RESEARCH ARTICLE

The local species richness of Dragonflies in mountain waterbodies: an indicator of climate warming?

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Abstract

With climate warming, many Odonata species are extending their geographical area. In Switzerland, as in many parts of the world, this phenomenon may lead to a regional increase in species richness. The local richness (the richness of individual waterbodies) is also expected to increase, particularly in the alpine or subalpine areas where the waterbodies are particularly species–poor. Based on the species richness recorded in 109 waterbodies scattered all across Switzerland, a model is presented here relating the local species richness (adult dragonflies) to environmental variables, including the mean annual air temperature. This model predicts a sharp increase in species richness for alpine or subalpine waterbodies, which is expected to double or even treble before the end of this century. This increase would mainly be the consequence of the immigration of eurythermal species extending their geographical range, together with potential local extinctions of the cold stenothermal species.

Introduction

Global changes, and particularly climate warming, are likely to have various impacts on Odonata (see other chapters of this book), such as a shift in species' geographical distribution, an earlier timing of emergence, or a shorter duration of the aquatic live

stage. In the northern hemisphere, the northerly shift in the geographical distribution of several species will lead in many areas to an enrichment of the regional species pool, mainly resulting from an increase in the number of eurythermal species. Such an increase will largely encompass the associated decrease in the number of cold stenothermal species. A regional increase in species richness has already been reported in many European states such as Switzerland, Germany, Netherlands, Belgium, or UK. Similar changes are also expected to occur with altitude. Indeed, the elevation gradient is often claimed to mirror the latitudinal gradient (Rahbek 1995), hence conditions at higher altitudes resemble conditions at higher latitudes (Ricklefs 1990).

If the regional increase in species richness is now an evidence, changes in the local richness (richness of a given ecosystem, e.g. pond, stream, wetland) were at the moment poorly documented (but see the example of permanent vegetation plots, in Pauli et al. 2007). Nevertheless, such changes would undoubtedly occur, especially in areas where the local richness is low. This is particularly the case in altitude (or high latitude), where local species richness is clearly lower than in lowlands (or lower latitude) (e.g. Oertli et al. 2008). Many alpine ponds in Switzerland do not presently host any Odonata species (or only a few), whereas it is common to observe ten to twenty species in lowland ponds.

The present case study aimed to predict the expected changes in the local species richness as a consequence of various scenarios of temperature elevation. For this purpose, the species richness of adults Odonata was assessed in 109 ponds distributed in all altitudinal regions (and therefore thermal regions) of Switzerland. This data set is used to relate the species richness of the ponds with the mean annual air temperature.

Material and methods

Measure of local species richness and environmental variables

A set of 109 ponds scattered in the four altitudinal belts of Switzerland (collinean, montane, subalpine, and alpine; Figure 1) was investigated between 1996 and 2002. This set represents a broad range of thermal conditions with mean annual air temperature ranging from –2.2°C to 12.1°C (Figure 2). The sampling of adult Odonata and the assessment of species richness were standardised and followed the PLOCH method (Oertli et al. 2005), for which a representative species list is gathered during two sampling days (at the end of spring and summer). To account for sample-size inadequacies (i.e. it is unlikely to perform the same sampling effort on each pond), the measured species richness is further corrected by means of Chao estimator of true richness (see Oertli 2008; Oertli et al. 2002; 2005).

About a hundred of environmental variables were also measured, at the local and regional scales, including water physico-chemistry (e.g. pH, nutrients, conductibility, transparency), morphometry (e.g. pond area, depth), watershed characteristics (geology, land use), connectivity (isolation from other waterbodies), and climatic data (air
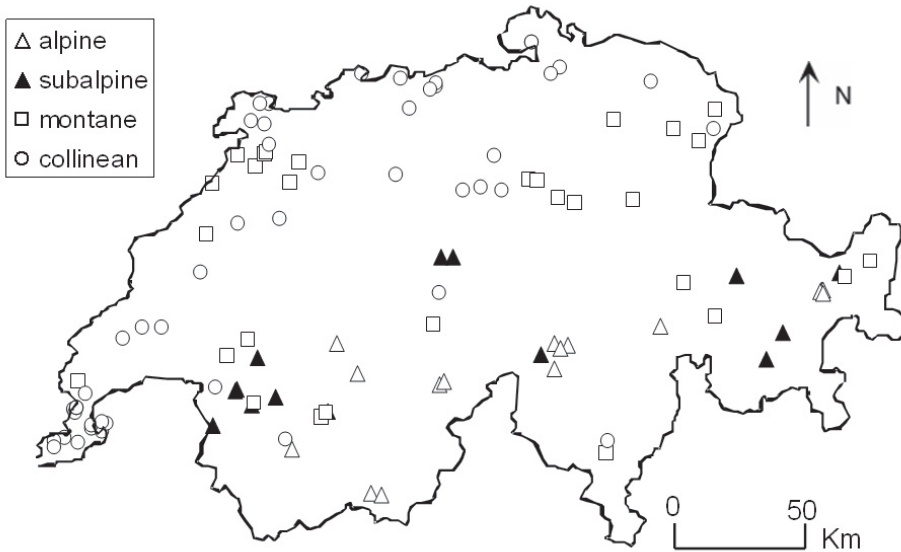
Figure 1. Distribution of the 109 sampled ponds in Switzerland, with indication of their altitudinal belt.
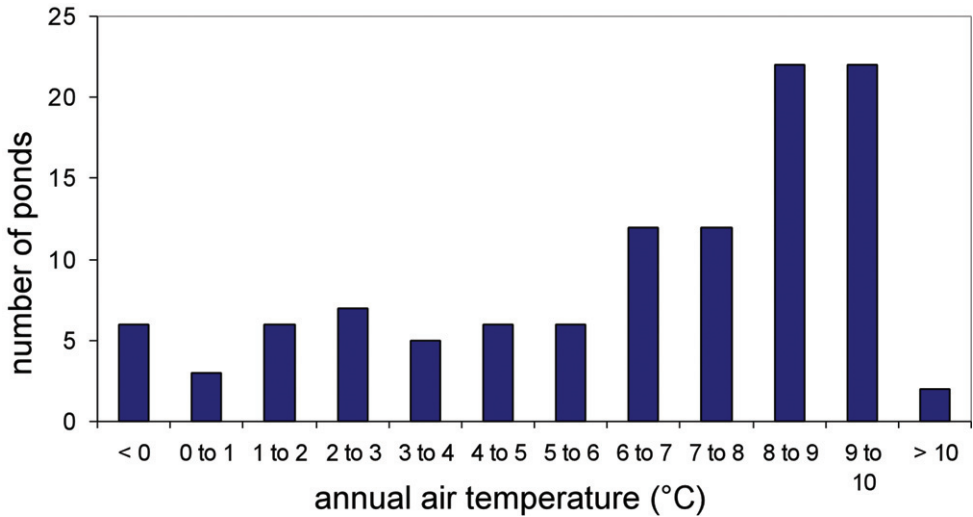

Figure 2. Range of mean annual air temperature covered by the 109 sampled ponds. Annual mean air temperature was calculated on the basis of monthly values from 115 climate stations and of a digital terrain model with a 25-m grid (data from the Swiss Federal Institute for Forest, Snow and Landscape Research).

temperature, quantity of precipitations, cloud cover, evapotranspiration, solar radiation). For additional information on sampling procedure and pond characteristics, see Oertli et al. (2002, 2005).

Statistical analyses

In a first descriptive step, correlation coefficients (Spearman's "ϱ") served to assess the relationships between species richness and mean annual air temperature, and each environmental variable.

A stepwise linear regression procedure (LR) was then used to model the relationship between estimated Odonata species richness and the annual mean air temperature (also including the other significant environmental variables), by setting the probability to 0.05. The model was used to predict the changes in species richness for two "virtual" alpine and subalpine ponds (each one with a surface area of 3300 m^2) in response to global change. The typical alpine pond had a mean annual air temperature of 0.6°C and the typical subalpine pond of 3.4°C. The temperature increases ranged between +1.8°C to +4.0°C, and were based on seven emission scenarios: the six IPCC scenarios for 2090–2100 (IPCC 2007) and the CH2070 scenario for Switzerland in 2070 (Hohmann et al. 2007).

Results

Relation between pond species richness and mean annual air temperature

From the correlation analysis, it resulted that species richness best correlated with, first, mean annual air temperature (r= 0.72), and then with altitude (r= - 0.67). These two variables were highly correlated (r= 0.99). Other important variables were identified by calculating their correlation with the residuals of the linear regression between species richness and annual air temperature. This analysis highlighted a significant relation with pond area (r= 0.47), proportion of the environment covered by forest (r= - 0.32), fish presence (r= 0.30), and mean pond depth (r= 0.23).

Based on these preliminary analyses, a selection of 15 variables was used to build the model (stepwise LR) relating the Odonata species richness to the air temperature: mean annual air temperature, pond area, pond age, mean depth, shore development, water conductivity, water transparency, pond eutrophication state, proportion of pond shaded, fish presence, proportion of pond area covered by floating vegetation or by submerged vegetation, proportion of agricultural landcover in the catchment, and proportion of the environment covered by forest and the connectivity in a radius of 1000 m.

The final model selected two variables, mean annual temperature and pond area, and showed that species richness (S) increased with an increase of temperature (T, in °C) or/and pond area (A, in m^2):

S = -4.65 + 1.34 * T° + 1.39 * log(A)
r^2= 0.51 p<0.0001

Prediction of the local species richness of mountain ponds as a function of different scenarios of temperature increase

The resulting model was used for the simulation of the impact of temperature increases on local species richness. For a given alpine or subalpine pond (fixed area of 3300 m²), we tested seven scenarios (Figure 3) representative of the trends predicted for the next 65 to 95 years. All seven scenarios evidenced a clear increase in Odonata species richness. The magnitude of this increase is particularly high, as the richness is likely to double, or even to treble in the case of alpine ponds. Whilst the species richness currently observed in an alpine pond is one species, this is expected to increase to three to six species during the next decades. In the case of a subalpine pond, species richness may rise from six (mean value currently observed) to 8–11 species.

Discussion

The predictions of climate warming presented here point out future drastic changes in the species richness of mountain waterbodies. For alpine ponds, the local richness of Odonata is likely to double or treble. This increase in local species richness of mountain waterbodies is the consequence of immigration events that will largely exceed extinction events. Indeed, in Switzerland, the present Odonata species pool is composed of 72 indigenous species (Gonseth and Monnerat 2002), the majority being eurythermal species associated with lowland waterbodies. Only seven species are restricted to altitude areas and can be considered as "cold stenothermal species". With the warming of the climate, many eurythermal species will extend their geographic distribution to higher altitudes, and will therefore be able to colonise mountain ponds from which they are currently absent. The extension of the geographical area to higher latitude has already been reported for European Odonata by Ott (2007). This phenomenon is likely to have also occurred along the altitudinal gradient through the highest elevations, though this has not been yet reported. Such altitudinal shift in geographical species distribution is also observed for plant species in the Alps (e.g. Pauli et al. 2007).

Beside the immigration of eurythermal species in waterbodies, it is noteworthy that extinction of currently established species will probably also occur. As a consequence of warming, the seven cold stenothermal species could disappear from their living waterbodies. The lower altitudinal limit of their geographical distribution could increase and could consequently lead to an upward shift of their habitats; in the long term, this could lead to species loss at a regional scale.

In Switzerland, the geographical area (and therefore the altitudinal distribution) of Odonata species is particularly well documented by the databases of the Swiss Centre for Fauna Cartography (CSCF) (see also the Swiss Atlas; Wildermuth et al. 2005). Odonata are absent of almost all high-elevation waterbodies (higher than 2500 m). Sixteen species are frequent above 1500 m (Figure 4), from which a first set of seven species can be considered as cold stenothermal due to their predominance in the upper
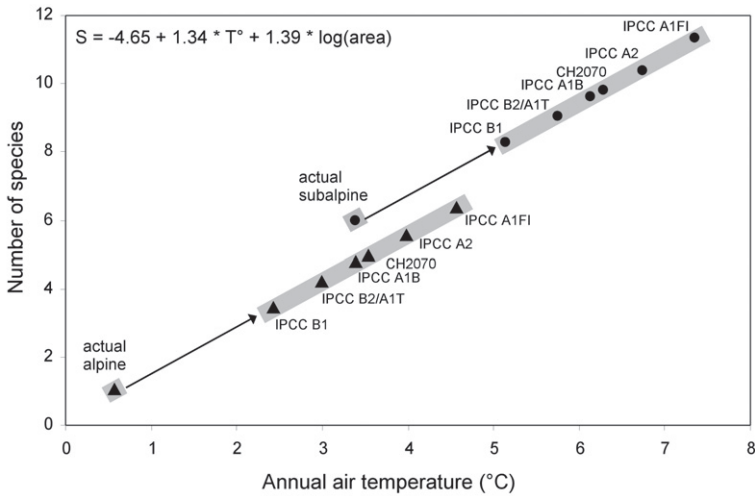
Figure 3. Potential change in the Odonata species richness (S) for an alpine and a subalpine pond as predicted by the stepwise LR equation according to seven climate change scenarios (six IPCC emission scenarios and the CH2070 scenario). "T°" is the annual mean air temperature. The two virtual ponds are typical of subalpine and alpine altitudinal belts, with a fixed area of 3300 m². For the alpine pond, present "T°" is 0.6°C, while it is 3.4°C for the subalpine pond

elevation areas: *Aeshna caerulea, A. juncea, A. subarctica, Coenagrion hastulatum, Leucorrhinia dubia, Somatochlora alpestris, S. arctica*. The most elevated altitudinal ranges are those of the boreo-alpine species *Aeshna caerulea* and *Somatochlora alpestris*, and are particularly narrow. Species belonging to this set are those presenting the highest risk of extinction at the local scale (waterbody), but also on the long range at the regional scale. A second set is composed by nine eurythermal species, characterised by a broad altitudinal distribution, mainly located below 1000 m. This set includes the candidate species to the colonisation of mountain waterbodies, and will be responsible for the increase of the local species richness.

The predictions of changes in local richness presented in this paper are potential values. They present a global trend that provides a baseline for describing biotic responses to warming. The magnitude of the changes, however, may be slightly different than that described here, being either higher or lower. Indeed, the predictive models are based on the change of only one parameter affected by climate change, i.e. mean annual air temperature. Other variables could interact with temperature and either diminish or increase the magnitude of the predicted changes. For example, variables such as the seasonal timing of warming (i.e. winter or summer), the quantity and frequency of precipitations, the number of days of ice cover, or the radiation (e.g. UVs), are factors potentially able to interfere directly with temperature, or to lead to secondary changes (e.g. hydrology, productivity, water chemistry). Land use, which could have many secondary consequences, is a relevant factor that is likely to greatly vary in mountain area (Maurer et al. 2006). Besides environmental factors, biotic variables should also be accounted for. The dynamics of the colonisation processes in both
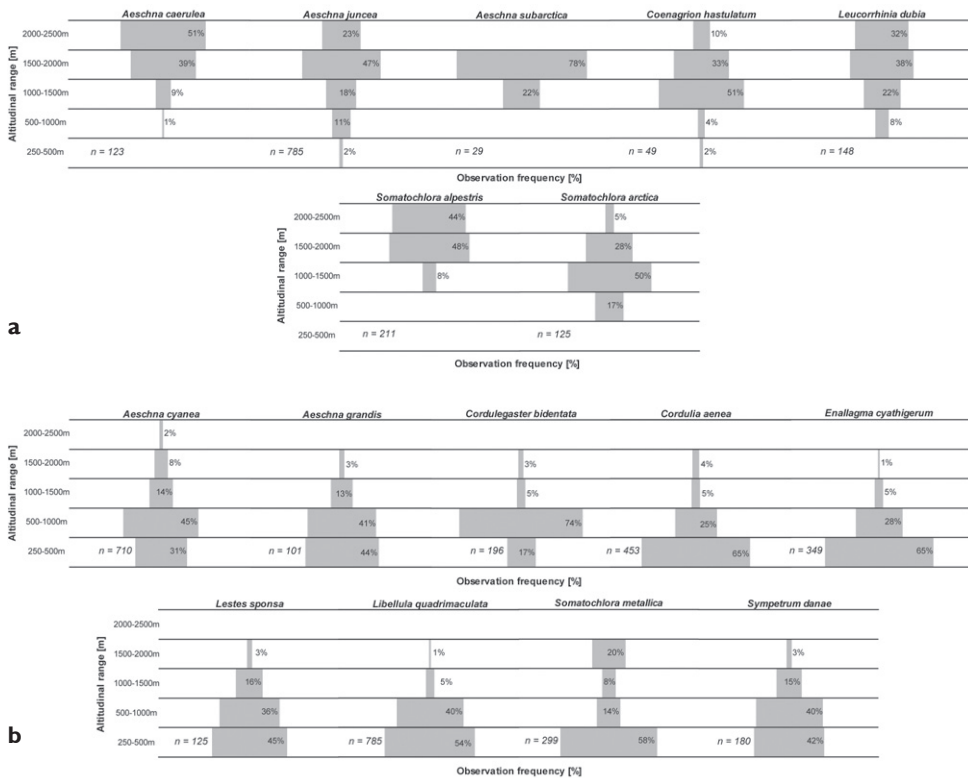
Figure 4. Altitudinal distribution in Switzerland of a set of 16 species frequently observed at high altitude (above 1500 m). **4a** The seven cold stenothermal species, expected to exhibit a decrease in their geographical area (at risk of extinction on the long range). **4b** The nine eurythermal species, likely to become more frequent at higher altitude. The data report observations of exuviae and subadults only, two life stages attesting the reproduction at the observed altitude. "n" indicates the number of observation. Data were gathered before 2003 (mainly between 1990 and 2002) by the Swiss Centre for Fauna Cartography.

space and time could be very complex, as they are species-specific. The time at which the upward dispersal begins, or the speed at which a species extend its distributional area, depend on its own biological or ecological characteristics. At the assemblage scale, this could result in a space-time overlapping and changing pattern of species distributions. As an example, Anisoptera are much more efficient fliers and active colonisers than Zygoptera. The latter group can nevertheless compensate this miss by an usually elevated number of individuals per population and by the passive dispersal by wind. Other biotic interactions, such as predation, may occur when an immigrant colonises a new pond. Local processes are therefore likely to present some resistance to immigration and to delay the increase in species richness.

With their small size and their relative simple community structure, ponds constitute ideal sentinel and early warning systems (De Meester et al. 2005). This is particularly true for alpine or subalpine ponds, characterised by species-poor communities (e.g. Oertli et al. 2007). Such systems should therefore be used for monitoring the

biotic impacts of climate changes. Monitoring should be conducted with a set of ponds situated at various altitudes and covering a large range of latitudinal scales, both in Switzerland and in other countries.

Among other invertebrates, Odonata is certainly one of the most suitable groups for conducting monitoring, either alone or, better, in conjunction with another indicator group (i.e. Oertli 2008). Indeed, the regional species pool of Odonata in altitude areas is small (e.g. Figure 4), but nevertheless large enough for conducting long range monitoring. Here, the local species richness has been shown to be a particular sensitive metric, hence being a good candidate to join the set of metrics used for long range monitoring. Local extinctions of cold stenothermal species, or colonisation of lowland species, are early warning events for mountain waterbodies that should be monitored.

Acknowledgement

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