

## 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)

Geert De Knijf<sup>a\*</sup>, Ulrich Flenker<sup>b</sup>, Cédric Vanappelghem<sup>c</sup>, Cosmin O. Mancid,  
Vincent J. Kalkman<sup>e</sup> and Heidi Demolder<sup>a</sup>

<sup>a</sup>Research Institute for Nature and Forest, Kliniekstraat 25, 1070 Brussels, Belgium; <sup>b</sup>German Sport University Cologne, Institute of Biochemistry, 50933 Cologne, Germany; <sup>c</sup>Rue de Bailleul 34, 62580 Thelus, France; <sup>d</sup>Babes-Bolyai University, Faculty of Biology and Geology, Cluj-Napoca, Romania; <sup>e</sup>European Invertebrate Survey, Naturalis – National Museum of Natural History, PO Box 9517, 2300 RA Leiden, The Netherlands

(Received 11 January 2010; final version received 4 April 2011)

It is expected that climate change will have a great impact on many species and habitats. This will be greater if populations are found at the edge of their range or are isolated, and could lead to regional extinction. Here we investigate the possible impact on two boreo-alpine dragonfly species, *Somatochlora alpestris* and *S. arctica*, at their range margins. Both species were unknown for most parts of south-eastern Europe. In 2007 we found 15 localities for *S. alpestris* and two for *S. arctica* in the Carpathian Mountains of Romania. Both species are there confined to mountain peat bogs. All localities are situated between 1300 m and 2100 m altitude, with the majority restricted to a small range between 1600 m and 1800 m. Based on the factor altitude we predict a hypothetical distribution map for *S. alpestris*. The underlying models exclusively rely on the ultimate factor “altitude” and explain more than 60% of the deviance. In addition, we assessed the impact of climate change for two scenarios: a 1.5°C temperature increase and a 3°C increase. The first resulted in altitudinal range shifts of +200 m and in a distributional shrinkage of 40%, the latter corresponds to an upward range shift of 600 m and a loss of 90% of the area. Habitat specialists, especially those at their margins of distribution, are hardly able to keep pace with climate change. It seems unlikely that mountain peat bogs will develop at rates comparable to those of current climate change. This may effect regional extinctions of boreo-alpine species.

**Keywords:** Odonata; dragonfly; Romania; *Somatochlora arctica*; *Somatochlora alpestris*; range shift; climate change; habitat; altitudinal distribution

### Introduction

Dragonflies are not only a popular group in ecological research (see Corbet, 1999 and references therein) but have also received much attention in biogeographical studies (e.g. Grant & Samways, 2007; Kalkman et al., 2008; Sternberg, 1998; Suhling, Martens & Marais, 2009; von Ellenrieder,

---

\*Corresponding author. Email: geert.deknijf@inbo.be

2010). The distribution of most species is very well documented, at least in Europe (d'Aguilar & Dommange, 1998; Dijkstra & Lewington, 2006). Even for less well-known parts of Europe, such as the Mediterranean area, including northern Africa and the major part of the Middle East, a distribution atlas has recently been published (Boudot et al., 2009). Nonetheless, there are still parts in Europe where our knowledge of the distribution of dragonflies is limited. This is the case for large parts of European Russia and the Ukraine (Skvortsov, 2010), for some areas in the south-eastern part of Europe, e.g. many countries of the former Republic of Yugoslavia, including Serbia, Bosnia and Herzegovina, Macedonia, and also for Romania.

Global climate is warming (IPCC, 2007). During the 21st century, global temperatures have been predicted to increase between 1.1 and 6.4°C. It is obvious that these changes will also affect habitats and the species therein present. Three potential responses to climate change are mentioned by Coope (1995): (a) the species can become extinct; (b) the species can adapt *in situ*; (c) the species can migrate to areas with a more suitable climate. Some adaptations can cause changes in behaviour and life history such as voltinism. Braune, Richter, Sondgerath and Suhling (2008) employed matrix population models to predict that the life cycle of *Gomphus vulgatissimus* will change from predominantly 4 to 3 years development time in Sweden, even assuming a modest warming scenario. Hassall, Thompson, French and Harvey (2007) demonstrated that changes in phenology of British Odonata are related to climate change. British Odonata advanced their flight period on average 1.51 days per decade or three days per degree rise in temperature. However, it is expected that most species would shift their ranges in response, rather than adapt to warmer temperature *in situ* (Huntley, 1991). These shifts in species distribution may occur towards higher latitudes and/or altitudes (Hickling, Roy, Hill, Fox & Thomas, 2006; Parmesan & Yohe 2003; Walther et al., 2002). In Western Europe, dragonflies have been shown to shift distributional ranges northwards in response to global warming. Hickling, Roy, Hill and Thomas (2005) give evidence for a northward range shift for 37 species of British Odonata at their range margins over the last 40 years.

The aim of this study is to examine the possible impact of climate change on two boreo-alpine species (Ander, 1950; Sternberg, 1998), *Somatochlora alpestris* (Selys, 1840) and *S. arctica* (Zetterstedt, 1840), at the presumed south-eastern edges of their distribution ranges in Europe. Both species are very rare in most parts of Europe and show a scattered distribution towards their southern range (Dijkstra & Lewington, 2006, pp. 230–232; Wildermuth 2008, pp. 380–384, 389–394). Both are typical of oligotrophic fens and peat bogs. We first investigated whether one or both species were present in the southern Carpathian Mountains in Romania. Secondly we assessed the impact of global climate change on *S. alpestris*. Habitat specialists which are spatially confined to highly fragmented landscapes (Thompson & Watts, 2006) and those confined to mountainous areas are particularly susceptible to negative impacts. This is especially the case for boreo-alpine species such as *S. alpestris* at their range margins. There will be almost no potential for adaptive shifts in ranges, except towards higher altitudes.

### ***Status in Europe***

The centre of distribution of *S. alpestris* and *S. arctica* within Europe is situated in Scandinavia (Dijkstra & Lewington, 2006, pp. 230, 232; Wildermuth, 2008, pp. 381, 390) and extends to north-eastern Europe for *S. arctica*. In Central Europe *S. alpestris* is restricted to mountainous areas (Wildermuth, 2008, p. 381) and is in particular widely distributed in the Alps (Boudot et al., 2009; Brockhaus, 1999; Kotarac, 1997, p. 150; Kuhn & Burbach, 1998, pp. 150–151; Raab, Chovanec & Pennerstorfer, 2006, pp. 184–185; Wildermuth, Gonseth & Maibach, 2005, p. 270). As well as in the Alps, the species further occurs in the Vosges in France (Grand & Boudot, 2006, p. 376), in some smaller mountain chains in Germany such as the Black Forest, Harz, Erzgebirge, Fichtelgebirge, Bohmerwald and Thüringerwald (Baumann, 2001; Brockhaus,

1990; Kuhn & Burbach, 1998, pp. 150–151; Sternberg, 2000), in the Sudety Mountains (Bernard et al., 2009, p. 142; Dolny et al., 2007, p. 477), and more to the east in the northern parts of the Carpathian Mountains (Bernard, Buczyński, Tończyk & Wendzonka, 2009, p. 142; Holuša, 2009). The species is absent from many mountains in south-western Europe (Boudot et al., 2009). The situation in south-eastern Europe and the Balkans is largely unclear, mostly due to the lack of appropriate fieldwork in these regions (see Boudot et al., 2009). Askew (2004, p. 150) and Dijkstra and Lewington (2006, p. 232) illustrated this by indicating a dot and a question mark respectively on the corresponding distribution map.

*S. arctica* is much more widely distributed in Europe than *S. alpestris*, although the latter is distinctly more common in mountainous regions. This is especially the case in north-eastern Europe, such as in Scandinavia (Wildermuth, 2008, p. 390) and in the Baltic countries, where *S. arctica* can be found in many places (Kalkman & Dijkstra, 2000), but also in the Alps (Wildermuth, 2008, p. 390). It also occurs in several places in heath and fenlands in the northern European lowland such as Belgium (De Knijf, Anselin, Goffart & Taily, 2006, pp. 162–163), the Netherlands (Nederlandse Vereniging voor Libellenstudie, 2002, p. 298), Germany (Müller & Schorr, 2001) and Poland (Bernard et al., 2009, p. 144). The species further occurs in the mountainous areas of Scotland and Ireland (Merritt, Moore & Eversham, 1996, p. 89) and in the Central Massif and the Pyrenees in France (Dommanget, Dommanget & Dommanget, 2002; Grand & Boudot, 2006, p. 378). *S. arctica* has recently been discovered in Bulgaria (Marinov & Simov, 2004).

## Materials and methods

### *Study site and sampling*

Within the framework of the preparation of a European atlas of dragonflies (Odonata), a European meeting was organised in July 2007 in Baile Herculane, situated in the south-western part of Romania between River Danube and the Carpathian Mountains. The objectives of the meeting were to do some fieldwork in order to update the Romanian Odonata database (see <http://dragonfly.nature4stock.com/>). The fieldwork was conducted in 2007 from 9 to 27 July. An area of  $c.180 \times 120$  km was prospected (see inset Figure 1), covering nearly the whole western part of the southern Carpathians. Special attention was paid to the dragonfly fauna of high altitudes. In total more than 100 localities, spread out around Baile Herculane, were investigated for their dragonfly fauna. For the fieldwork we split up into small groups in order to cover as many sites per day as possible. Adult dragonflies were sampled on warm sunny days between 10:00 h and 17:00 h, the local maximum of odonate flight activity.

Dragonflies were investigated by slowly walking round potential habitats or selected stretches thereof. All species and corresponding abundances were recorded. At each locality, we tried to capture at least one individual of *Somatochlora* species. All catches were checked with relevant literature (Bos & Wasscher, 2004, pp. 178–179, 182–183; Dijkstra & Lewington, 2006, pp. 230–232). More individuals were captured when present and most of them were released after identification. For most species, voucher specimens were collected. These have been placed in the collections of the respective authors. Exuviae were searched for in the vegetation adjoining the respective stretches of water. Surveys of each site lasted approximately one hour.

### *Data analysis*

Based on the altitudes of the surveyed localities we inferred a distribution map for *S. alpestris* for the southern Carpathian Mountains. This dataset contains sites where any dragonfly species was

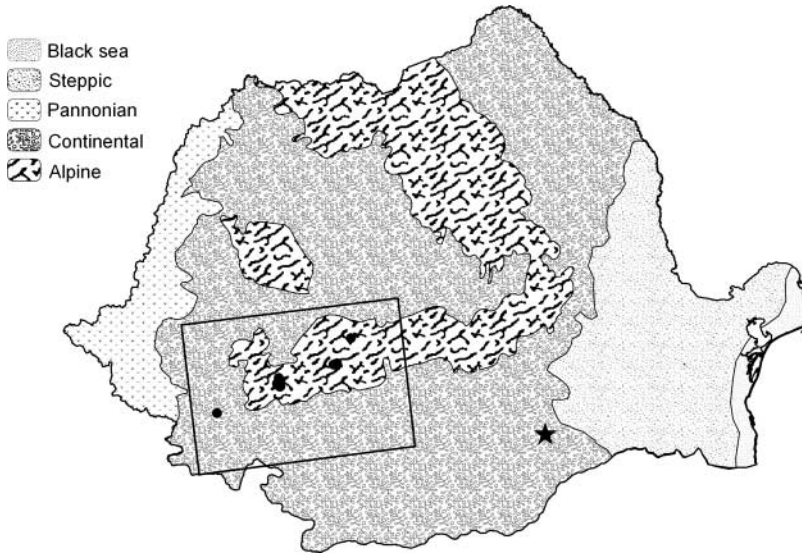


Figure 1. Map of Romania with situation of the different biogeographical regions. The inset corresponds with the investigated area during 2007 and is further used as a framework for assessing the present and future distribution of *Somatochlora alpestris*. Black dots represent the localities where *S. alpestris* was present. The location of the capital Bucharest is indicated by a star.

observed, with and without *S. alpestris*. But it contains also 13 investigated sites with apparently suitable habitat for dragonflies, but without actual records of dragonflies. These 13 localities are all situated at a minimum altitude of 750 m a.s.l. Without these, the dataset showed a sampling bias due to significant lack of sites with observations between 800 m and 1300 m a.s.l. (data not shown). In the southern Carpathians, this zone corresponds to steep and densely forested terrain with little suitable habitat for dragonflies. Moreover, this zone is, beneath the roads crossing it, very difficult to access and to investigate.

Data were evaluated exclusively on a binary scale, i.e. observed presence or absence of *S. alpestris* at a given location. The respective locations were characterized by longitude, latitude (degrees E and N) and altitude (m a.s.l.). Based on the total set of 76 localities, a generalized linear model (GLM) as well as a generalized additive model (GAM) was fitted to the data. Necessarily, both models assumed binomial distribution of the data.

Significance of the respective variables as well as the goodness of fit was assessed by likelihood statistics. Specifically, the adequacies of the models were expressed by the proportions of deviance explained. This is a measure similar to  $r^2$  in more classical regression models. Fitting GAMs and GLMs relies on likelihood maximisation rather than on minimisation of the residual variance. This renders  $r^2$  meaningless in the majority of applications. See Wood (2006) for a comprehensive introduction.

Altitude was the only independent variable for the GLM. The GAM initially also incorporated longitude and latitude. The GLM employed the logit link function and the linear predictor was a second order polynomial. The fit of the GLM therefore resulted in a Gauss-like response curve of *S. alpestris* to the factor altitude. The GAM was fitted with a two-dimensional smooth term for the coordinates and with a smooth term for the altitude. In contrast to the GLM, no specific response curve was assumed for any of the independent variables. The software used was “R” in its latest version (R Development Core Team, 2010) in combination with the “mgcv” library (Wood, 2006). Both fitted models were employed to predict the distribution of *S. alpestris* in the investigated region. The predictions were based on the GTOPO30 digital elevation model (USGS, 2010).

The predicted distributions then made it possible to assess the potential distributions of *S. alpestris* under two different scenarios of climate change. These scenarios featured an increase in temperature of 1.5°C and of 3°C, respectively. These fall within the range of the predicted global increase (IPCC, 2007). In a relatively benign scenario, we assumed a 100 m altitude shift per 0.7°C temperature increase and an increase of 1.5°C temperature. The more extreme scenario assumed a 100 m vertical shift per 0.5°C and a temperature increase of 3°C. We used altitude as a proxy for climate characteristics which can be observed in most mountain ranges. The values for temperature induced vertical shifts of ecological communities were taken from Nentwig, Bacher, Beierkuhnlein, Brandl and Grabherr (2004).

## Results

Out of more than 100 investigated localities in Romania, *S. alpestris* was found at 15 localities and *S. arctica* at two localities.

### List of localities and observations for *S. alpestris* and *S. arctica*

- Loc. 1a: 9 July 2007. Obarsia Lotrului (45°25'52" N, 23°39'53" E; altitude 1380 m). Peat bog. An estimated number of more than 20 individuals of *S. alpestris* and more than 30 individuals of *S. arctica* were seen; several of them were captured (obs. CV, COM, J.-A. Jorant, O. Pratte, N. Meziere) from both species, males and females. Territorial behaviour was also observed. One copulation of *S. arctica* was observed. Two specimens, one male and one female, were collected and are held in the collection of COM.
- Loc. 1b: 22 July 2007. Obarsia Lotrului – Lacul Vidra (45°25'57" N; 23°39'55" E; 1360 m). This locality is situated in the vicinity of Loc. 1a and it is supposed that there is an exchange of individuals between them, so they could be considered one locality of a very huge peat bog of more than 10 ha. More than 20 males and females of *S. alpestris* and at least five individuals of *S. arctica* were found by GDK & HD.

### List of localities and observations for *S. alpestris*

- Loc. 2: 9 July 2007. Lacul Vidra (45°25'37" N, 23°37'11" E; 1360 m). Small pond nearby Cabana. Fifteen individuals of *S. alpestris* were seen by CV, COM, J.-A. Jorant, O. Pratte & N. Meziere. Also territorial behaviour and oviposition in *Equisetum* sp. vegetation was observed. No exuviae could be found although we paid special attention to them.
- Loc. 3: 16 July 2007. Semenicultei Mountains, Statitunea Semenice (45°10'40" N, 22°03'24" E; 1440 m). Peat bog near Gozna peak. One male of *S. alpestris* was collected by CV, COM, J.-A. Jorant, O. Pratte & N. Meziere.
- Loc. 4: 24 July 2007. Retezat Mountains, small streams near lake Buta (45°19'04" N, 22°53'48" E; 1850 m). VJK & A. Wouters found one male of *S. alpestris* flying nearby some small streams close to the lake.
- Loc. 5: 25 July 2007. Retezat Mountains, surroundings of Cabana Buta, (45°19'17" N, 22°54'13" E; 1650 m). 33 larvae of *S. alpestris* were found in the mud of a completely dried out pool by VJK & A. Wouters.
- Loc. 6: 24 July 2007. Retezat Mountains, Taul dintre Brazi, (45°23'48" N, 22°54'13" E; 1740 m). Five adults and one ovipositing female of *S. alpestris* were seen by COM.
- Loc. 7: 23 July 2007. Retezat Mountains, Refugiul Poiana Pelegii, (45°20'02" N, 22°53'30" E; 1633 m). One male of *S. alpestris* was seen by GDK & COM.

- Loc. 8: 24 July 2007. Retezat Mountains, peat bog above Refugiul Poiana Pelegii (45°20'23" N, 22°53'00" E; 1700 m). Capture of one male of *S. alpestris* by GDK & HD.
- Loc. 9: 24 July 2007. Retezat Mountains, peat bog between Refugiul Poiana Pelegii and Refugiul Salvamont Bucura (45°20'40" N, 22°52'40" E; 1800 m). One adult of *S. alpestris* was observed by GDK & HD.
- Loc. 10: 24 July 2007. Retezat Mountains, south of Lacul Bucura (45°21'10" N, 22°52'20" E; 2050 m). One adult of *S. alpestris* was captured by GDK.
- Loc. 11: 24 July 2007. Retezat Mountains, peat bog between Lacul Ana and Lacul Liu, (45°21'00" N, 22°52'10" E; 1950 m). Twenty males, three females, one copula and one female ovipositing of *S. alpestris* were noticed by GDK.
- Loc. 12: 22 July 2007. Retezat Mountains, c.400 m NW Cabana Buta, SE slope of Vf. Buta (45°19'20" N, 22°54'09" E; c.1750 m). At least two males of *S. alpestris* were observed by UF & S. Gräff.
- Loc. 13: 23 July 2007. Retezat Mountains, Bucura valley, c.500 m NW of the camping ground at the mouth of the Bucura creek (45°20'35" N, 22°54'28" E; c.1650 m). One male of *S. alpestris* was photographed by UF & S. Gräff.
- Loc. 14: 26 July 2007. Cindrel Mountains, c.3.8 km SW Paltinis, northern slope of the saddle between Vf. Surdu and Vf. Batrana (45°37'55" N, 23°53'58" E; ca 1,750 m). At least two males of *S. alpestris* were observed simultaneously by UF & S. Gräff. Three larvae were collected from a pond. All were determined as *S. alpestris*. Four exuviae were collected, found floating in the water. The identification of the exuviae was not entirely clear, but probable.

### **Habitat in Romania**

Localities 1a and 1b, the only sites for *S. arctica*, were found at the foot of a ridge close by the road and the river valley. They were separated from each other merely by a small wooded fringe and were therefore considered a single entity. Locality 1b was a more than 10 ha transition mire, with local patches of raised bog. The vegetation was dominated by *Sphagnum* mosses. A small stream flowed through the peat bog. Several small fens, usually only a few square metres in size were spread out in the mire. To the south, almost bordering the road, there were several ponds which were characterised by *Sphagnum* and *Carex* vegetation. Locality 3 was situated near a tourist resort. During the time of inspection, the peat bog was very dry due to the drainage effect of a central ditch, and the extreme warm and dry weather during summer 2007. Except from the drainage ditch, no open water could be found in the surroundings of this locality. Localities 4–13 were all situated within the mountain range of the Retezat National Park. They were all situated in the subalpine and alpine zone of the mountain range. The greatest abundances of individuals were found where alpine lakes adjoined peat bogs and where the bank featured plants such as *Carex*, *Equisetum* and *Sphagnum*. Some localities were situated in open woodland composed mainly of *Pinus mugo* or *Picea abies* (Loc. 8). Others (Loc. 11) were completely situated within alpine pastures without trees or merely with some low bushes of *Salix*. *S. alpestris* could not be found in alpine lakes with rocky littorals. In some cases (Locs 7, 8, 9), adults of *S. alpestris* were seen flying over dry peat bog vegetation remote from open water. Locality 14 was situated far more to the east than the other localities in the Retezat Mountains. It was a small pond, obviously artificial, and was surrounded by peat bog with *Sphagnum* vegetation and by alpine pasture. Most of the localities, especially those housing larvae or larger numbers of imagines of *S. alpestris*, were characterised by the presence of vegetation on peaty soil at parts of the shoreline. Most of them also exhibited floating *Sphagnum* mosses. At several localities, parts of the shoreline were formed by peaty mud or similar organic matter (detritus).

### Altitudinal gradient and the impact of climate change

All parameters of the GLM were significant at  $p < 0.05$ . The reduction of deviance versus the Null-model was significant at  $p < 0.001$ . The combined smooth term for longitude and latitude of the GAM turned out to be non-significant and was removed from the model. The remaining smooth term for the factor altitude was significant at  $p < 0.001$ . The GLM as well as the GAM explained more than 60% of the total deviance (67% and 64%, respectively). The factor altitude can therefore be assumed to largely control the distribution of *S. alpestris* within the given range and area. Figure 2 shows the corresponding response curves from both models. The GLM and the GAM exhibit virtually identical maxima (1689 and 1701 m, respectively) but the GAM suggests a somewhat broader tolerance. Although more than 100 localities ranging from altitudes of a few hundred metres to more than 2300 metres were surveyed, we only found *S. alpestris* and *S. arctica* at higher altitudes in the investigated area. Figure 2 also illustrates the altitudinal

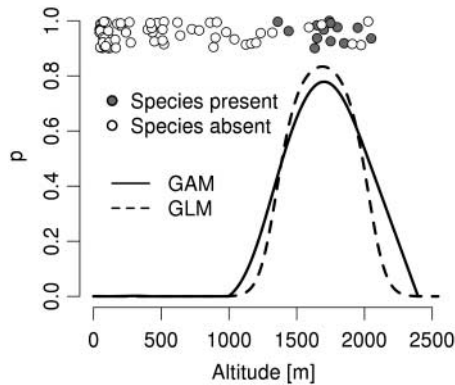


Figure 2. Response curves of *Somatochlora alpestris* to the factor “altitude” based on different statistical models (GLM and GAM). The value of the response function ( $p$ ) corresponds to the probability that at least one specimen of *S. alpestris* was observed at a habitat suited for the reproduction of Odonata at a given altitude. See text for details of the modelling process. The locations of the circles correspond to the altitudes of the investigated locations.

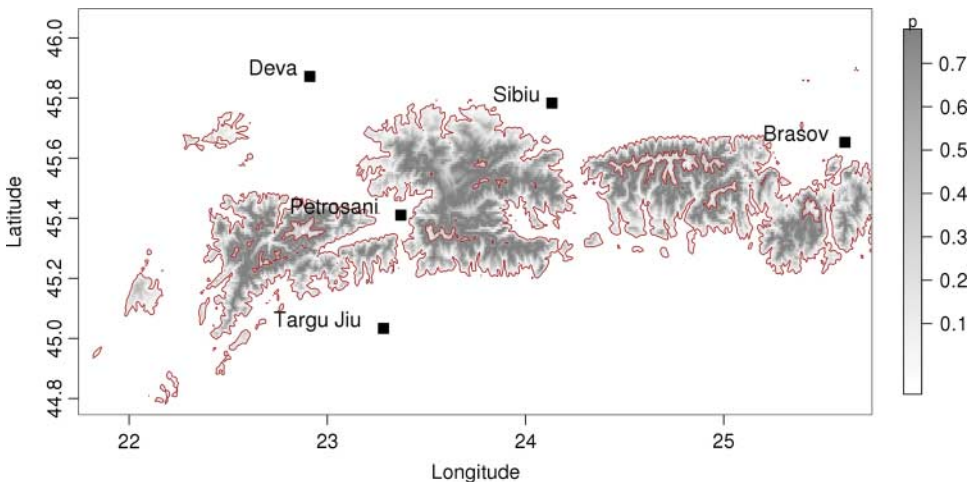


Figure 3. Predicted distribution of *Somatochlora alpestris* in the southern Carpathian Mountains based on the GAM-calculated response curve to the factor “altitude”. See text for detailed model properties.  $p$ , coded by shading of bar along right hand axis, represents the probability that the species can be observed at any habitat apparently suited for the reproduction of Odonata in the region. Contour lines represent elevations of 1000 and 2000 m a.s.l. The locations of the major cities in the relevant area have been added to facilitate orientation.

distribution of the different localities of *S. alpestris*. They were all situated between 1300 m and 2010 m. According to the statistical models the gross of the potential habitats of *S. alpestris* in the southern Carpathians will fall in this range with only small uncertainty (confidence interval of the fitted GAM, not shown). Based on the fitted GAM and a digital elevation model, we produced a distribution map of *S. alpestris* for the southern Carpathian Mountains (Figure 3). The range is remarkably large and *S. alpestris* may be expected to be comparably widespread in this region.

The possible changes of the distribution of *S. alpestris* within the southern Carpathian Mountains in Romania induced by climate changes are shown in Figure 4a for scenario 1 with 1.5°C temperature increase and 100 m altitude shift per 0.7°C, and in Figure 4b for scenario 2 with 3°C temperature increase and 100 m altitude shift per 0.5°C. Scenario 1 resulted in a shift in altitude of roughly 200 m and in a distribution shrinkage of 41%. Under scenario 2, the possible distribution of *S. alpestris* shrank dramatically, with a 600 m altitudinal shift resulting in a loss of 91% of the area. For this estimation, the regions with an expected probability of  $p_e > 75\%$  for the presence of *S. alpestris* were considered. Other values of  $p_e$  changed the estimated range losses only marginally.

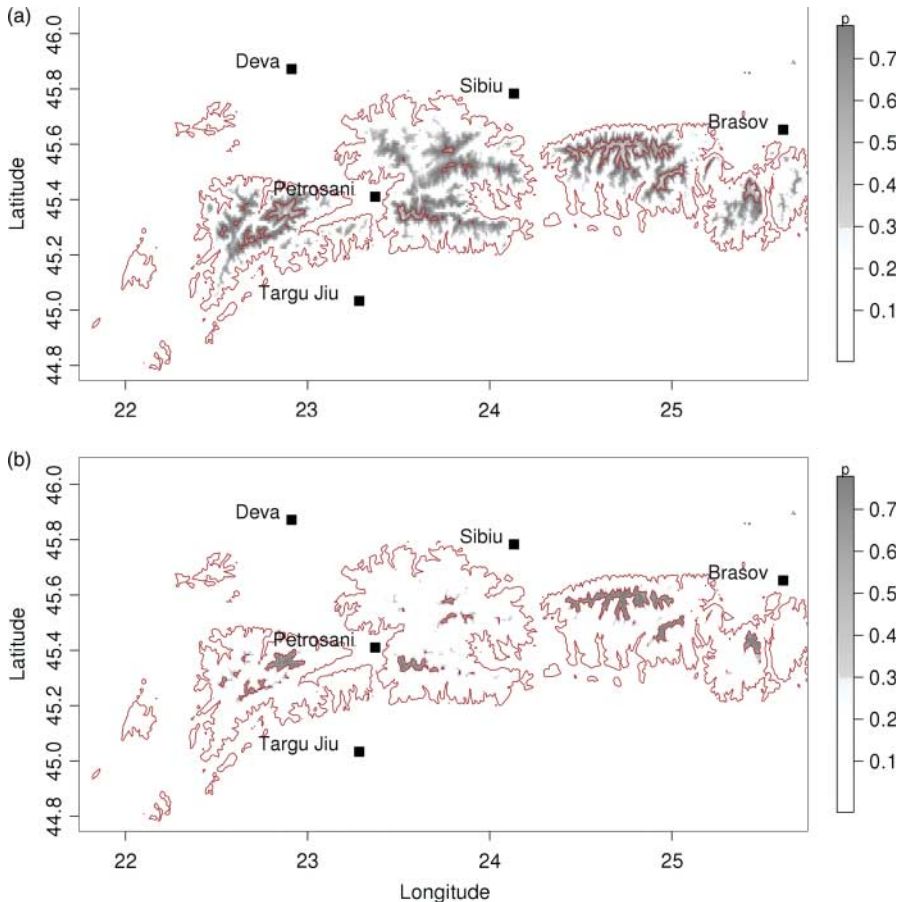


Figure 4. Predicted distribution of *Somatochlora alpestris* in the southern Carpathian Mountains assuming the GAM-calculated response curve in Figure 2.  $p$ , coded by shading of bars along right axis, represents the probability that the species can be observed at any habitat apparently suited for the reproduction of dragonflies in the region. Contour lines represent elevations of 1000 and 2000 m a.s.l. The locations of the major cities in the relevant area have been added to facilitate orientation. Distribution (a) for a temperature increase of 1.5°C, and a vertical ecological shift of 100 m per 0.7°C; and (b) for a temperature increase of 3.0°C, and a vertical ecological shift of 100 m per 0.5°C.



## Discussion

### *Distribution*

Altogether *Somatochlora alpestris* was found at 15 localities, with reproducing populations being present at least at seven of them (Locs 1a, 1b, 2, 5, 6, 11, 14), and *S. arctica* was detected at two localities. Therefore, both species should be considered as part of the Romanian dragonfly fauna. The two localities of *S. arctica* were separated by several hundred metres of open forest. Since this species has often been seen foraging in open forest adjacent to the reproduction sites (Wildermuth, 2008, p. 388), commuting flights between the two localities may well be expected. Our observations of *S. arctica* represent the first fully documented records from Romania. Paina (1977) mentioned the species for Romania, but gave no details about the locality and the habitat where the species was found. His observation was therefore considered very doubtful and consequently had been omitted from the corresponding European distribution map in Dijkstra and Lewington (2006, p. 230). *Somatochlora alpestris* obviously has a much wider distribution within Romania. However, except for our observations, only a few old and sometimes also very doubtful records exist. The species was first mentioned by Ieniştea (1956), where one male was collected (leg. Vasile Decu) in the end of July 1955 near the Scropoasa Reservoir, not very far from Sinaia at the place named “Seven Izvoare” (“Seven Springs” at c.1200 m, 45°18'34" N, 25°25'11" E). This record had also been cited by Cîrdei and Bulimar (1965, pp. 208–210). Schneider (1972) collected a single larva identified as *S. alpestris* in July 1967 in the Retezat National Park near Lake Judele at an altitude of c.1990 m (45°20'44" N, 22°50'22" E). The larva was deposited into the collection of the Natural History Museum in Sibiu (Romania), but its identity has not been verified. A doubtful, third record was published by Vintilă (1989) who claimed to have observed a *S. alpestris* in the summer of 1986 near Caldarusani Lake at an altitude of c.90 m a.s.l. (44°40'13" N, 26°16'37" E), c.30 km north of Bucharest. As far as we know, no material was collected. This location is situated in the lowland area of Romania. The lake itself is bordered by a small fringe of reed vegetation and does not seem at all suitable for reproduction of *S. alpestris*. Finally, a male and female were found in a private collection which was examined in 2008 by COM. These specimens were collected at Lacul Doamnei at an altitude of c.1940 m a.s.l. (45°36'17" N, 24°35'58" E), in Muntii Fagaras nearby Sibiu on 25 July 1994 by M. Goia.

Altogether, the present and the historical records demonstrate that the species is present over a distance of c.270 km from west to east in the southern Carpathian Mountains or nearly the whole southern arch. Sited at latitudes of c.45°20'N, the Romanian populations belong to the southernmost ones, not only within Europe, but even within the species' global distribution (Wildermuth, 2008, pp. 389–394). They are situated approximately 300 km south of the ones recently found in the Ukraine (Holuša, 2009). *S. arctica* has a broader range within Europe and it can also be found outside mountain ranges and outside Scandinavia (e.g. Dijkstra & Lewington, 2006, p. 230; Müller & Schorr, 2001; Nederlandse Vereniging voor Libellenstudie, 2002, pp. 298–300). But our findings of *S. arctica* also fall outside the main area of distribution within Europe (Dijkstra & Lewington, 2006, p. 230; Wildermuth, 2008, p. 390). These new populations are relatively close to the very isolated one, recently found in Bulgaria (Marinov & Simov, 2004).

### *Habitat*

Our results suggest that *S. alpestris* and *S. arctica* are largely limited to mountain peat bogs in Romania. *S. alpestris* was found in transition mires, raised bogs, fens and small alpine ponds surrounded by peat bog vegetation. At the localities where larvae of *S. alpestris* were found or

where several individuals were seen, vegetation was always present at the bank. Most notably *Sphagnum* mosses were found. Trees were also present in a wider area, but always less than 300 m away from the water. Besides the vegetation, these sites were characterised by the presence of peaty mud or similar organic matter (detritus), sometimes only at parts of the shoreline. These substrates are important for the hibernation of larvae under the ice and for the survival during extended dry periods in summer, which can result in temporary desiccation of shallow waters (Wildermuth et al., 2005, pp. 276–277).

The habitat preferences of any given odonate species may change significantly depending on local conditions. Populations occurring in Central or South-east Europe may inhabit environments different from those in Scandinavia (Sahlén & Ekestubbe, 2001). Populations at the edge of their range are, in general, more confined to a narrow range of habitat characteristics. In Romania, *S. alpestris* was only found at high montane and subalpine peat bog complexes, to which the species may be confined here. This is in accordance with the habitat preferences in other Central European countries such as Austria (Raab et al., 2006, pp. 184–185) and Switzerland (Wildermuth et al., 2005, pp. 270–273). Knaus and Wildermuth (2002) found that the major proportion of the adult *S. alpestris* population disappeared from their study site after emergence. Only a small proportion returned to the breeding site after maturation. The authors demonstrated that many individuals shuttled between neighbouring ponds and some did so between waters located up to 2 km apart from each other. We thus also expect an exchange of individuals at least between the localities within the Retezat National Park (Locs 4–13), which are only situated several hundred metres from each other and which have to be considered to represent a metapopulation. As the water bodies in the National Park differ significantly in structural characteristics such as size depth and vegetation, some of them will be more suitable than others for larval development. Some will probably not produce imagines in each year, and the species may be periodically or permanently extirpated from these localities.

Even though we did not find exuviae of *S. arctica* in Romania, we assume that this species is breeding in the smallest and shallowest water bodies within the mire. The habitat here consists of transition mires with seepage water bodies often smaller than one square metre. These seepage waters locally form tiny rivulets which flow through the peat bog. The hollows in bogs can rather be classified as wet depressions instead of water bodies. These narrow habitat preferences by *S. arctica* correspond to those in other European mountain ranges (Kotarac, 1997, p. 104; Raab et al., 2006, pp. 186–187; Wildermuth, 1986; Wildermuth et al., 2005, pp. 274–277). In South and Central Sweden (Sahlén, 2006), *S. arctica* has its preferred habitat in forest lakes which are dominated by peat, waters of bog characters with *Sphagnum* mosses, waters with low nutrient levels and waters with emergent vegetation. In north-western Europe (Bouwman & Groenendijk, 2007; De Knijf et al., 2006, pp. 162–163; Nederlandse Vereniging voor Libellenstudie, 2002, p. 298) the species is confined to a similar vegetation structure with very tiny open water in wet heaths and in lowland peat bogs instead of mountain peat bogs.

### **Statistical modelling**

GLMs and GAMs are now considered useful tools to model and to predict the distributions of species (Guisan & Zimmermann, 2000; Guisan, Edwards & Hastie, 2002). It is advantageous that data analyses based on these techniques may be performed on the binary scale, i.e. observed presence or absence. In fact, the information present in abundance is thus ignored. But the reliable estimation of abundances in ecological fieldwork is generally difficult, if not impossible. This particularly applies to species such as *S. alpestris* or *S. arctica* which tend to appear at possible reproduction sites for only short intervals. For numerous reasons, the search for larvae or exuviae also will typically yield heavily biased abundances.

A critical point is the possible sampling bias in areas where there are only few and very characteristic potential habitats. This particularly applies to habitat specialists such as those investigated here. Specifically, at high altitudes even generalist species will be absent in otherwise well suited habitats. If the dataset is then restricted to the presence of the targeted species the apparent probability of occurrence will necessarily approximate unity. This will finally result in a dramatic over-estimation of the potential occurrences and more generally in biased response curves. Therefore also 13 potential habitats without any actual dragonfly records have been included. At lower altitudes, this is certainly inappropriate as absence of Odonata can confidently be interpreted as fundamental lack of the particular habitat's suitability for reproduction. At higher altitudes however, this will rather reflect the significance of ecological gradients within the suitable range and perhaps also stochastic episodes of colonization and extirpation.

Ecological modelling by GLMs basically presumes a defined shape of the respective species' response curve to the investigated factors. The probability  $p$  to observe at least one specimen of the respective species at a given location may be modelled by a linear combination of predictor variables via a link-function. Here, the logit link  $\ln(p/(1-p))$  in combination with a second-order polynomial as linear predictor was chosen. This results in a bell-shaped response of  $p$  to altitude and conveniently allows for the estimation of the species' ecological optimum. Apart from that, the response of a species to an ecological factor is not necessarily Gaussian (Oksanen & Minchin, 2002). The advantage of GAMs is largely given by the fact that the shape of the response curve is estimated by a smoothing term rather than being defined beforehand. In this study, the GAM response curve turned out to be very similar to the one calculated by the GLM. However, the GAM suggests a somewhat larger tolerance. The GAM fit initially also featured a two-dimensional smoothed term for longitude and latitude. This factor turned out to be insignificant and was hence removed. Taking into account this and the large proportion of deviance explained by both models (c.65%), it can be concluded that altitude is the most important factor that controls the distribution of *S. alpestris* within the investigated area. The factor is to be considered ultimate in that it certainly does not immediately have a physiological effect on the viability of *S. alpestris*. Rather the existence of suitable habitats will be reflected in these findings. While other factors, such as precipitation and temperature, will in fact have effect on the distribution of *S. alpestris* proximately, it is hardly possible to incorporate them into our models. This is mostly due to the fact that in turn they depend on the altitude more or less immediately. Such collinearities will result in over-parameterized models which often will not even converge. Moreover, the "law of parsimony" virtually prohibits the incorporation of redundant factors.

### *Altitude and climate change*

We assume that the vertical distribution of *S. alpestris* in the southern Carpathian Mountains in Romania mainly falls between 1300 and 2100 m a.s.l. More than half of the sites however were restricted to an even smaller range between 1600 and 1800 m a.s.l. The localities with proven reproductive populations (Locs 1a, 1b, 2, 5, 6, 11, 14) were situated between 1360 and 1950 m a.s.l. This is in accordance with the situation in Switzerland (Wildermuth et al., 2005, p. 270) where the vertical distribution of the localities falls between 800 and 2700 m a.s.l. and where more than 60% are situated between 1600 and 2100 m. Populations in Switzerland however are restricted to the zone between 900 and 2440 m a.s.l. (Wildermuth, 2008, pp. 264–269). Similarly, in Austria the species is mostly restricted to the subalpine zone between 1600 and 2300 m (Raab et al., 2006, pp. 184–185). More relevant than the absolute altitude a.s.l. is the local climate, which can be expressed by the thermal steps (see Wildermuth et al., 2005, pp. 59, 270). In Switzerland, *S. alpestris* is nearly completely restricted to the alpine and mountain vegetation zone, with an average annual temperature of max. 6°C. *Somatochlora arctica* has been found only at two sites

(1360 m and 1380 m) in Romania so far. Wildermuth et al. (2005, pp. 274–277) state that nearly 90% of the area in which *S. arctica* is present in the Swiss Alps lies between 800 and 1900 m. *Somatochlora arctica* is less restricted to mountain ranges in Europe as it occurs also in peat bogs in the lowlands of northern and western Europe. Towards the southern part of its distribution, it seems to be limited to mountains. This can be explained by the absence of peat areas outside the mountain ranges in southern Europe.

The trend of *S. alpestris* in the southern Carpathian Mountains during recent decades is not known, due to the lack of data prior to our study in 2007. We do not know whether *S. alpestris* in the southern Carpathian Mountains is now more common than in the past, or scarcer. It is not impossible that *S. alpestris* has benefited from the rise in temperature and that this enabled us to observe the species at different localities in Romania. Flenner and Sahlén (2008) observed that over a time span as short as 10 years, formerly rare species have become more frequent in Swedish forest lakes. These benefits, e.g. higher survival rate of immature individuals, can be very temporary, but paradoxically can convert into complete disappearance of the species over longer periods as a consequence of possible changes in the habitat themselves or of altered species competition and abundances (Flenner & Sahlén, 2008).

Our results demonstrate that *S. alpestris* may be widespread throughout the southern Carpathians in Romania (Figure 3a). The strong habitat preferences for peat bogs and peat bog pools suggest that the species will not occur at every accessible body of water within the mountains. High altitude lakes, for example, are often characterised by a rocky substrate and by lack of any higher vegetation. Most of the streams present are also flowing too fast to allow for development of peat areas alongside the stream. The true distribution will therefore be much smaller.

Most organisms are confined to specific elevational zones as a result of microclimatic constraints imposed by ambient temperature and water availability on species metabolisms (Weathers, 1997) and on their preferred habitats or vegetation types (Martin, 2001). This, together with climate and geological history, has contributed to the distribution patterns of many taxa. Pleistocene glaciations have led to widespread migration, range restrictions and survival in disjunct refugia (Ohlemüller et al., 2008; Sternberg, 1998), like *S. alpestris* in many parts of Europe (Dijkstra & Lewington, 2006). Our scenario may appear over-simplistic, but the close to linear relationship between temperature and the altitudinal distributions of given biocoenoses is well established. A study on the extinction risk of all landbirds by Serkercioglu, Schneider, Fay and Loarie (2008) revealed that 97% of the variation was explained by the elevational limitation of range size. Populations of many highland taxa will likely decrease as global warming forces them to move to higher elevations (Pounds, Fogden & Campbell, 1999; Shoo, Williams & Hero, 2005), resulting in reduction in range size and leading to greater extinction risk (Thomas et al., 2004). Even at a very modest temperature increase of 1.5°C we can already infer a loss of c.40% of the potential localities (Figure 4a). A more probable situation, a rise of 3°C, will result in a very pronounced shrinkage of the distribution (90% loss of the area; Figure 3b) and 600 m altitudinal shift. This corresponds very well with the results found by Ubukata (2000) for Japan, where a temperature increase of 2.5°C corresponded with a horizontal shift of 400 km northwards and a vertical shift of 400 m. One of the species which should be especially affected is *S. alpestris*, which would become a relict species in the mountains of Hokkaido, northern Japan.

It cannot be excluded that in addition to elevation range other variables are also very important. But it will be helpful to bear in mind that proximate factors (e.g. local temperature, precipitation and habitat availability) are to a large degree determined by ultimate factors, principally regional climate and altitude. Most of the proximate factors affecting the reproductive success of *S. alpestris* and *S. arctica* will be more or less collinear with altitude. Phenomenologically, this may be inferred from good fits of the models presented here. As has been discussed, the restrictions to comparably narrow altitude ranges are in good accordance to findings in other regions.

In the winter and spring prior to our study in 2007, the southern Carpathian Mountains experienced a dramatic decrease in precipitation, resulting in the complete desiccation of many streams, rivers, ponds and lakes over several months, resulting locally in hard crusts forming in potential habitats in the alpine zone. Evidently, these will be not suitable any more to support successful development of larvae. This phenomenon induced by extremely hot and dry periods has occurred in several years during the last decade in Romania (COM). This supports our assumptions concerning the potential negative impacts of global warming on the distribution of *S. alpestris*. Complete withering was already observed by us at three localities (Locs 7, 8, 9) in the alpine zone.

Dragonflies, especially anisopterans, are in general considered excellent fliers (Corbet, 1999, p. 340) and thereby able to colonize rapidly newly created habitats. The high degree of habitat specialization of *S. alpestris* and *S. arctica* may, however, result in a failure to colonize higher situated habitats within the fragmented and unsuitable environment in the mountains in Romania. A greater challenge will be faced in the shift of habitat to higher altitudes. At present, most high mountain lakes in Romania are not suitable as reproduction sites. It is unlikely that peaty vegetation or, above the tree line, water bodies with a substrate of organic matter will emerge within the next decades at higher altitudes. Even if *S. alpestris* were already able to colonize alpine lakes at higher altitudes, it is unlikely that it would find these specific favoured larval habitats there. This is because development of vegetation and ground with organic matter takes a long time. In the Alps the upper distribution limit of *S. alpestris* is probably correlated with the presence of small water bodies characterised by organic mud (Wildermuth, 2008, p. 307). Due to increasing temperatures, detrimental changes to the vegetation and habitat structure are also to be expected at the current locations. The succession of peat bog pools can be the consequence of (partly) drying out, but may also be accelerated by fallout of nutrients (e.g. nitrate) with precipitation. This will finally result in changes of the habitats so that these are no longer suitable for larval development of *S. alpestris*. In our assessment, we merely employed the average temperature as an independent variable. However, the effects of extreme events such as prolonged hot and dry periods might be even more important. In the hot and dry summer of 2003, some local populations became extinct in Switzerland because of complete desiccation of larval habitat (H. Wildermuth, personal communication). For most aquatic species these events are more likely to be fatal than continuous long-term changes.

In addition, increase of temperatures can lead to colonization of the present localities by other dragonfly species which will give rise to competition between invaders and less competitive inhabitants, such as *S. alpestris*. For example, *Anax imperator* currently seems to be expanding northward in Europe (e.g. Flenner & Sahlén, 2008). The range of this native African species is limited by cold climates, and additionally its habitat preferences largely prevent the problems often resulting from other invasive species. This, however, might rapidly change in the future. *A. imperator* is known to behave extremely aggressively, successfully chasing off other territorial odonates from potential reproduction sites. Even more important is that the larvae are fierce predators, habitat generalists and do particularly well in fishless habitats. From this, it is quite possible that habitat specialists, such as many boreo-alpine species will come to be outperformed by generalists. Ultimately, this process will also be driven by warming climates.

## Acknowledgements

Many persons kindly assisted us during the fieldwork in Romania: Julie-Anne Jorant, Nicolas Meziere and Olivier Pratte (France), Oliver Brauner, Sabine Gräff and Marco Olias (Germany), Anna Macagno, Fabio Pupin, Elisa Riservato, Francesco Tomasinelli and Franziska Werth (Italy), Fierman Baarspul, Iris Niemeijer, Marcel Wasscher and Anke Wouters (The Netherlands), Paweł Czachorowski, Stanisław Czachorowski and Bogusław Daraz (Poland) and Elena Dyatlova (the Ukraine). Isha De Knijf (Belgium) provided a cheerful note during the fieldwork. Finally, thanks are due to Frank Suhling, Hansruedi Wildermuth and Gerald Louette for their valuable comments on an earlier version of this paper. Cosmin O Manci

gives thanks for the financial support provided by the Sectoral Operational Programme Human Resources Development, Contract POSDRU 6/1.5/S/3 – ‘Doctoral studies: through science towards society’.

## References

- Ander, K. (1950). Zur Verbreitung und Phänologie der borealpinen Odonaten der Westpaläarktis. *Opuscula entomologica*, 15, 150–156.
- Askw, R.R. (2004). *The Dragonflies of Europe*. Colchester: Harley Books.
- Baumann, K. (2001). Habitat und Vergesellschaftung von *Somatochlora alpestris* und *S. arctica* im Nationalpark Harz (Odonata: Corduliidae). *Libellula*, 20, 47–67.
- Bernard, R., Buczyński, P., Tończyk, G. & Wendzonka, J. (2009). *A Distribution Atlas of Dragonflies (Odonata) in Poland*. Poznan: Bogucki Wydawnictwo Naukowe.
- Bos, F. & Wasscher, M. (2004). *Veldgids Libellen. (Vierde druk)*. Utrecht: Koninklijke Nederlandse Natuurhistorische Vereniging (KNNV).
- Boudot, J.-P., Kalkman, V.J., Azpilicueta Amorin, M., Bogdanovic, T., Cordero Rivera, A., Degabriele, G., Dommanget, J.-L., Ferreira, S., Garrigós, B., Jovic, M., Kotarac, M., Lopau, W., Marinov, M., Mihokovic, N., Riservato, E., Samraoui, B. & Schneider, W. (2009). Atlas of the Odonata of the Mediterranean and North Africa. *Libellula Supplement*, 9, 1–256.
- Bouwman, J. & Groenendijk, D. (2007). New records of *Somatochlora arctica* in northwestern Lower Saxony (Odonata: Corduliidae). *Libellula*, 26, 35–40.
- Braune, E., Richter, O., Sondgerath, D. & Suhling, F. (2008). Voltinism flexibility of a riverine dragonfly along thermal gradients. *Global Change Biology*, 14, 470–482.
- Brockhaus, T. (1990). Zum vorkommen von *Somatochlora alpestris* (SEL.) und *Somatochlora arctica* (ZETT.) im Erzgebirge (Insecta, Odonata: Corduliidae). *Faunistische Abhandlungen Staatliches Museum für Tierkunde Dresden*, 17, 97–100.
- Brockhaus, T. (1999). Ein Nachweis von *Aeshna subarctica elisabethae* Djakonov 1922, und *Somatochlora alpestris* (Sélys, 1840) im Hochmoor Sijec auf der Pokljuka, NW Slowenien (Anisoptera: Aeshnidae, Corduliidae). *Exuviae*, 6, 11–13.
- Cîrdei, C. & Bulimar, F. (1965). *Fauna of Popular Republic of Romania, Insecta – Odonata Order*. Bucharest: Bucuresti Academeie RPR. [In Romanian; English title].
- Coope, G.R. (1995). Insect faunas in ice age environments: why so little extinction? In: J.H. Lawton & R.M. May (Eds.) *Extinction Rates* (pp. 55–74). New York: Oxford University Press.
- Corbet, P.S. (1999). *Dragonflies: Behaviour and Ecology of Odonata*. Colchester: Harley Books.
- d’Aguilar, J. & Dommanget, J.-L. (1998). *Guide des Libellules d’Europe et d’Afrique du Nord* (2nd ed.) Lausanne-Paris: Delachaux et Niestlé.
- De Knijf, G., Anselin, A., Goffart, P. & Taily, M. (Eds.) (2006). *Dragonflies (Odonata) of Belgium: distribution – evolution – habitats*. Brussels: Dragonfly Society Gomphus in collaboration with the Research Institute for Nature and Forest (INBO).
- Dijkstra, K.-D.B. & Lewington, R. (2006). *Field guide to the dragonflies of Britain and Europe*. Dorset: British Wildlife Publishing.
- Dolný, A., Bába, D., Waldhauser, M., Holuša, O., Hanel, L. & Lizler, R. (2007). *The dragonflies of the Czech Republic. Ecology, conservation and distribution*. Hradec Králové: Tata Publishers.
- Dommanget, C., Dommanget, T. & Dommanget, J.-L. (2002). Inventaire cartographique des Odonates de France (Programme INVOD). Bilan 1982–2000. *Martinia* 18, *Supplément 1*, 1–68.
- Fleener, I. & Sahlén, G. (2008). Dragonfly community re-organisation in boreal forest lakes: rapid species turnover driven by climate change? *Insect Conservation and Diversity*, 1, 169–179.
- Grand, D. & Boudot, J.-P. (2006). *Les Libellules de France, Belgique et Luxembourg*. Mèze: Biotope (Collection Parthénope).
- Grant, P.B.C. & Samways, M.J. (2007). Montane refugia for endemic and Red Listed dragonflies in the Cape Floristic Region biodiversity hotspot. *Biodiversity and Conservation*, 16, 787–805.
- Guisan, A. & Zimmermann, N.E. (2000). Predictive habitat distribution models in ecology. *Ecological Modelling*, 135, 147–186.
- Guisan, A., Edwards, T.C. & Hastie, T. (2002). Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecological Modelling*, 157, 89–100.
- Hassall, C., Thompson, D.J., French, G.C. & Harvey, I.F. (2007). Historical changes in the phenology of British Odonata are related to climate. *Global Change Biology*, 13, 933–941.
- 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.
- Hickling, R., Roy, D.B., Hill, J.K., Fox, R. & Thomas, C.D. (2006). The distribution of a wide range of taxonomic groups are expanding polewards. *Global Change Biology*, 12, 450–455.
- Holuša, O. (2009). New records of *Cordulegaster bidentata* and *Somatochlora alpestris* in the Ukrainian Carpathians (Odonata: Cordulegasteridae, Corduliidae). *Libellula*, 28, 191–201.
- Huntley, B. (1991). How plants respond to climate change – Migration rates, individualism and the consequences for plant-communities. *Annals of Botany*, 67, 15–22.

- Ieniște, M.A. (1956). Contribution to the knowledge of the dragonfly fauna from Sinaia area. *Analele Universității C.I. Parhon – București, Seria Științele Naturii*, 12, 151–153. [In Romanian; English title].
- IPCC [International Panel on Climate Change] (2007). *Fourth Assessment report: the physical science basis*. Cambridge: Cambridge University Press.
- Kalkman, V.J. & Dijkstra, K.-D.B. (2000). The dragonflies of the Bialowieza area, Poland and Belarus (Odonata). *Opuscula Zoologica Fluminensia*, 185, 1–19.
- Kalkman, V.J., Clausnitzer, V., Dijkstra, K.-D.B., Orr, A.G., Paulson, D.R. & Van Tol, J. (2008). Global diversity of dragonflies (Odonata) in freshwater. *Hydrobiologia*, 595, 351–363.
- Knaus, P. & Wildermuth, H. (2002). Site attachment and displacement of adults in two alpine metapopulations of *Somatochlora alpestris* (Odonata: Corduliidae). *International Journal of Odonatology*, 5, 111–128.
- Kotarac, M., (1997). *Atlas of the dragonflies (Odonata) of Slovenia; with the Red Data list*. Miklavz na Dravskem Polju, Slovenia: Atlas Faunae et Florae Sloveniae 1. Center za Kartografijo Favne in Flore.
- Kuhn, K. & Burbach, K. (1998). *Libellen in Bayern*. Stuttgart (Hohenheim): Bayerischen Landesamt für Umweltschutz und vom Bund Naturschutz in Bayern e.v..
- Marinov, M. & Simov, N. (2004). *Somatochlora arctica* (Zett.) and *Leucorrhinia dubia* (Vander L.) new for the fauna of Bulgaria (Anisoptera: Corduliidae, Libellulidae). *Notulae Odontologicae*, 6, 34–35.
- Martin, T. E. (2001). Abiotic vs. biotic influences on habitat selection of coexisting species: climate change impacts? *Ecology*, 82, 175–188.
- Merritt, R., Moore, N.W. & Eversham, B.C. (1996). *Atlas of the dragonflies of Britain and Ireland*. London: Institute of Terrestrial Ecology/The Stationary Office.
- Müller, J. & Schorr, M. (2001). Verzeichnis der Libellen (Odonata) Deutschlands. *Entomofauna Germanica*, 5, 9–44.
- Nederlandse Vereniging voor Libellenstudie (2002). *De Nederlandse libellen (Odonata). Nederlandse Fauna 4*. Leiden: Nationaal Natuurhistorisch Museum Naturalis, KNNV Uitgeverij & European Invertebrate Survey-Nederland.
- Nentwig, W., Bacher, S., Beierkuhnlein, C., Brandl, R. & Grabherr, G. (2004). *Ökologie*. Heidelberg: Spektrum.
- Ohlemüller, R., Anderson, B.J., Araujo, M.B., Butchart, S.H.M., Kudrna, O., Ridgely, R.S. & Thomas, C.D. (2008). The coincidence of climatic and species rarity: High risk to small-range species from climate change. *Biology Letters*, 4, 568–572.
- Oksanen, J. & Minchin, P.R. (2002). Continuum theory revisited: what shape are species responses along ecological gradients? *Ecological Modelling*, 157, 119–129.
- Paina, M. (1977). Zoogeographical consideration of dragonfly fauna (Insecta, Odonata) from Romania. *Nymphaea*, 5, 381–409. [In Romanian; English title].
- Parmesan, C. & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421, 37–42.
- Pounds, J.A., Fogden, M.P.L. & Campbell, J.H. (1999). Biological response to climate change on a tropical mountain. *Nature*, 398, 611–615.
- Raab, R., Chovanec, A. & Pennerstorfer, J. (2006). *Libellen Österreichs*. Wien, New York: Springer.
- R Development Core Team (2010). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from: <<http://www.R-project.org>>.
- Sahlén, G. (2006). Specialists vs. generalists in the Odonata – the importance of forest environments in the formation of diverse species pools. In: A. Cordero Rivera (Ed.) *Forests and Dragonflies* (pp. 153–179). Sofia, Moscow: Pensoft Publishers.
- Sahlén, G. & Ekestubbe, K. (2001). Identification of dragonflies (Odonata) as indicators of general species richness in boreal forest lakes. *Biodiversity and Conservation*, 10, 673–690.
- Schneider, E. (1972). *Somatochlora alpestris* Selys (Odonata) in Retezat Mountains – a second record for Romanian Carpathians. *Studiși Comunicări, Științele Naturii, Muzeul Brukenthal Sibiu*, 17, 273–275. [In Romanian; German summary].
- Sekercioglu, C.H., Schneider, S.H., Fay, J.P. & Loarie, S.R. (2008). Climate change, elevational range shifts, and bird extinctions. *Conservation Biology*, 22, 140–150.
- Shoo, L.P., Williams, S.E. & Hero, J.M. (2005). Potential decoupling of trends in distribution area and population size of species with climate change. *Global Change Biology*, 11, 1469–1476.
- Skvortsov, V.E. (2010). *The dragonflies of Eastern Europe and Caucasus. An illustrated guide*. Moscow: KMK Scientific Press.
- Sternberg, K. (1998). The postglacial colonization of Central Europe by dragonflies, with special reference to southwestern Germany (Insecta, Odonata). *Journal of Biogeography*, 25, 319–337.
- Sternberg, K. (2000). *Somatochlora alpestris* (Selys, 1840) – Alpen-Smaragdlibelle. In: K. Sternberg & R. Buchwald (Eds.) *Die Libellen Baden-Württembergs. Band 2: Großlibellen (Anisoptera)* (pp. 236–250). Stuttgart: Ulmer.
- Suhling, F., Martens, A. & Marais, E. (2009). How to enter a desert – Patterns of Odonata colonisation of arid Namibia. *International Journal of Odonatology*, 12, 287–308.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., De Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., Van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L. & Williams, S.E. (2004). Extinction risk from climate change. *Nature*, 427, 145–148.
- Thompson, D.J. & Watts, P.C. (2006). The structure of the *Coenagrion mercuriale* populations in the New Forest, southern England. In: A. Cordero Rivera (Ed.) *Forests and Dragonflies* (pp. 239–258). Sofia, Moscow: Pensoft Publishers.

- Ubukata, H. (2000). The impact of global warming in insects. In: A. Domoto, K. Iwatsuki, T. Kawamichi & J. McNeely (Eds.) *A Threat to Life: The impact of climate change on Japan's biodiversity* (pp. 61–70). Gland and Cambridge: Tsukiji-Shokan Publishing and IUCN, Japan.
- USGS (2010). GTOPO30. Available from: [http://eros.usgs.gov/#/Find\\_Data/Products\\_and\\_Data\\_Available/gtopo30\\_info](http://eros.usgs.gov/#/Find_Data/Products_and_Data_Available/gtopo30_info) (accessed 8 September 2010).
- Vintilă, C. (1989). The dragonfly fauna (Odonata) of the lake Căldărușani (Romania). *Travaux du Muséum d'Histoire Naturelle "Grigore Antipa"*, 30, 101–104. [In Romanian; French summary].
- von Ellenrieder, N. (2010). Odonata biodiversity of the Argentine Chaco biome. *International Journal of Odonatology*, 13, 1–25.
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, E. & Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, 416, 389–395.
- Weathers, W.W. (1997). Energetics and thermoregulation by small passerines of the humid, lowland tropics. *Auk*, 114, 341–353.
- Wildermuth, H. (1986). Zur Habitatwahl und Verbreitung von *Somatochlora arctica* (Zetterstedt) in der Schweiz (Anisoptera: Corduliidae). *Odonatologica*, 15, 185–202.
- Wildermuth, H. (2008). *Die Falkenlibellen Europas. Corduliidae. Die Neue Brehm-Bücherei 653*. Hohenwarsleben: Westarp Wissenschaften.
- Wildermuth, H., Gonseth, Y. & Maibach, A. (Eds.) (2005). *Odonata – les Libellules en Suisse*. Fauna Helvetica 11. Centre Suisse de Cartographie de la Faune / Schweizerische Entomologische Gesellschaft, Neuchâtel.
- Wood, S.N., (2006). *Generalized Additive Models: An Introduction with R*. CRC Press: Chapman and Hall.