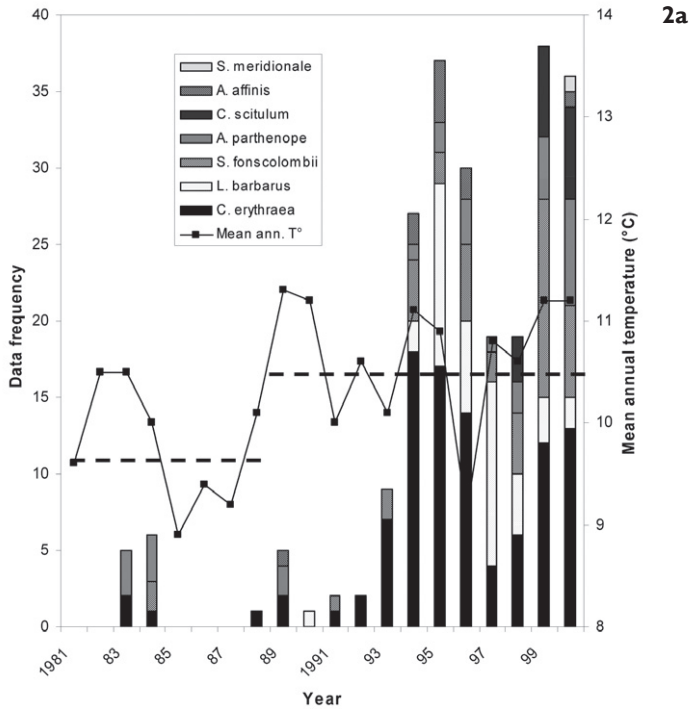
Because of being widely skewed, distribution of trends (as measured by percentage of change) were submitted to non-parametrical tests (with SAS System), to test hypotheses of (1) median diverging from zero (sign test) and of (2) medians differing between groups of species (median test).

## Results

### Southern species with changing status

For seven southern species which were former rare, there has been an increasing number of observations during the last two decades (Fig. 2a). The data were still very restricted during the eighties, and very much more numerous during the second half of the nineties, from 1994 onwards, years which experienced summer heat records. The number of species concerned has clearly increased too. The pattern is globally similar when using relative frequency rate of observation (Fig. 2b), behalf of the first bars which are higher than before the correction due to low sampling efforts before 1989. The observations of these seven ‘new colonists’ species are still, proportionally, more than four times higher in the nineties than in the eighties (G-test of independence, with William’s correction:  $G_{adj} = 60.3$ , 1 df,  $P < 0.001$ ).

Table 1 gives a synthetic view of the observations done about these seven rare southern species, by decreasing order of frequency. Six of these species had been already noted before 1981: some individuals were already caught during the XIXth century, during hot summers and at least two of them reproduced sometimes, as reported by de Selys-Longchamps, namely *C. scitulum* and *S. meridionale*. Evidences of successful reproduction exist now for all these species, even if casual for some. *Crocothemis erythraea* is one of the first and most numerous of these new colonists noted in Belgium and is now a regular breeder on still waters in Wallonia (Fig. 3a). *Lestes barbarus* has appeared later but also in great numbers; its establishment seems less stable however than *C. erythraea*, and a decrease is worth to notice in the last years (Fig. 3b). Like as for other species, true waves of migrants have been noticed some years in Wallonia, as in other countries of north-western Europe, generally



**Figure 2.** Temporal pattern of observations of seven southern species in Wallonia during the last two decades (period 1981 – 2000). **2a** Observation number **2b** Relative frequency.

**Table 1.** Data frequency of seven Southern Odonata species in Wallonia during the last two decades. First date and type of reproduction evidences are indicated for each species.

Species	Data				First reproduction reported
	before 1980	1981–1990	1990–2000	Total	
<i>Crocothemis erythraea</i>	yes	6	94	109	1993 (egg-laying, emergences)
<i>Lestes barbarus</i>	yes	1	41	48	1996 (egg-laying, emergences)
<i>Sympetrum fonscolombii</i>	yes	2	39	51	1998 (egg-laying, emergences)
<i>Anax parthenope</i>	no	8	20	28	2000 (egg-laying, >1 year population)
<i>Coenagrion scitulum</i>	yes	0	15	23	1999 (egg-laying, >1 year population)
<i>Aeshna affinis</i>	yes	1	9	13	1995 (>1 year population)
<i>Sympetrum meridionale</i>	yes	0	1	9	2000 (emergence)
Total (southern spp.)	6 spp.	18	219	237	
Total (all spp.)	3345	6436	16956	23392	

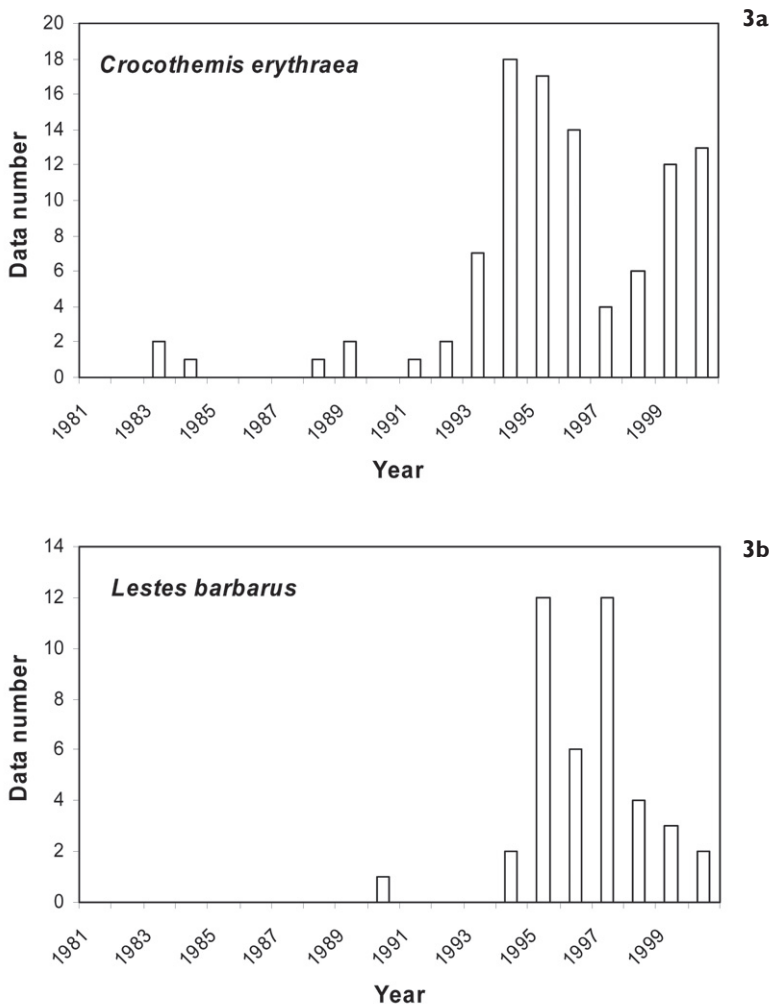
during periods of hot and humid winds from the south (sirroco) (Ott 2000, 2001; Parr et al. 2004).

The data about these species are distributed all over the territory of Wallonia, but more species have been observed in the hottest regions like Lorraine, Fagne-Famenne and the Hainaut and Brabant provinces (Fig. 4). Appearances were in general very sudden and wide over the territory for most species, and a slow geographic progression taking several years has been noticed for only one species, *Coenagrion scitulum* (Vanderhaeghe 1999; Goffart 1999, 2000, 2001).

### Trends of the southern species

The results of the analysis made on all the southern species known in Wallonia are summarised in Table 2. Eleven species, out of 14, show a positive trend in terms of the number of grid cells occupied between both periods, against one with negative trend and two with a stable situation. The global median of their trends (+81%) differs thus significantly from zero (sign test:  $P = 0.0063$ ). The same is true when looking at their observation rate per visit with twelve positive trends and two negative ones (median = + 82%; sign test:  $P = 0.0129$ ). However, only six species show a significant increase of at least one of both variables, probably because of too low absolute numbers of grid cells or observations. Only one species seems to decline, *Orthetrum brunneum*, a pioneer species, but the figure is not significant for the change in UTM1 and significant only at the level 0.1 for the change in OBS. *Coenagrion mercuriale* is also unique by the fact that it presents a positive change for one variable (UTM1) and a negative one for the other (OBS), both insignificant.

When pooling all 14 southern species together, there were 62% more grid cells occupied during the second period to compare to the first one (146 in p2 vs 90 in p1; G-test for goodness of fit, with William's correction:  $G_{adj} = 13.4$ , 1 df,  $P < 0.001$ ) and



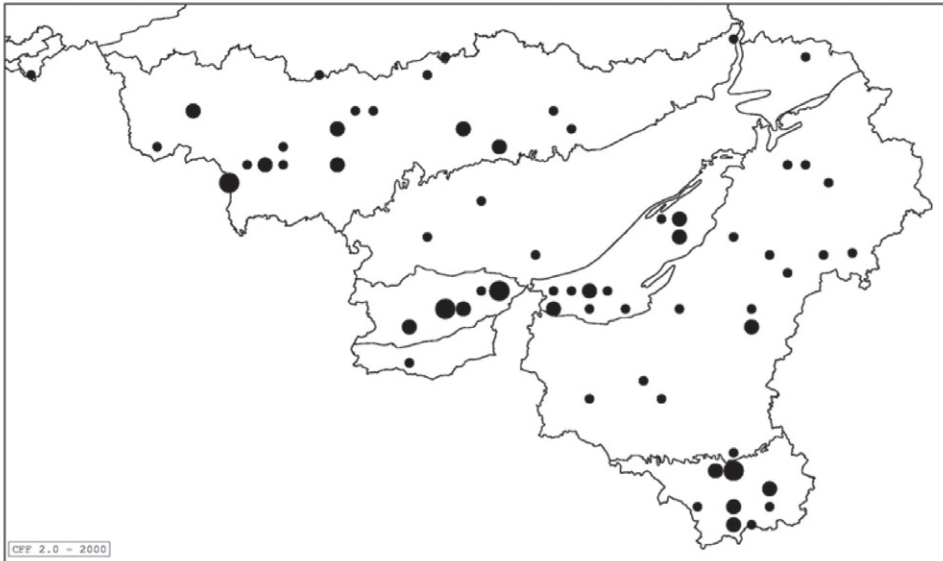
**Figure 3.** Temporal pattern of records of the two most frequent southern species. **3a** *Crocothemis erythraea* **3b** *Lestes barbarus*.

65% more observations per visit (321/1398 in p2 vs 203/1457 in p1; G-test for goodness of fit:  $G_{adj} = 31.9$ , 1 df,  $P < 0.001$ ).

### Trends comparisons of the whole regional fauna

The comparison of species grouped by distribution type shows that the global trend of the southern species presence differ significantly from that of the other groups, namely the mid-european species and the northern spp., whatever the variable considered, UTM1 (median test:  $X^2 = 7.9$ , 2 df,  $P = 0.019$ ) or OBS (median test:  $X^2 = 11.22$ ,





**Southern species (total: 7 spp.)**

- > 3 spp.
- 2 - 3 spp.
- 1 sp.

**Figure 4.** Distribution of seven new colonising southern species (same as on Fig. 2) during the period 1990–2000. Natural regions are (from north to south): **1** Loess region north of Meuse and Sambre, **2** Condroz **3** Fagne-Famenne, Calestienne **4** Ardenne **5** Lorraine.

2 df,  $P = 0.0037$ ) (Fig. 5): the first ones are globally expanding when the others are more or less stable or in decline. Note this last trend, although not significant (median UTM1 = -33%, sign test:  $P = 0.453$ ; median OBS = -31%, sign test:  $P = 0.125$ ), for the northern species, in particular.

When comparing species groups classified by main habitat type (Fig. 6), the differences are weaker and not significant, probably due to the great variances of species trends in each group. But a tendency is worth to notice: species characteristic of eutrophic still waters show more positive trends, than ones from mesotrophic and oligotrophic waters (the species from the last habitat having a negative median, which do not differ significantly from zero with the variable UTM1 (sign test:  $P = 1.0$ ) but well with the variable OBS at the level of 0.01 (sign test:  $P = 0.063$ )). However, this tendency is not significant, even when pooling mesotrophic and oligotrophic dragonflies together against eutrophic species. Interestingly, the positive trend of the eutrophic species (at least with the variable UTM1 : median = 16%) appears clearly to stem from the southern components of this group (Fig. 7), which is much increasing (median UTM1 = 150 %, sign test:  $P = 0.0156$ ; median OBS = 307 %, sign test:  $P = 0.0156$ ) and show highly significant differences with the non-southern subgroup (median test UTM1: X2

**Table 2.** Change in frequency of 14 southern species in Belgium between the periods 1989–1994 (p1) and 1995–2000 (p2). Comparison of the number of grid cells with observation (UTM1) and of the observation rate per visit (OBS). Statistical significance level (G-test of independence, adjusted): +  $P < 0.10$ ; \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ ; ns = non-significant  $P > 0.10$ .

NB: three other southern species were not included in this table because of (1) impossibility of evaluation due to insufficient occurrences (*Sympetrum meridionale*) or (2) their status of scarce vagrants (*Gomphus simillimus* and *Onychogomphus uncatus*).

Species	Grid cell nb > 1989	Grid cell nb sampled p1 & p2	Percent change (UTM1)	Sign. Level	Percent change (OBS)	Sign. Level	Trend synthesis
<i>Gomphus pulchellus</i>	142	51	0%	ns	22%	ns	Unchanged
<i>Erythromma viridulum</i>	90	36	61%	ns	70%	**	Expansion
<i>Erythromma lindenii</i>	54	21	900%	***	872%	***	Expansion
<i>Crocothemis erythraea</i>	40	21	45%	ns	85%	*	Expansion
<i>Lestes barbarus</i>	23	11	350%	*	861%	***	Expansion
<i>Orthetrum brunneum</i>	23	11	-22%	ns	-50%	+	Unchanged ?
<i>Sympetrum fonscolombii</i>	20	9	350%	*	466%	***	Expansion
<i>Oxygastra curtisii</i>	16	4	100%	ns	125%	ns	Expansion?
<i>Sympetma fusca</i>	16	7	33%	ns	9%	ns	Expansion?
<i>Anax parthenope</i>	11	6	150%	ns	307%	*	Expansion
<i>Coenagrion mercuriale</i>	10	3	50%	ns	-32%	ns	Unchanged?
<i>Coenagrion scitulum</i>	8	1	1000%	ns	1000%	-	Expansion?
<i>Aeshna affinis</i>	4	5	100%	ns	80%	ns	Expansion?
<i>Ceriagrion tenellum</i>	1	1	0%	ns	10%	ns	Unchanged?

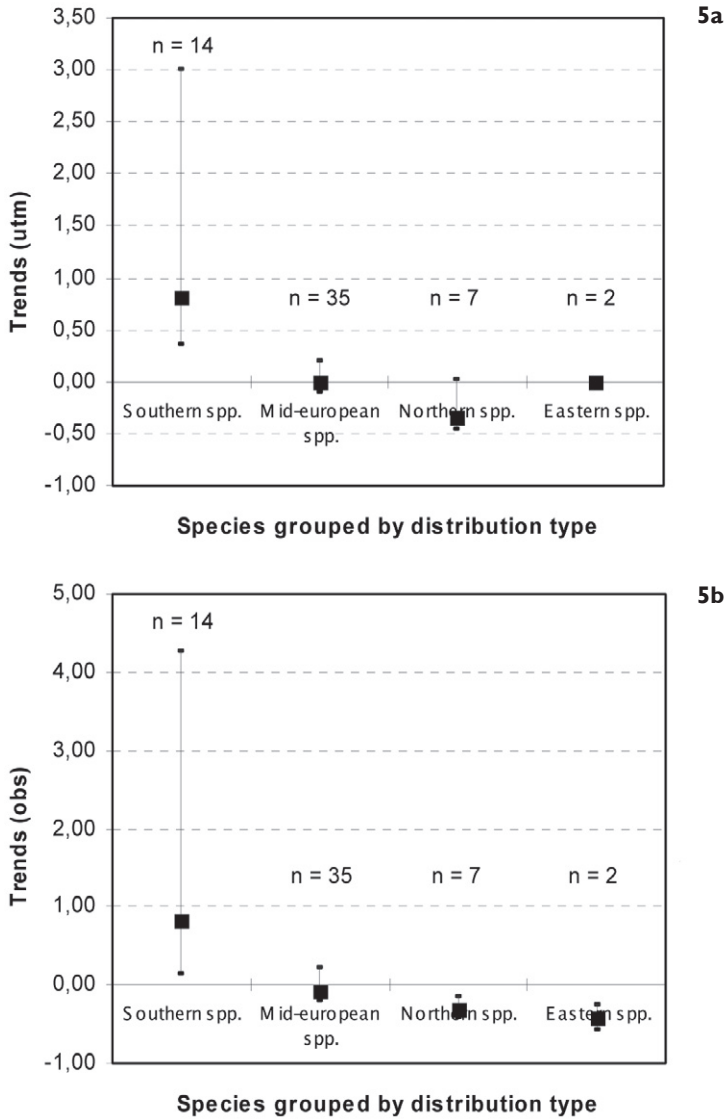
= 11.37,  $P = 0.0007$ ; median test OBS,  $X^2 = 10.81$ ,  $P = 0.001$ ). Moreover, the non-southern sub-group is maybe experiencing a decline, as appears from the significant decrease of the observation rate per visit (median OBS = -16.5%, sign test:  $P = 0.0117$ ).

The whole fauna (all 59 species) appears to be globally stable, as the median trend equal zero with the variable 'number of grid cells of 1 km square with observation' (UTM1) (sign test:  $P = 0.576$ ) and -2.7% with the 'observation rate per visit' (OBS) (sign test:  $P = 0.603$ ). There is a good correlation between the changes measured with the variables UTM1 and OBS (Spearman corr. coeff. = 0.677,  $P < 0.0001$ ).

## Discussion

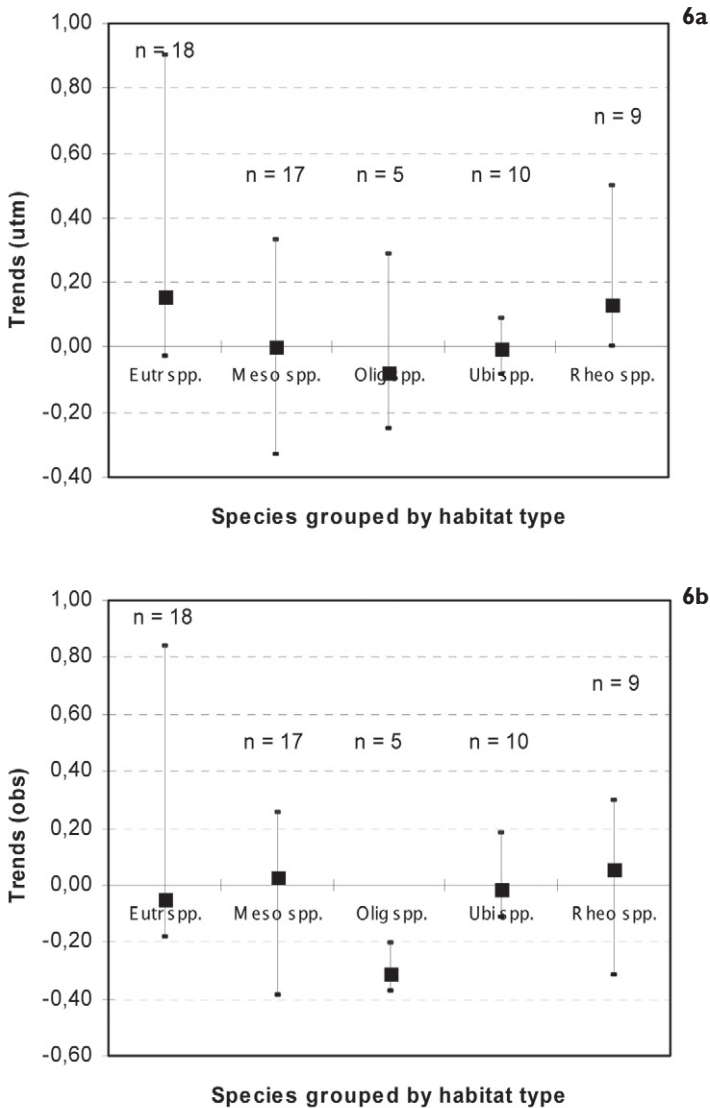
### Expansion or sampling increase?

Although there has been a sensible increase of recording effort about dragonflies over the years in Wallonia, especially since the start of the survey and monitoring scheme in 1989, we obtained convincing evidences of a global expansion of southern species during the eighties and the nineties. Indeed, the use of a method of trend analysis coping with the variation of sampling in space as in time and applied on the more



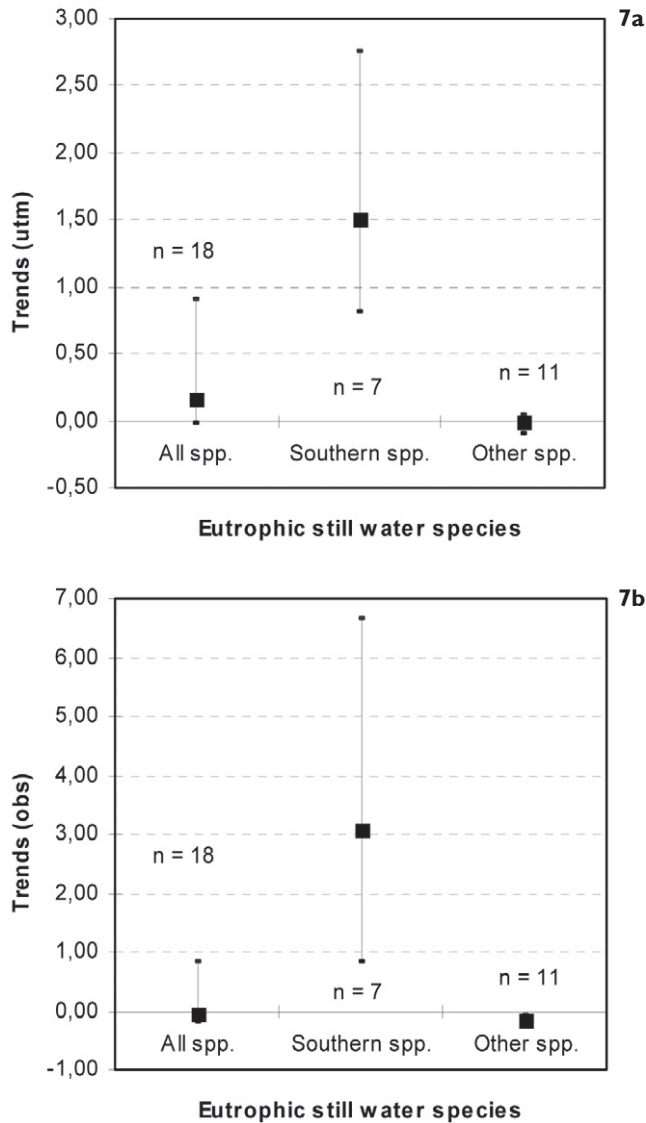
**Figure 5.** Median trends and interquartile range of 58 species (from 61) grouped by distribution type. The only montane species (*C. bidentata*) is not shown. **5a** Percentage of change in UTM1 **5b** Percentage of change in OBS.

comprehensive data from 1989 to 2000, gave still significant increases for the group of 14 southern species pooled together, from which 13 showed a positive change of at least one of both variables selected, significant for six of them (Table 2). These analyses should be viewed as rather conservative as only the presence of species were considered in grid cells or per visit and not their abundance. For many of these species, numbers on sites rose also, as their frequency over the territory.



**Figure 6.** Median trends and interquartile range of 59 species (from 61) in relation to their habitat preferences. **6a** Percentage of change in UTM1 **6b** Percentage of change in OBS.

Incidentally, there is a more obvious indication of the reality of expansions, which is the enrichment in species on particular sites, which have been regularly sampled. For instance, at the lake of Virelles, there were around 23 species observed per year in the early nineties (p1), and about 29 species per year at the end of the same decade (p2). The difference is due to the arrival and establishment of diverse southern species, like *Erythromma lindenii*, *Anax parthenope*, *Crocothemis erythraea* and *Sympetrum fonscolombii*.



**Figure 7.** Median trends and interquartile range of eutrophic species ( $n = 18$ ) dissociated in southern ones ( $n = 7$ ) and non-southern ones ( $n = 11$ ). **7a** Percentage of change in UTM1 **7b** Percentage of change in OBS.

### Patterns of change in southern species

In which concern the seven new colonists (Fig. 2), two of them (*A. parthenope* and *S. fonscolombii*) are well known as migratory species: they can take advantage of rising air currents to ascend to higher altitudes and then be carried by winds for long distances, probably about several hundred kilometres (Corbet 1999). They were often noticed together on the same sites, the same day, in southern Belgium as in the neighbouring regions, often after events of warm humid southerly winds (Parr

et al. 2004). Along with *C. erythraea*, these species were the first to arrive in Wallonia during the hot summers of 1983 and 1984. But it seems that, in the eighties, these waves of immigrants were not followed by establishment of the species. Similar scenarios probably happened already in the past, as suggested by old records of these species, as early as in the XIXth century. The very quick pattern of colonisation on a wide front of some other species, like *L. barbarus*, *C. erythraea* and to a lesser extent *A. affinis*, suggest that these southern dragonflies can also travel with winds on rather long distances. However that may be, the new thing of the last decade is that all these species were observed on several consecutive years (except *S. meridionale*) and were able to reproduce, or even establish populations in our region. These changes are paralleled by the evolution of mean annual temperatures which showed also a significant rise during the nineties in Belgium. Similar events have been reported for the same dragonfly species in all adjacent countries of Western Europe (Ott 2000, 2001; Parr et al. 2004). This change of status, from migratory behaviour to residency, has also been picked out recently for several migratory Lepidoptera in Britain, whose arrivals as migrants in the past proved to be strongly associated with temperatures in France (Sparks et al. 2005).

The eight other southern species mentioned in Table 2 were already present before the eighties in Wallonia and all of them had probably resident populations. For six of them, their range size and/or their frequency on the territory increased during the nineties. The only species which apparently decreased during the time interval, *Orthetrum brunneum*, is actually a pioneer species mainly thriving in recently created biotopes in Wallonia: the observed pattern could result from the method used to measure trends, which can record the disappearance of the species on older places but has fewer chances to detect colonisation events on newly created sites (evicted from the analysis if they were not surveyed during the first six years' period). The case of *Coenagrion mercuriale*, with opposite changes of both variables, can be explained maybe by the apparently rather dynamic colonising success of the species during the nineties, but its unstable situation (low persistence or decline) on many new (or old) sites in Wallonia (Goffart et al. 2001).

**Table 3.** Synthesis of the predictions following from the three explaining hypotheses for changes of species occurrence.

Hypotheses Predictions	Habitat change (eutrophication)	Intrinsic population dynamics	Climate change
Expanding species	Eutrophic spp	No particular group	Southern spp
Decreasing species	Oligo- & meso-trophic spp	No particular group	Northern spp
Temporal synchronisation	Yes, moderately	No	Yes, highly
Habitat selected by expanding species	Eutrophic waters	Diverse waters	Hot waters

## Explaining hypotheses

The main predictions that can be formulated from the three potential causes considered *a priori* to explain expansions or contractions of geographical ranges (and increase or decrease of populations) are synthesised in Table 3.

The first one, dealing with the groups of species expected to extend, points obviously in favour of the climate change hypothesis. Indeed, the group of the southern species is the only one presenting a consistent positive trend, which has been observed on most of its species (Figure 5). The group of eutrophic species, even if it shows a slight tendency to rise, has proved to be highly heterogeneous in this matter. Moreover, its trend was clearly brought over by the southern species included in this group (Figure 7). If eutrophication had significantly spread during the twelve years interval and had represented a main driving force for southern species, it should have favoured also the non-southern species eutrophic thriving in this kind of habitat. This was not the case and even some species showed maybe signs of declining numbers in this latter sub-group.

The second line of predictions, related to the declining species, cannot help to discern between hypotheses of climate change and habitat change, but it adds to the first ones to disqualify the hypothesis of ‘intrinsic population dynamics’. Indeed, there is a tendency for northern species and oligotrophic species to decline, but the trends are not sufficiently consistent: these two groups include few species from which most are in common. Hickling et al. (2005) have found already that dragonfly species were shifting faster at their northern range margin than at their southern margin in Britain, as did also Parmesan et al. (1999) for butterflies at the European scale.

The prediction about temporal synchronisation seems again to point out to the climate change hypothesis, as several southern species have colonised the region in a very short period (a decade) and immigration events sometimes occurred simultaneously during warm summer periods.

Concerning habitats predictions, these have not been yet strictly tested in Wallonia, but it is worth to notice that new southern colonists were found (1) on many kinds of waters, including oligotrophic ones, where breeding has been often noticed, like in sand pools and, most of the time, (2) on thermally favourable regions (Fig. 4) and habitats (sunny and shallow waters that can warm up more quickly during the good season), supporting again the climate change hypothesis.

In conclusion, global warming appears to be the main explaining cause to the observed pattern of expansion of southern species, even if other factors could also have played a role.

## Perspectives

From this and previous studies, it appears that dragonflies can be viewed as useful indicator for climatic change effects. This can be assigned to their generally high capacities

of dispersal and movement (Corbet 1999) which make them not too sensitive to the available habitat network (Travis 2003). In contrast, many butterflies will have little opportunity to expand northwards in fragmented landscapes, due to their low mobility and highly specialised requirements, as already shown in Great Britain (Warren et al. 2001; Hill et al. 2002). For the most mobile Odonata, namely the ‘migrant’ species like *A. parthenope* or *S. fonscolombii*, their movement propensity even give them the ability to track yearly climatic fluctuations and to change their range annually, with quick advance or retreat phases, but with the inconvenience that longer time series are needed in order to distinguish year-to-year variation from the long-term trends.

Further studies will be needed to better investigate the precise link between climate parameters and dragonfly range shifts, population trends, larval development, reproductive success, migration movements or impacts on aquatic communities.

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