Changes in ranges:
invertebrates on the move

Proceedings of the 13th International Colloquium
of the European Invertebrate Survey,
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European Invertebrate Survey – the Netherlands
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CONTENTS

Opening address

Jan Krikken

Our museum has been involved in EIS affairs for a very long time. EIS-the Netherlands has organisationally been a part of our museum, and the Dutch office is still supported through the museum.

The biodiversity community to which we all belong, is at this moment passing some digital landmarks. We are not there yet, but it seems that taxonomists and their biogeographical and ecological associates have, at last, got their act together by establishing through the OECD (Organisation for Economic Cooperation and Development) a complex global megascience organisation intended to set standards in the digital connectivity and exchange of biodiversity information. Copenhagen has the honour of hosting the GBIF (Global Biodiversity Information Facility) of the OECD, and we, naturally, wish our colleagues there all the best.

In this context of informatics I hope that your colloquium programme will show more affinity to biodiversity informatics and the relevant Europe-wide initiatives than is immediately apparent from most of the titles on the list of papers I have seen. I know that some of the contributors are aware of what is nowadays called data mining or KDD (Knowledge Discovery in Databases), but my plea is, from within your organisation, to more coherently and pro-actively approach the organisations that are going to be responsible for biodiversity informatics on the European and national levels and grab (at least some of) the initiative and not to re-invent the wheel. Your council may have paid attention to this during the weekend, but anyway, don't underestimate current developments.

You are – as I understand from preparatory signals – concerned, like I am, with the interest of politicians and administrators in invertebrate studies, and you wish to put a couple of things right. There are, and I'm sure you are all certainly aware of this, various reasons for being concerned, and many of you are more than competent to underpin your arguments as to why invertebrates, 'the little things that run the world', as Ed Wilson phrased it, really matter. I recommend however to go through a thorough Australian book about invertebrate studies, entitled 'The other 99%', before you arrive at your final declaration. I still have to see, from Europe, convincing arguments why the little things are as important as, or even more important, than the big things. Yes, some studies and probably enough factual data are there, but much remains to be done in the way of a convincing synthesis for politicians and administrators. This Australian book may help you there.

In my position, one of my concerns of course is funding. Many of the groups you are studying are heavily in the domain of non-professionals, and administrators tend to think that collections and data in this domain are there as a free for all, public property. The cost for a complete digitisation of the collections of recent animals in this museum, i.e. retrospective entry of label data, would easily run into a 45 million Euro, if the gross time required for recording per object (one or more specimens with the same label) is set at ten minutes. For the Dutch participation in the OECD GBIF megascience project the Dutch Department of Education, Science and Culture appears to have set aside 790 000 Euro, which can hardly be called a mega-sum. I realise fully, having been a president of the Netherlands Entomological Society, comprising numerous amateur entomologists, for more than a decade, that gathering faunistic data is fun, but one can hardly blame politicians and administrators for not taking invertebrate faunistics seriously if these data are gathered and given away for free. Even if this museum calculates the project costs of organising and archiving the data, so essential for subsequent data mining, others, I'm sure, would give data away for free, spoiling the pressure on potential funding agencies.

The overall picture is not really as gloomy as I may have suggested here. It's just that I have invertebrate biogeography at heart, and, incidentally, don't forget that, although EIS is slightly older, it is hardly a decade ago that the term biodiversity started to pop up. The media are paying an unstoppable amount of attention to biodiversity, and, increasingly, show documentaries on invertebrate diversity. Raising awareness as to the importance of biodiversity is crucial, it is the business of this museum, and I am sure that your meeting will also contribute by focussing on the changes in ranges and the long-term effects of human intervention. I wish you a very successful conference.

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Global warming and the change of butterfly distributions: a new opportunity for species diversity or a severe threat (Lepidoptera)?

Nils Ryrholm

Abstract

In order to assess the influence of climatic changes on the distribution of insects, the ranges of non-migratory European butterfly species have been studied. This study revealed that the northern limits of 32 (64%) of 52 species have expanded northwards during the 20th century. The southern limits of ten (25%) of 40 species have retracted northwards. The example of the Peacock butterfly (*Inachis io*) is given to illustrate the response to climatic changes of a species of which the range is not restricted by habitat choice. The northern limit of its range shows a considerable shift to the north during warm periods, and a southward retraction during cooler periods. Several other species showed the same pattern. These results are followed by a discussion of the impact of climate change on species diversity.

Key words: Lepidoptera, Europe, changes in ranges, climate change, *Inachis io*.

Introduction

During recent decades the climate on Earth has clearly become warmer, especially in the northern hemisphere. Whether or not this is due to human induced changes in climate or part of normal global climate fluctuations is still not fully understood. However, an increasing number of scientists believe that the rapid changes observed are caused by human activities.

Whatever the cause, the mean temperature in Europe during the past century has risen 0.8ºC, displacing isotherms 120 km northwards on average. In comparison, the mean temperature during the last ice age was approximately 4ºC lower in Scandinavia than it is today. The recent changes are also more pronounced in northern than in southern Europe.

Insects have short life cycles and often a high reproduction and dispersal capacity. Therefore they have the ability to react relatively quickly to changes in climate. As shown in our study, a number of butterfly species have responded to the recent climatic change by shifting their entire European range northwards. New habitats have become available further north due to the warmer climate and thus allowing northward expansion. In southern Europe many habitats have become too hot and dry, thus causing local extinctions of the species at their southern range limit.

Changes in ranges of European butterflies

The results of a study done in co-operation with a number of European and American butterfly ecologists have shown that a large number of European butterfly species have recently responded to the ongoing changes in climate (often called global warming; Parmesan et al. 1999). In this work we studied non-migratory butterfly species with distributions not restricted by habitat or host plant demands. These species belong to all families of butterflies and use different hibernation strategies. Data were compiled for the period 1900-1997. For the northern border analysis 52 species were used. The use of a very conservative classification method revealed that 33 (64%) of these had expanded their habitats significantly northwards, 17 species (34%) remained stable and one (2%) retracted southwards. However, observations from the years after 1997 indicate that several species in the last two groups have actually started to expand as well. For the southern border analysis 40 species were used. Using the same method 10 species (25%) were found to retract northwards, 28 (70%) remained stable and two (5%) expanded southwards. As could be expected, if these shifts are due to climatic change, the reactions are stronger in the north than in the south (see below). Of these species 35 could be used in an overall range analysis: 22 species (63%) shifted northwards, ten (29%) remained stable and two (6%) expanded southwards. Taken together these results clearly show that butterfly populations can respond quickly to changes in climate both at their southern and their northern range limit.

Examples

Here distribution data on the peacock butterfly (*Inachis io* Linnaeus, 1758*)* are used to show in more detail how a species' northern range limit in Sweden has varied as a response to different variations in summer temperatures (fig. 1) during the past hundred years. Since the larvae of this species feed on the common nettle (*Urtica dioica*) in various types of habitats, changes in land use etc. cannot explain the observed fluctuation.

In the beginning of the last century, the species had its northern range limit in south-central Sweden at 60º N (fig. 2). As the climate, particularly the summers, became warmer during the 1930-1940s, the species' range expanded dramatically. At the same time a number of other butterfly species expanded their ranges in Sweden and *Ladoga camilla* (Linnaeus, 1764) established itself in southern Sweden. The northernmost populations of *Inachis io* during this period occurred more than 620 km north of its northern limit at the previous turn of the century (fig. 3).

A climate deterioration which peaked during the 1960s with a number of wet and cool summers (fig. 1) resulted in a retraction of the range of *Inachis io* nearly back to the northern range limit of the species some 60 years earlier (fig. 4). During this period many other species showed a similar pattern, *Parnassius apollo* (Linnaeus, 1758) declined dramatically and *Ladoga camilla* became extinct in Sweden.

In the warm summers of the 1980s *Inachis io* again started to expand strongly, only to revert to the 'baseline' in the extremely wet and cold summer of 1987. During the mainly warm summers in the 1990s the species has once again established itself in the lowland areas of northern Sweden (fig. 5), thus showing an expansion capacity of at least 600 km in less than ten years! Many other butterflies and other insect species with different host plants and differing life cycles, for instance *Aporia crataegi* (Linnaeus, 1758), *Argynnis paphia* (Linnaeus, 1758) and *Plebicula amanda* (Schneider, 1792), have shifted their distribution range northwards during the same period. Despite the increasing habitat fragmentation, periods of warmer summers clearly allow a number of species to expand towards the north.

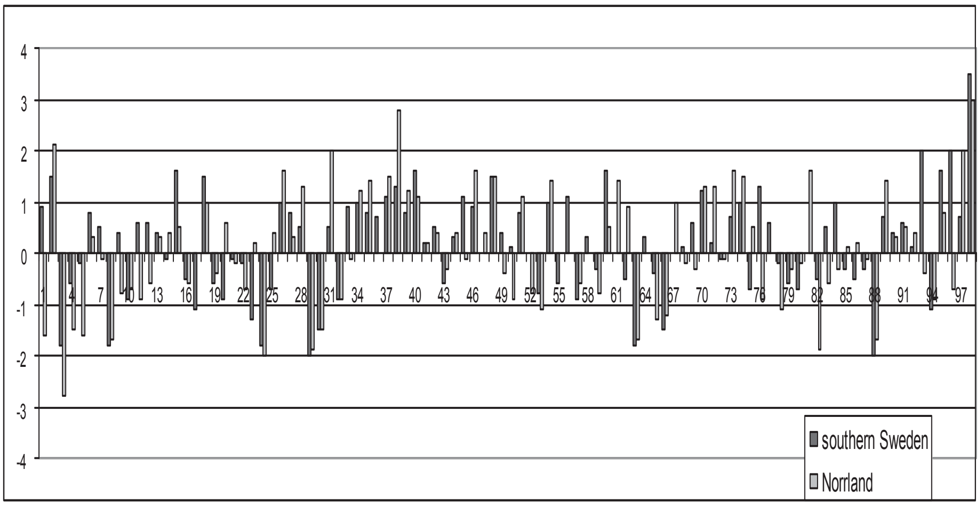

Figure 1
Mean summer (June-August) temperatures in southern (dark) and northern (light) Sweden 1900-1999.

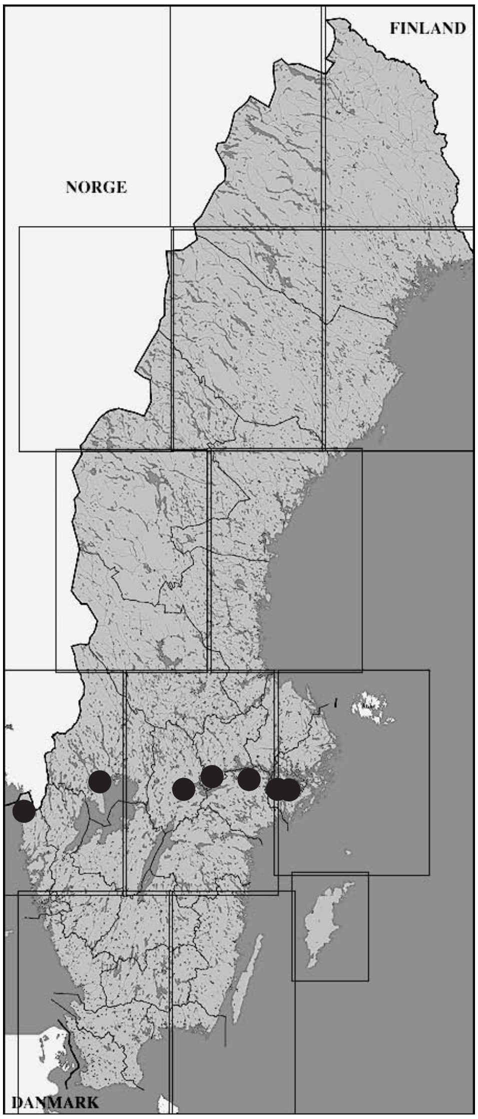

Figure 2
Northernmost finds of *Inachis io* in Sweden during the period 1900-1910.

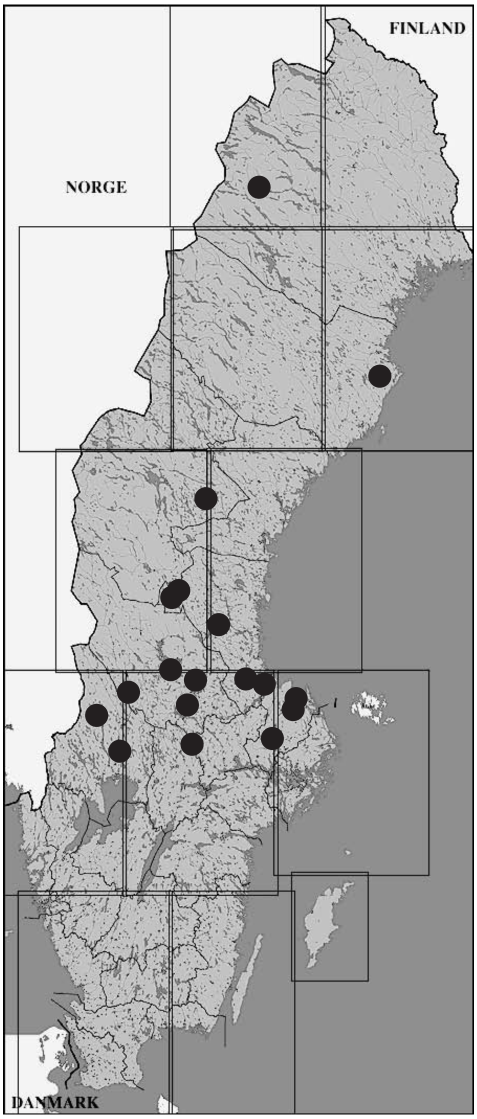

Figure 3
Northernmost finds of *Inachis io* in Sweden during the period 1931-1940.

Discussion

Throughout Europe the increasing demands of the human population and more 'rational' land use is continuously causing habitat destruction and fragmentation, leaving less and less suitable habitats for any kind of flora or fauna. This is most pronounced in western Europe with its high human population density where extremely few suitable habitats are left. If the climate continues to get warmer in southern Europe this will lead to new difficulties for European wildlife. The combination of changing climate and continuously declining habitats may lead to an increasing number of extinctions of species, especially on their

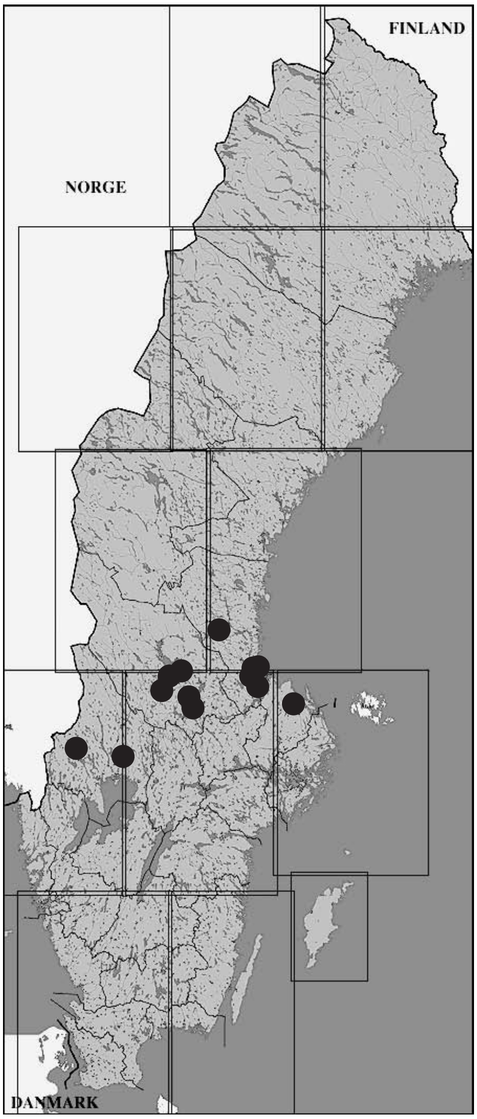

Figure 4
Northernmost finds of *Inachis io* in Sweden during the period 1961-1970.

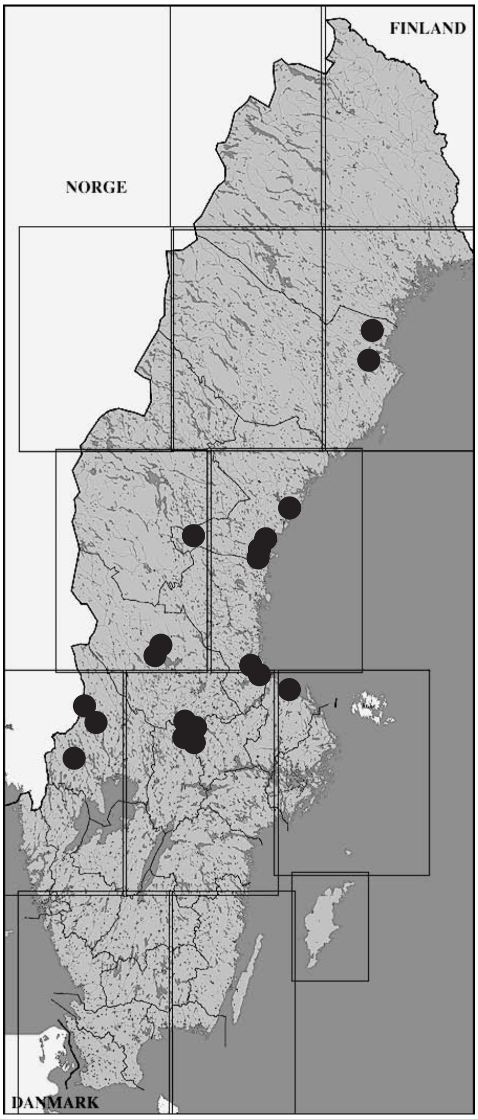

Figure 5
Northernmost finds of *Inachis io* in Sweden during the period 1991-1997.

southern range limit, as they are 'forced' further north and into areas with dense human populations where no suitable habitats are left. The further suitable habitats are from each other, the higher the risk for species to become extinct. Species like *Inachis io* which have a high dispersal capacity and low habitat demands may perhaps find suitable areas to colonise. However, those species with low dispersal capacity or high habitat demands will have severe problems in finding new habitats when their old ones become unsuitable. The degree of fragmentation in a landscape will determine the survival/extinction rate of species in a changing climate. The more fragmentation, the higher the extinction risk even at moderate levels of climate change. Insect populations living in a highly fragmented landscape will have much less chance to survive any climatic change (warmer/dryer – cooler/wetter) than those living in more undisturbed areas. These perspectives must be taken into account in the European conservation work of today in order to compensate for the changes of tomorrow.

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The apparent influence of climatic change on recent changes of range by European insects (Lepidoptera, Orthoptera)

John F. Burton

Abstract

For several years I have been collecting data concerning changes in the ranges of European insects, especially Lepidoptera and Orthoptera. The vast majority of those species which have altered their ranges since 1850 have spread to the north, north-west or west (e.g. 96% of the Lepidoptera expanding their ranges). Of the smaller number of species where the range has contracted, the majority (e.g. 75% of the Lepidoptera) have retreated southwards, south-westwards or south-eastwards.

I have attempted to correlate these range changes with the main climatic fluctuations from 1850 to the present. Throughout this long period of predominately warming climate in Europe, those insect species which have been expanding their ranges have done so in steadily increasing numbers, especially since 1975, thus coinciding with the marked increase in temperatures worldwide associated with the anthropogenic greenhouse effect.

Key words: climate change, range change, Europe, insects, Lepidoptera, Orthoptera, greenhouse effect.

Introduction and climatic background

This paper is concerned with the apparent influence of climate changes on changes in range by European insects over the past century and particularly with current trends. However, it is necessary to view such relatively recent events against the background of the climatic history of the interglacial period within which we are living.

It is, of course, well known that during the Pleistocene ice ages the fauna and flora of the northern hemisphere retreated southwards when the climate cooled and caused the ice sheets to expand outwards from the North Pole, advancing northwards again as the ice retreated during those frequent periods when, to a greater or lesser degree, the climate warmed up again (Beirne 1952). The whole process went into reverse when next the climate cooled and so on. Because warm and cold interludes of variable durations and extent have alternated right up to the present time, this back and forth process has continued to some degree ever since the ice-sheets massively retreated at the end of the last (or Weichselian) glaciation, some 10 000 years ago, and the present Holocene interglacial epoch, commonly known as the post-glacial, began.

Following the 500 years or so of the ‘little ice age’, which was at its coldest in the 17th century and did not finally end until about 1850, we have experienced a climatic amelioration which lasted till about 1950, followed by another climatic deterioration that caused some climatologists and others (Calder 1974) to predict the end of our interglacial and the onset of a new ‘ice age’ (glaciation). At the time, this did not seem at all improbable as some warm interludes between the most recent glaciations were of similar length to that attained by the present one. However, these predictions proved unfounded when the present climatic warming became evident about 1975. This warming is, of course, attributed, with much justification, to the pollution caused by human activities which has resulted in the anthropogenic greenhouse effect.

Europe’s flora and fauna have responded to such climatic fluctuations as they have always done in the past, the extent depending upon the severity of the climate. Many of the consequences of the gradual climatic amelioration after 1850 are, fortunately, well documented. This warmer, but generally wetter phase reached its peak in the 1930s and 1940s when the summers became hotter and drier, and the winters distinctly colder. It enabled many species of birds and insects, for example, to extend their breeding ranges northwards and/or north-westwards, sometimes at the expense of closely related northern species which, at the same time, withdrew the southern limits of their ranges northwards as well (Burton 1995, 1998, Parmesan et al. 1999, Williamson 1975). The largely maritime-type climate did not suit all species with a Central European or Mediterranean centre of distribution; except in the drier 1930s and 1940s, these tended to contract their ranges eastwards or south-eastwards where conditions were drier and more stable. Examples among insects include the lepidopterans *Aporia crataegi* (Linnaeus, 1758) and *Tyta luctuosa* (Denis & Schiffermüller, 1775), the tettigoniid *Ephippiger ephippiger* (Fiebig, 1775), the gryllid *Gryllus campestris* Linnaeus, 1758 and the acridid grasshopper *Psophus stridulus* (Linnaeus, 1758) (Burton 1975, Heath & Emmet 1983, Kleukers 1997, Pratt 1983). From 1950, when the climate of the northern hemisphere, particularly that of the Arctic and Subarctic, began to cool and hard winters also became more frequent farther south in Europe, there was again a trend to a southwards expansion of the ranges of northern zone species and a contraction southwards of those of the temperate zone, although a good many species which had been expanding northwards in response to the earlier amelioration continued to do so, carried along by the momentum of their expansion. So this north-south movement and back of animals in reaction to strong climatic oscillations was nothing new, but a continuation of a process which has been happening, to a greater or lesser extent, throughout the ice ages.

Figure 1
Roesel's bush-cricket *Metrioptera roeseli*, a rapidly expanding species in Britain and north-western Europe. Photo Roy Kleukers.

About 1975 the anthropogenic greenhouse effect began to neutralize the previous, apparently natural, climatic deterioration; by 1980, the global warming it produced was beginning to overwhelm it in at least some regions of the northern hemisphere (Burton 1995, Gribbin 1990). Not surprisingly, the complex and, for a time, opposing climatic trends have been reflected in correspondingly complex, even apparently paradoxical, effects on birds, insects and other wildlife. Since 1980, however, most of the temperate-zone and Mediterranean-zone species have recovered from the set-backs they suffered during the climatic deterioration and have resumed their advance northwards, while some of the arctic and other northern species have retreated again. Those advancing north have been joined by a large number of other species, especially by those whose breeding range is centred on the Mediterranean.

Problems involved in assessing the responses to climate change

In this paper I have concentrated on the apparent effects on European insects of climate changes since about 1850. It is, of course, not easy to prove that observed changes in the behaviour of animals are, in fact, due to climate change rather than other causes. Man's growing influence on the terrestrial environment as well as on the climate is now so profound and complex that it has greatly complicated the situation compared with that existing prior to historic times. It is, for instance, difficult to unravel the precise causes of changes in the distribution of species when so many other factors are involved, such as habitat fragmentation and loss, the intensification of agriculture, afforestation and disafforestation, horticultural expansion (including the introduction of alien plants), industrial pollution and the use of insecticides. It is probable that in many cases climate change is not the sole factor; a combination of two or more factors may be involved. The reponses of animal species may take the form of alterations not only in breeding range and abundance, but also in such factors as migration patterns, number of annual generations, overwintering abilities, interactions with other organisms, and phenology. Because of the specific theme of this colloquium, I have confined myself in this paper to describing changes in distribution.

Changes in geographical range since 1850

For space reasons, I am obliged to restrict my examples to a few of the more notable species of the Lepidoptera, Orthoptera and Hymenoptera which are altering their ranges, apparently as a consequence of climate warming.

Lepidoptera

Of 245 species of Macrolepidoptera and Pyralidae whose breeding distributions have, to my knowledge, altered since 1850, 201 (82%) have expanded their ranges at some time or another in one or more directions, the vast majority, 193 species (96%) to the north, north-west or west. Of the 77 species which have contracted their ranges, 58 (75%) have retreated southwards, south-westwards or south-eastwards. The reason why the combined total of expanding and contracting species is greater than the total number of species (245) involved is that, within this lengthy period, some species (like the butterflies *Pararge aegeria* (Linnaeus, 1758) and *Polygonia c-album* (Linnaeus, 1758)) have both contracted and expanded their ranges at different times. Moreover, some other species (like *Parnassius apollo* Linnaeus, 1758) and *Lycaena tityrus* (Poda, 1761)) have expanded their ranges at the northern limit and contracted at the southern limit during the same period of time (Parmesan et al. 1999).

A further analysis of the 201 species which have expanded their ranges reveals that 68 (34%) were doing so in the period of gradual climatic warming from 1850-1949, 105 (52%) in the years 1950-1974 (a period of climatic deterioration in western Europe) and 169 (84%) in the years from 1975-1999 inclusive, a period of escalating climatic warming fuelled by a marked increase in the influence of the anthropogenic greenhouse effect. An examination of the 77 species which have contracted their ranges since 1850 shows that 32 (42%) were doing so in the period from that year to 1949, 30 (38%) in the years 1950-1974 and 35 (45%) in 1975-1999 inclusive. Thus the number of species contracting their ranges has been fairly uniform from 1850 to the present.

On the whole, those species which began expanding their ranges after 1850 continued to do so and were joined by many more species as the climatic amelioration became more noticeable after 1920. It appears that, as a consequence of the impetus built-up during the very warm decades of the 1930s and 1940s (apart from the winters), the majority of these species maintained their range expansions in spite of the temporary checks resulting from the relatively brief climatic deterioration from about 1950 to 1975.

Davis (1989) remarked that for ‘most species, constraints on dispersal will cause a time-lag between the climate becoming suitable for establishment and their actual appearance’. My own study of the influences of climatic change on European birds (Burton 1995) tended to to confirm this as does my current work on European Lepidoptera. I believe the responses of so many species, and the directions in which they are expanding, strongly suggest that climate change is the main factor operating. It is probably working also on other species which have yet to reveal any obvious tendency to alter their present ranges. Some of them may be inhibited from expansion through ecological competition with closely related species which already occupy the territory into which they might otherwise expand.

Regardless of the factors, or combination of factors, involved, it is clear from the foregoing details that the vast majority of European Lepidoptera that altered their geographical distributions to a greater or lesser extent since 1850 expanded them in a northerly direction. Furthermore, a majority of those that contracted their breeding ranges since that year did so in a southerly direction. This, in itself, and taking into account the known fluctuations of the European climate during the same period, indicates that climatic factors are involved in some way. It appears that these species have been, and still are, responding to the climatic warming that has occurred for the greater part of the period. Bearing in mind the known responses of animal and plant species to the glaciations and their aftermath during the ice ages, this is to be expected.

The general results so far obtained from my own investigations are similar to those of Parmesan et al. (1999) who, in a sample of 35 non-migratory species of European butterflies, found that in the 20th century 63% have extended their ranges to the north by 35-240 km and only 3% to the south. These percentages compare fairly closely with mine for the same period for 231 species of European Lepidoptera (butterflies and moths) of which 75% have extended northwards and 1% southwards.

As Parmesan et al. (1999) found in their study of European butterflies, many of those species expanding their ranges have done so across large tracts of unsuitable territory and in spite of habitat fragmentation and loss. In this respect, my findings support their conclusion that ‘several of these species have extended northwards across heavily cultivated landscapes that are clearly less suitable for those species than they were a hundred years ago’. For example, such species of Lepidoptera as *Brenthis ino* (Rottemburg, 1775), *Coenonympha tullia* (Müller, 1764) and *Deltote bankiana* (Fabricius, 1775) have expanded their ranges in Europe in spite of significant habitat loss. On the other hand, other species (like *Hecatera dysodea* (Denis & Schiffermüller, 1775) and *Hypena rostralis* Linnaeus, 1758) that have contracted theirs have done so without any obvious loss of habitat (Burton 1998b).

Although analyses of my data strongly suggest the influence of climatic change on the observed alterations in the distributions of European Lepidoptera, other factors, such as habitat change may, nevertheless, also play a part. I have attempted to look for this: for instance, I have begun analyses of those Lepidoptera expanding their ranges whose larvae feed on coniferous trees and also of those that feed on a variety of cultivated plants, because it is sometimes stated (for instance by Owen & Duthie 1982, concerning the spread of *Lithophane leautieri hesperica* Boursin, 1957) that the range expansions of some of these species can be wholly explained by the increasing cultivation and therefore spread of such plants into new areas. However, my results so far do not support the contention that this is the sole cause. They suggest the same link to climatic fluctuations since 1850 as found for the majority of other species investigated; in fact, reflecting the same general pattern in time and direction. As concluded by Parmesan et al. (1999): ‘Consistency across taxa and continents indicates that butterfly species in the northern hemisphere are shifting generally northwards in response to a common environmental change’.

As also pointed out by Parmesan and her cooperators, Europe has warmed by about 0.8°C during the 20th century, shifting the climatic isotherms northwards by an average of 120km and ‘nearly all population-dynamic studies have concluded that butterflies, and insects in general, are sensitive to temperature’. They commented further that, although the correlational nature of their study limited their ability to determine causal factors, the sum of knowledge of butterfly biology, including numerous experimental studies, implied that the northwards shifts represented responses to increased temperatures.

I have only sufficient space to mention a few of the most notable examples of species altering their geographical ranges in response to climate warming and I have therefore decided to single out two butterflies with a characteristically Mediterranean-South European centre of distribution. As with several species of North African birds, the butterfly *Danaus chrysippus* (Linnaeus, 1758) has considerably increased and extend-

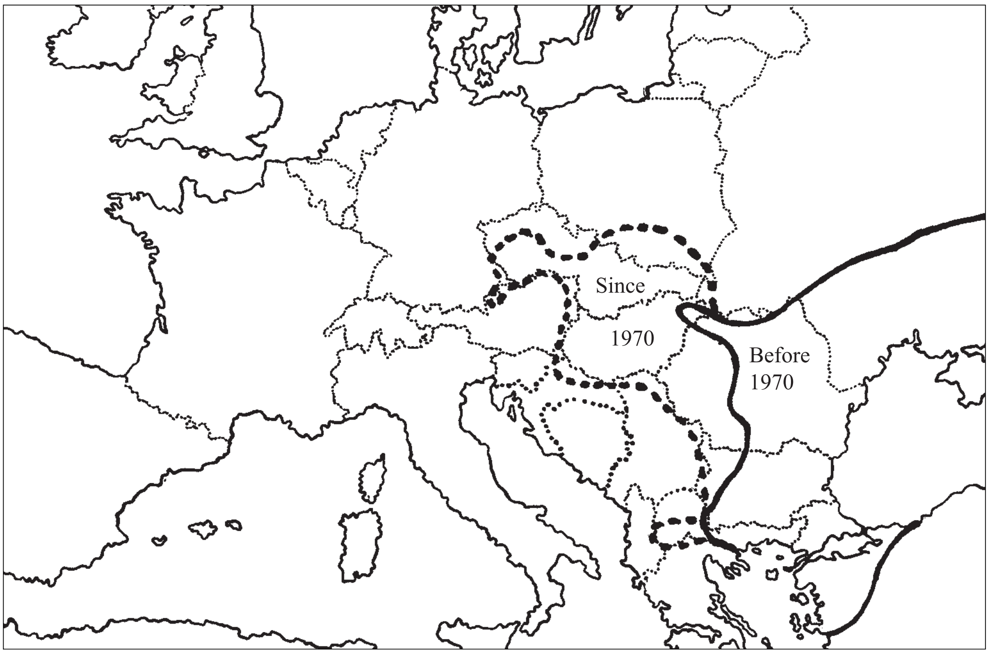

Figure 2
The range expansion of the butterfly *Colias erate*. The continuous line indicates the approximate limit of its distribution before 1970 and the broken line its expansion up to 31 January 2000 (Burton 1988, updated from Kudrna 2000 with his permission)

ed its range in the North African coastal regions in the past two decades, and from there has colonised parts of the southern coastal regions of Spain, Corsica, Sardinia, Italy, Malta, Greece and elsewhere along the 'underbelly' of Europe (Bretherton 1984, Borgo et al. 1992, Hensle 2000, Kleinekuhle 1999, Martin & Gurrea 1988, Owen 1991). Another North African butterfly *Colotis evagore nouana* (Lucas, 1849) has also begun the colonisation of the Spanish south coast (Tarrier & Leestmans 1997).

With regard to those Lepidoptera of truly European origin, the following are examples of a number of species that are currently spreading northwards or north-westwards (since the 1970s or earlier) on the European mainland, apparently in response to recent climatic warming: the Lepidoptera *Apamea illyria* Freyer, 1852, *Araschnia levana* (Linnaeus, 1758), *Autographa buraetica* (Staudinger, 1892), *A. mandarina* (Freyer, 1845), *Brenthis ino*, *Chlorantha (Actinotia) hyperici* (Denis & Schiffermüller, 1775), *Colias erate* (Esper, 1805) (fig. 2), *Cucullia artemisiae* (Hufnagel, 1766), *C. fraudatrix* Eversmann, 1837, *Erebia ligea* (Linnaeus, 1758), *Libythea celtis* (Laicharting in Fuessly, 1782), *Lithophane leautieri hesperica*, *Lycaena tityrus*, *Macdunnoughia confusa* (Stephens, 1850), *Opigena polygona* (Denis & Schiffermüller, 1775), *Pararge aegeria*, *Polygonia c-album* and *Staurophora celsia* (Linnaeus, 1758) (Burton 1992, 1997, 1998b, Emmet & Heath 1989, Hill et al. 1999, Hreblay et al. 1991, Schulze 1993, 1995). Some of these species seem to be on the point of attempting the colonisation of south-east England, as many others have done during the 20th century (Burton 1997).

Orthoptera

Grasshoppers, bush-crickets and their allies are very sensitive to temperature and are especially characteristic of hot, sunny regions. Their numbers and species diversity decline the farther north one travels. Only a few species occur as far

Figure 3
The distribution and expansion of range of the tettigoniid *Conocephalus discolor* in north-western Europe. Black area and black circles: distribution before 1980; open circles: records from 1 January 1980 to 1995; dotted line: records from 1996 to 31 December 2000 (updated from Kleukers et al. 1996 with records from Roy Kleukers and John Widgery, and reproduced by courtesy of Roy Kleukers and the Editor of the Entomologist's Gazette).

north as the subarctic zone or at high altitudes in alpine regions. Therefore, the Orthoptera are particularly good indicators of climate change.

One of the best examples of an almost certain response to the warming of the climate in north-western Europe since 1975 is the small tettigoniid *Conocephalus discolor* (Thunberg, 1815) (fig. 3) which has considerably expanded its range to the north in western Europe (Kleukers et al. 1996). Up to that year it was confined in Britain to a few footholds on the extreme south coast of England, but has since broken out of them to spread northwards at a remarkable speed towards and beyond the River Thames (Burton 1991). It has now reached Suffolk and even south-east Wales (Widgery 2000a, b). The advanced 'guards' often prove to be very long-winged and more mobile individuals capable of extended flights which develop as a result of overcrowding (Ando & Hartley 1982).

Another tettigoniid that has been expanding its previously limited range in Britain and increasing rapidly is Roesel's bush-cricket *Metrioptera roeselii* (Hagenbach, 1822) (fig. 1). Up to about 1980 it was mainly confined to grassland, especially in marshes, around the estuaries of south-eastern England as far north as the Humber. Since that year, however, it has been spreading farther inland, colonising much of the Home Counties as far west as Oxfordshire, and even penetrating into Wiltshire, Gloucestershire and Somerset and north-west to the Lancashire coast. In mainland Europe, the steady northward advances over the past two decades of the tettigoniids *Phaneroptera falcata* (Poda, 1761), *Meconema meridionale* Costa, 1860, *Conocephalus discolor*, and *Oecanthus pellucens* (Scopoli, 1763), and the acridid grasshopper *Chorthippus mollis* (Charpentier, 1825) (Kleukers et al. 1996, Kleukers 1997) are thought to be associated with the present climate warming, although *M. meri-*

dionale is known to obtain transport on vehicles (Kleukers et al. 1996), as I have seen for myself with my own car. The distributions of this and *Oecanthus pellucens* are centred on the Mediterranean, but they now extend as far north as the Low Countries and North-central Germany.

In Britain, the acridid grasshopper *Chorthippus albomarginatus* (De Geer, 1773), which formerly had a mainly coastal distribution, often sharing the same low-lying habitats as Roesel's bush-cricket, has been spreading farther inland in England since the early 1980s, especially in the Midland counties, and also farther northwards in Yorkshire (Burton 1991, Widgery 1999).

Over the past decade there has been increasing evidence that several other species with previously limited distributions are expanding their ranges in England, including the tettigoniids *Meconema thalassinum* (De Geer, 1773), *Platycleis albopunctata* (Goeze, 1778), *Tettigonia viridissima* Linnaeus, 1758 and *Conocephalus dorsalis* (Latreille, 1804), the acridids *Stenobothrus lineatus* (Panzer, 1796) and *Omocestus rufipes* (Zetterstedt, 1821), and the tetrigid *Tetrix subulata* (Linnaeus, 1758) (Widgery 2000a).

Hymenoptera

A number of species of Hymenoptera have expanded their ranges north and north-westwards in Britain in recent years, including the hornet *Vespa crabro* Linnaeus, 1758, the wasps *Dolichovespula media* (Retzius, 1783), *D. saxonia* (Fabricius, 1775), the bee wolf-wasp *Philanthus triangulum* (Fabricius, 1775) (fig. 4) and the sphecid wasp *Nitela borealis* Valkeila, 1974 (Else 1991-1997). *Dolichovespula media*, *D. saxonia* and *Nitela borealis* have all colonised South-east England from the European mainland. The very large bee *Xylocopa violacea* (Linnaeus, 1758), a mainly southern European species, has been spreading north-westwards in Germany since 1936 and especially since 1985 in central Europe in general (Otten et al. 1995), so it is not unexpected that it is now appearing almost annually in England and may be attempting to colonise (Else 1991-1999). Likewise, the wasps *Dolichovespula media* and *D. saxonia* have also been spreading northwards in Germany since the 1980s and elsewhere in Central Europe, as has the wasp *Polistes dominulus* (Christ, 1791) (Otten et al. 1995).

Figure 4
The bee wolf-wasp *Philanthus triangulum*, a species which has expanded its range northwards in Britain in recent years. Photo Aart Noordam.

Concluding remarks

These accounts of alterations in the geographical ranges of various insects do not in themselves prove without doubt that such distributional changes are due to the effects of climate change, but their broad correlation with known climatic oscillations over the past two centuries, as documented by climatologists, is highly suggestive that climate has been a primary influence in many cases, if not all. Absolute proof is difficult to obtain, but the circumstantial evidence is, I believe, strong. For instance, the similar directional changes in the distribution of a wide range of species, whether they are closely related to each other or not, indicates that climate change is a highly probable cause and driving force, even though other factors, such as habitat loss and fragmentation, afforestation and the cultivation of potential larval foodplants in new areas, may be involved to some extent. As mentioned earlier, some species at least have spread in spite of loss of habitat. If warming continues, it is a reasonable guess that further species will invade Britain from the European mainland.

As has been pointed out by various authors (Barkham 1994, Moss 1998), a warming climate will inevitably cause changes in habitats in the British Isles and elsewhere in Europe, particularly in montane regions and along low-lying coasts where inundation by the sea due to rising sea-levels will be a growing problem. Therefore, more changes in distribution can be anticipated. Without doubt, the current changes in the climate are providing plenty of opportunities for interesting study, not only by professional biologists, but also by amateur naturalists, especially when in co-operation with the professionals.

Acknowledgements

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Recent changes in distribution of dragonflies in Switzerland (Odonata)

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Abstract

In 1998 the Swiss Centre for the Cartography of Fauna (CSCF) initiated 'Odonata 2000'. This project aimed at testing a method for periodical reassessment of Red Lists in Switzerland. The study was carried out on Odonata and consisted of the resampling of known localities of threatened species and the sampling of new localities. Based on the number of sites where a given species has been found in the periods 1970-1998 and 1999-2000, trends were calculated for each species. The results show that since 1994 three species have disappeared from Switzerland, nine species have declined, two species have increased and 64 species have remained stable. *Crocothemis erythraea*, *Lestes virens*, *Nehalennia speciosa*, *Sympetrum depressiusculum* and *S. pedemontanum* are discussed as examples of the different trend categories. The authors conclude that the situation is worse than in 1994 and that the conservation of threatened species should not only focus on their last remaining habitats, but also on increasing the number of favourable sites.

Key words: Odonata, Switzerland, faunistics, Red List, conservation, trends.

Introduction

In 1998, the Swiss Centre for the Cartography of Fauna (CSCF) was contracted by the Swiss Agency for Environment, Forest and Landscape (SAEFL) to develop a strategy and a program for a periodical reassessment of the Red List of threatened species in Switzerland. The first version of this Red List (Duelli 1994) included 376 vertebrates and more than 2000 invertebrates.

In order to evaluate the proposed strategy, we elaborated a pilot project dedicated to dragonflies referred to as 'Odonata 2000'. Its aim was to test a practical method enabling us to revise Red Lists of other groups in the next decade. As a first priority, we selected groups representative of the principal macro-habitats of the country: prairies (Rhopalocera, Orthoptera), freshwater ecosystems (Trichoptera, Plecoptera, Ephemeroptera and Mollusca) and forests (Coleoptera: Cerambycidae, Buprestidae and Diptera: Syrphidae). The project was founded by SAEFL from January 1999 to December 2001.

Partners

From the beginning, we asked seven experienced odonatologists to help guiding the project and organizing fieldwork in different regions of Switzerland. Furthermore, in 1999, we requested participation in the fieldwork to all active odonatologists and received 55 positive answers.

Methods

The general strategy used to generate or to reassess red lists was based on: a. resampling of known sites (fig. 1), b. sampling of areas for which we had few or no previous records (fig. 2). The chosen strategy was effective because the distribution of dragonflies in Switzerland is well known due to the publication of an atlas (Maibach & Meier 1987) and of several canton inventories in the 1990s.

Given the logistic and financial difficulties to gather a statistically significant number of new samples within known sites and for every species, we decided to concentrate on 'target species' to plan fieldwork. The choice of target species was based on the following criteria:

1. international Red List status, namely all the species listed in the Bern Convention and in the Habitat Directive (Helsdingen et al. 1996);
2. national Red List status as mentioned in the Red Databook of 1994 (Maibach & Meier 1994);
3. national and regional distribution;
4. habitat vulnerability;
5. expert opinions.

According to these criteria we selected 37 target species among the 81 Odonata species ever recorded in Switzerland.
In the resampling program, we sampled only the sites where target species were known to have reproduced with certainty or with high probability. Criteria for assessing reproduction were derived from Chovanec (1999) and Lehmann (1990). This procedure was chosen in order to eliminate observations of isolated individuals susceptible to be incidentally observed in an unfavourable environment. For those species that have been mentioned in less than 15 sites in one or several of the six main biogeographical regions of the country, all of these sites were revisited. For more common species, only a fraction of the known sites was revisited.

The new prospective sampling effort was concentrated on lakes and ponds at high altitude and on wetlands. In 2000, the prospective sampling was only realised in regions where the resampling program itself had been fully completed in 1999. We considered a target species absent from a reproductive site, when three unsuccesful visits were made during the optimum of its flight period, under good weather conditions. Therefore, chosen sites were visited a minimum of one time and a maximum of three times. During each visit, all observed species at the site were recorded. Abundances of larvae, exuviae, tenerals, males, females or tandems, copulation and oviposition were also reported.

Trend evaluation was based on the comparison of the number of sites where a given species has reproduced during the first period (1970-1998) and the number of sites where it has been found again during the second period (1999-2000), with or without proof of reproduction. As a weighting criterion, we used the number of positive sites of the second period, which had been unsuccessfully visited in the first one. This measure, which integrates possible modifications of local species distribution, was selected because it was proven to be efficient at recapturing stable trends for common species.

Trend formula : $trend_i = [(p21_i - p1r_i) + n2_i] / p1r_i * 100$

where for species i :
p1: between 1970-1998
p2: resampling in 1999/2000
p21: both in p1 and p2
$trend_i$ = trend (in %)
$p1r_i$ = number of presences in period 1 revisited in period 2
$p21_i$ = number of presences in both periods ($p21_i$ is a subset of $p1r_i$)
$n2_i$ = number of new presences among sites already visited for any species in period 1 (weighting index)

Limitations

Of course, this approach has its limitations. The sampling strategy having been targeted on particular species, information and trends for other species were sometimes hard to interpret because: a. numerous sites hosting common species were only partially sampled, b. species with a flight period in spring or fall (*Brachytron pratense* (Müller, 1764), *Sympecma fusca* (Vander Linden, 1820) and some *Sympetrum*) were locally underrecorded. In order to correct for this bias, supplementary visits targeted on these species were organized in 2001.

Changes in distribution ranges

Examples were chosen according to the calculated trends to represent different scenarios: stability, expansion, regression and extinction.

***Sympetrum depressiusculum* (Sélys, 1841)**
(trend = 4.8%, p21 = 15, p1r = 21, n2 = 7)
In the past, this species was probably widespread in the whole Swiss plateau and at low altitudes in alpine valleys (fig. 3). With the intensive drainage of the big marshes, it progressively disappeared in a large part of the west side of the country, but remained in big populations in central Switzerland (fig. 4).
The trend calculated between the two considered periods indicates the stability of the species. We also point out that some new sites were found during the second period.

***Crocothemis erythraea* (Brullé, 1932)**
(trend = 44.0%, p21 = 18, p1r = 25, n2 = 18)
Until 1969, this Mediterranean species was an

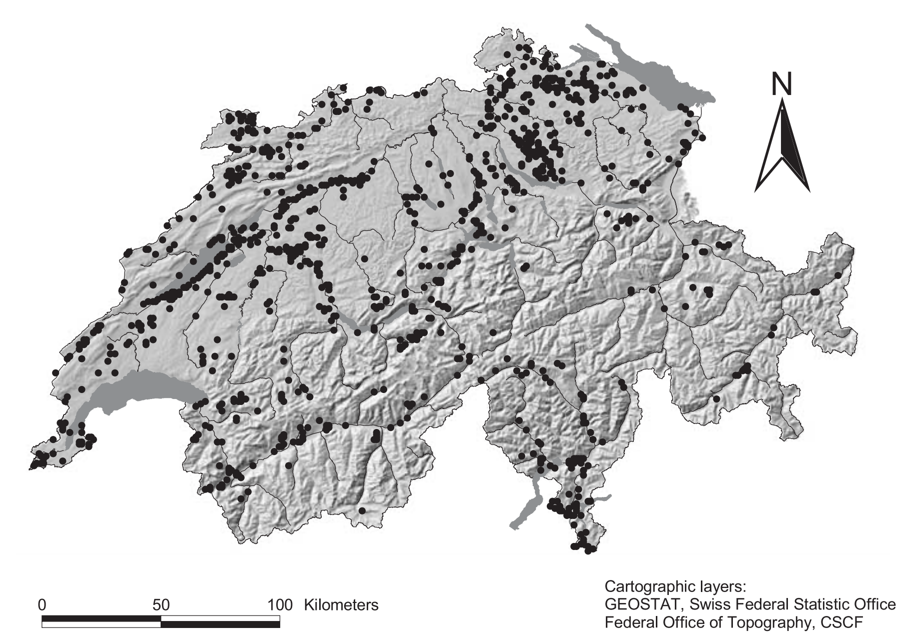

Figure 1
1 km squares revisited between 1999 and 2000.

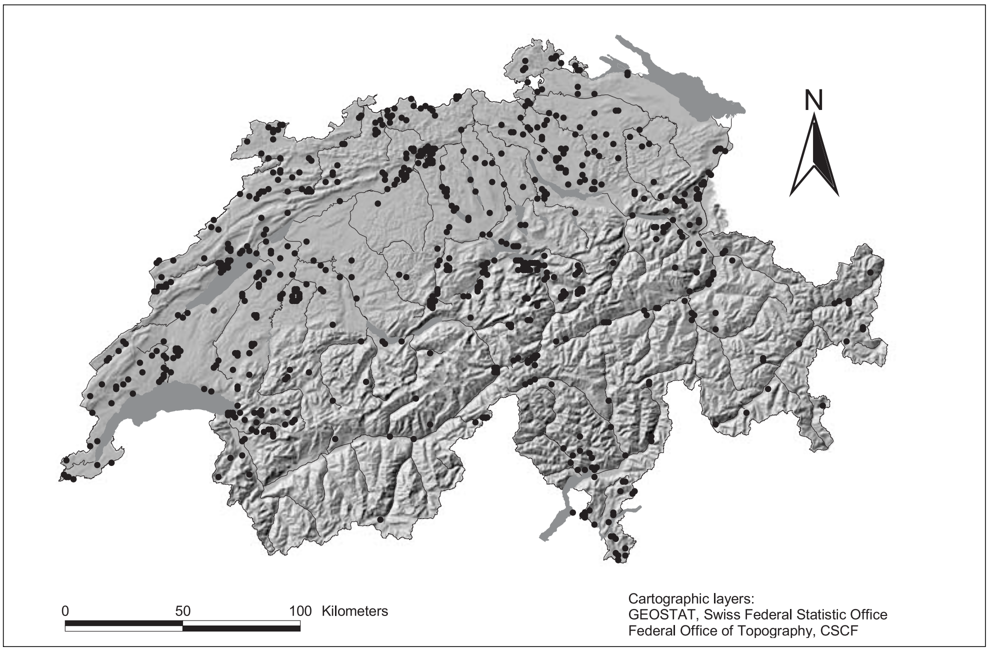

Figure 2
1 km squares visited for the first time in 1999 and 2000.

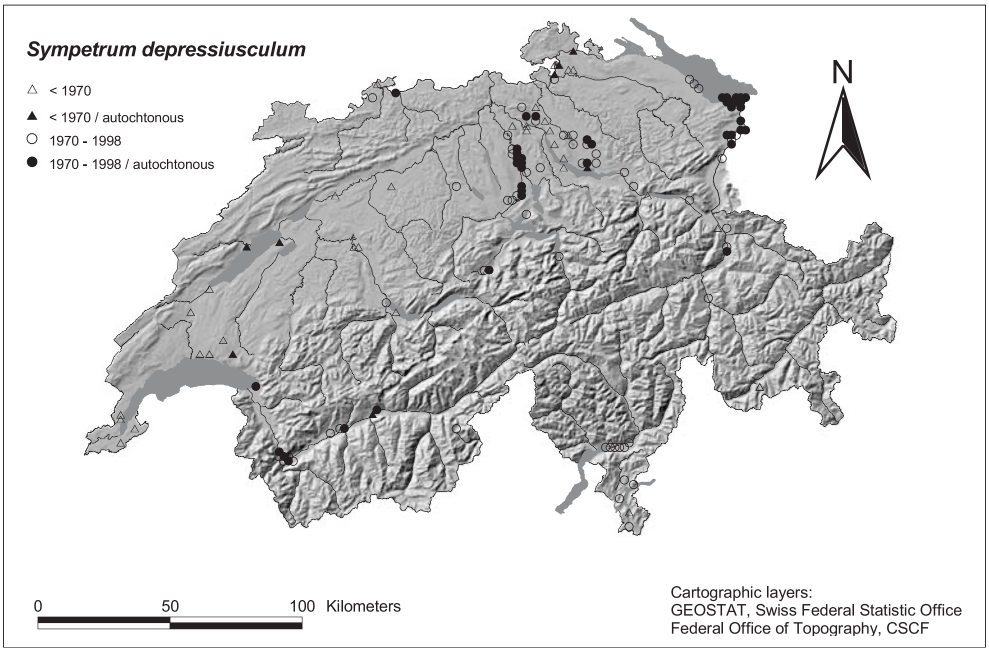

Figure 3
Distribution of *Sympetrum depressiusculum* before 1999.

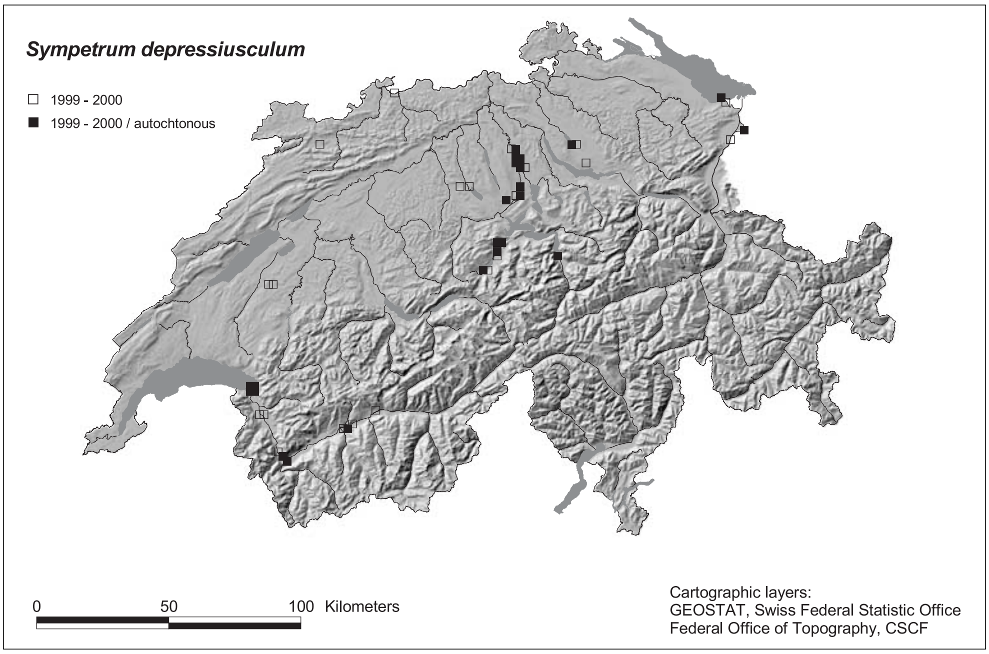

Figure 4
Distribution of *Sympetrum depressiusculum* since 1999.

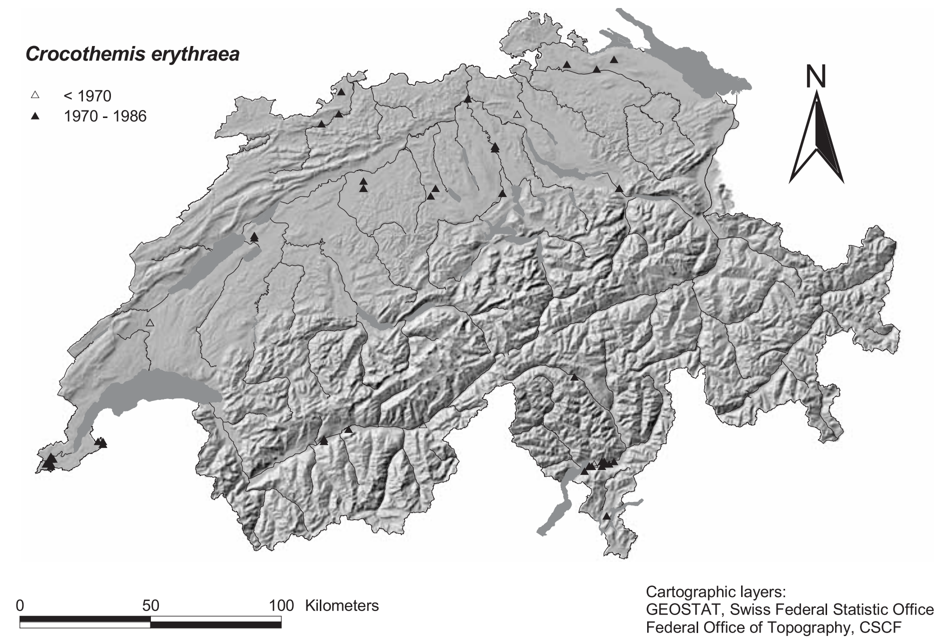

Figure 5
Distribution of *Crocothemis erythraea* before 1987.

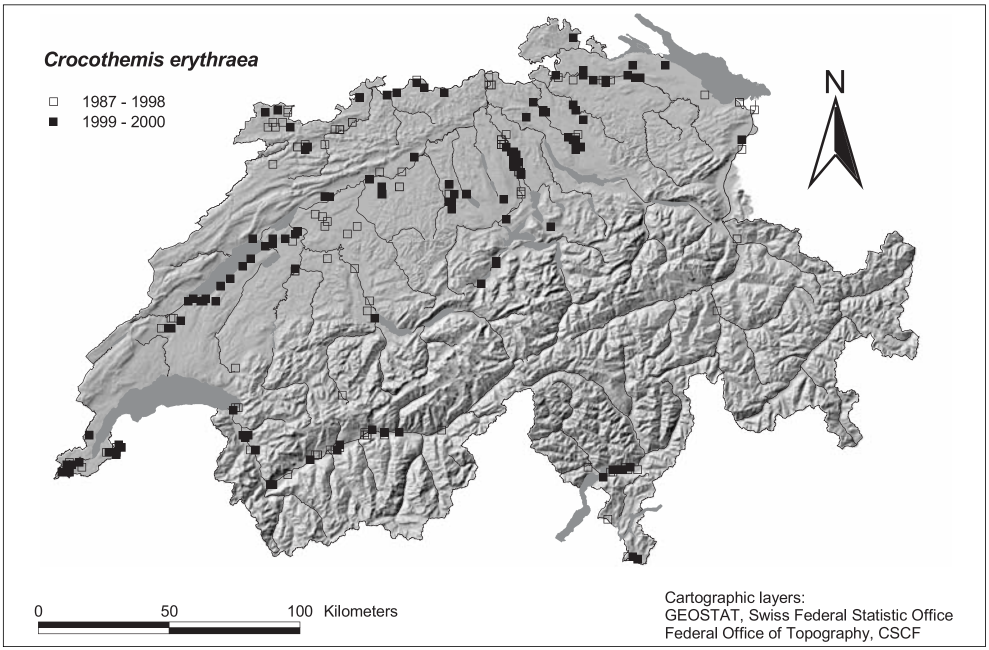

Figure 6
Distribution of *Crocothemis erythraea* since 1987.

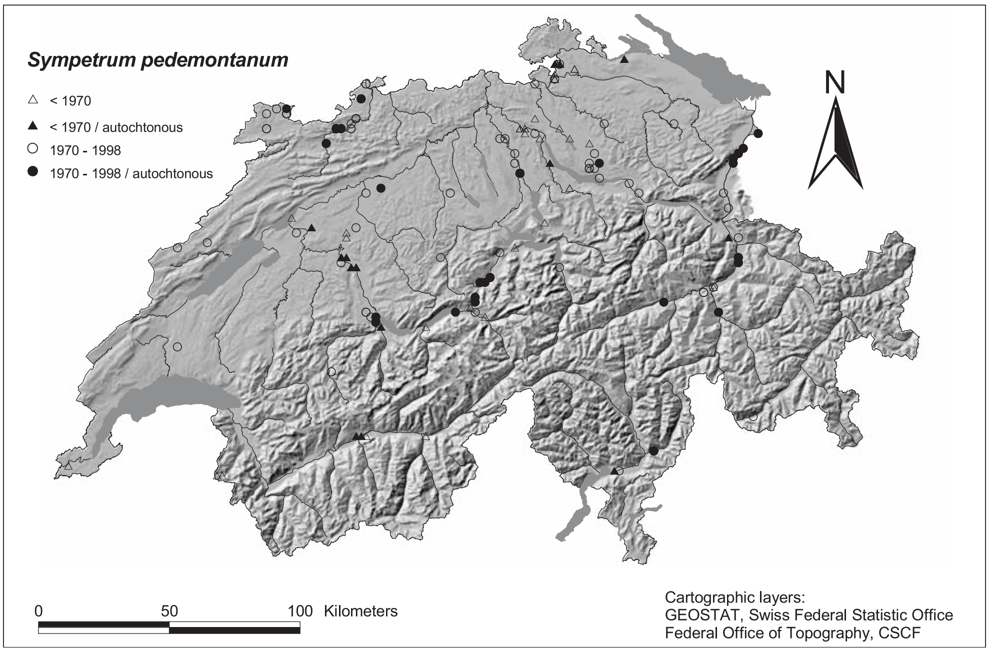

Figure 7
Distribution of *Sympetrum pedemontanum* before 1999.

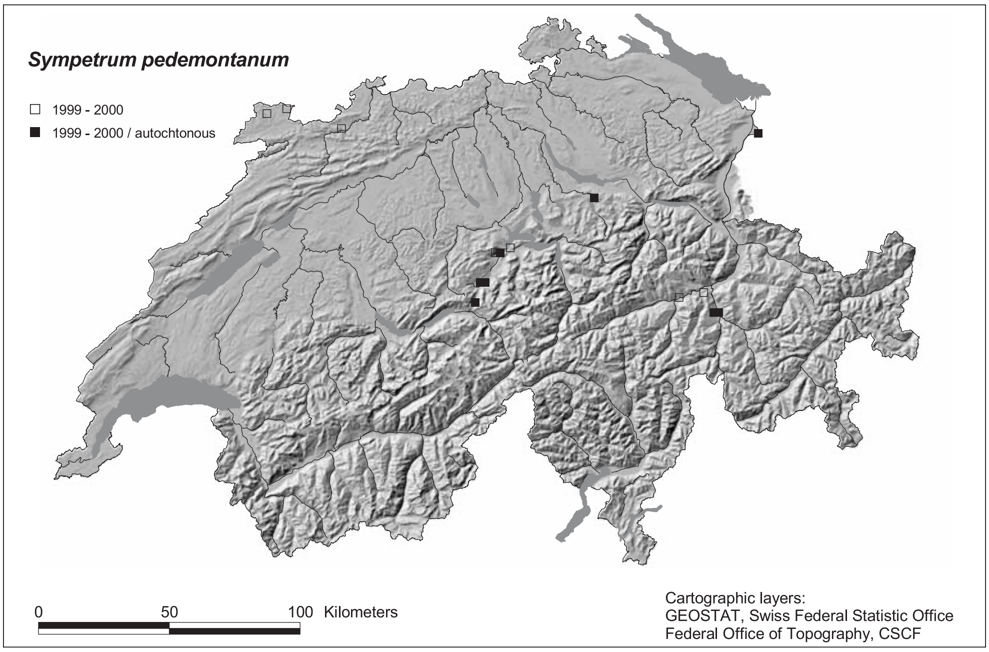

Figure 8
Distribution of *Sympetrum pedemontanum* since 1999.

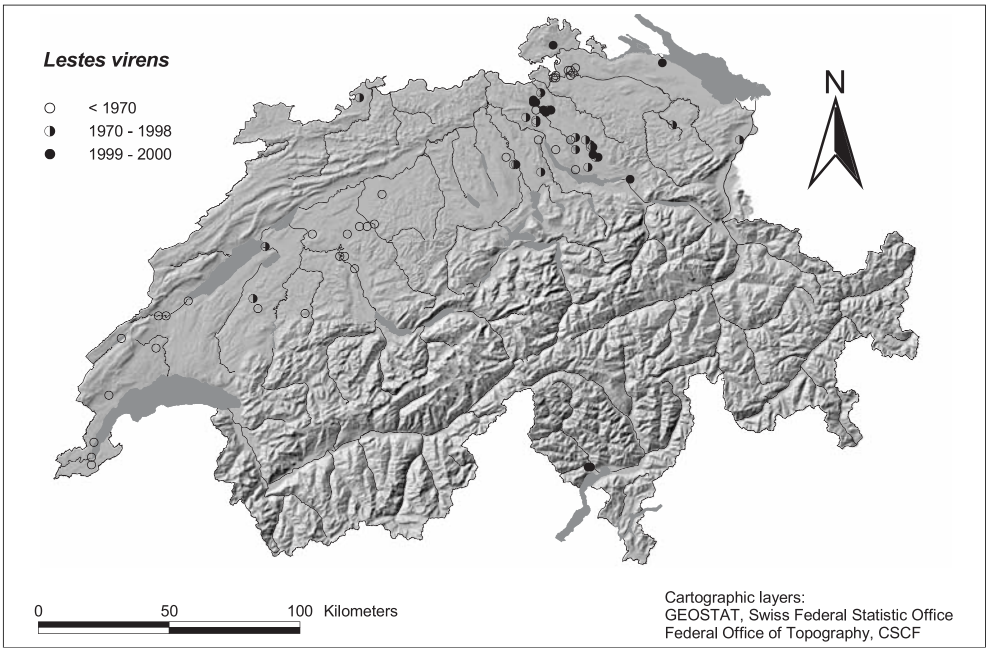

Figure 9
Distribution of *Lestes virens*.

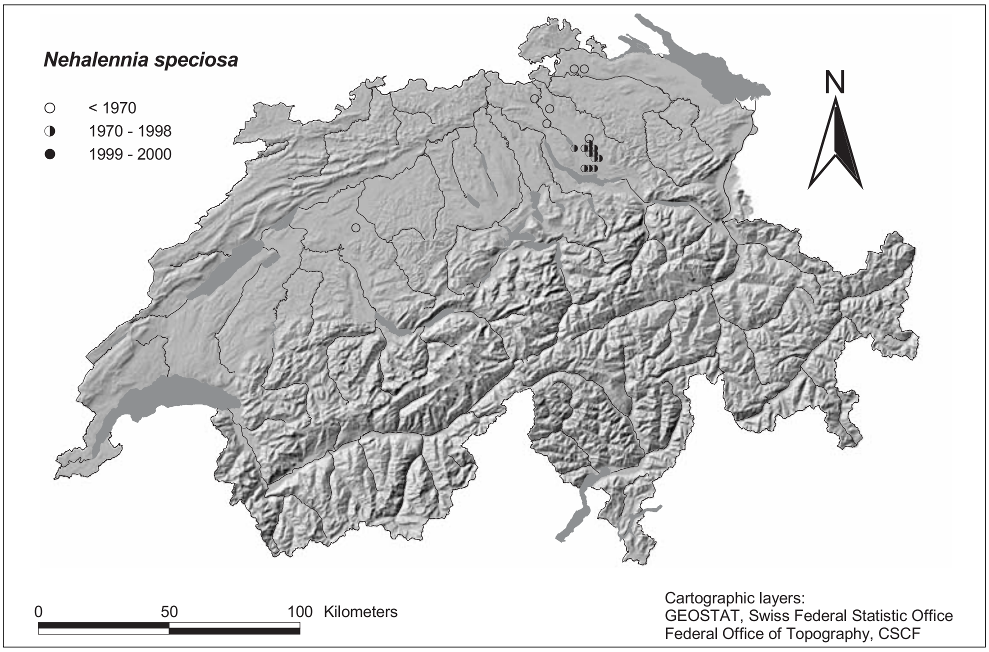

Figure 10
Distribution of *Nehalennia speciosa*.

occasional migrant with sporadic reproduction in Switzerland (fig. 5). Now the species is quite common in the low areas of the country with many regular reproduction sites. The main expansion of its range began in Switzerland at the end of the 1980s (fig. 6).

***Sympetrum pedemontanum* (Allioni, 1766)**
(trend = -43.8%, p21 = 8, p1r = 16, n2 = 1)
This species has taken advantage of the creation of numerous gravel pits and other artificial habitats during the 1960s and 1970s (fig. 7). Between 1999 and 2000 it only maintained stable populations in the central part of Switzerland and in several isolated localities (fig. 8). The probable reasons for this significant regression are the destruction of numerous pits and/or the natural succession of the pioneer ponds.

***Lestes virens* Rambur, 1842**
(trend = -57.9%, p21 = 7, p1r = 19, n2 = 1)
In the past, this species was probably widespread in the entire Plateau region. Between 1970 and 1998, it showed a strong regression in the western and central part of the country. During the last period, its regression continued in the western part and began in the eastern part of the country. Today it is extinct in many regions (fig. 9).

***Nehalennia speciosa* (Charpentier, 1840)**
(trend = -100%, p21 = 0, p1r = 11, n2 = 0)
This has always been an isolated and rare species in Switzerland, because the country is situated at the southern limit of its European range. In the beginning of the 1970s the species was recorded in nine sites North of the Lake of Zürich (Demarmels & Schiess 1977). The species was not found during the project and was last recorded by Hansruedi Wildermuth in 1990 at Wetzikon near Zürich in low numbers (less than ten males). The reasons of this dramatic decline are the isolation of the Swiss populations and the catastrophic effects of two very dry summers between 1975 and 1995. It is now considered as regionally extinct by odonatologists (fig. 10).

Result summary

The final reassessment of the Red List status of all Swiss species is made with the following criteria:

- calculated trends;
- ecological knowledge (e.g. vulnerability, phenology);
- Red List status in 1994 (the reason we took this into account is that stability, little expansion or regression are insufficient to justify a change of the initial status of species);
- expert opinion.

The main modifications of the Swiss odonatological fauna since 1994 are the following:

- three species have disappeared;
- nine species show a decline which justifies a higher Red List status;
- two species show a significant expansion which justifies a lower Red List status;
- 64 species are considered as stable or at least do not show trends which would justify a modification of their initial status.

Discussion

Our results show that 16% (12 species) of the Swiss fauna shows a significant negative trend since 1994 that might change their Red List status. At first glance the new Red List for Odonata of Switzerland will be quite similar to the one of 1994. In reality, we consider that the situation is worse than it seems to be, because many of the most threatened species of the Red List of 1994 have disappeared or are already almost extinct. This observation shows us that the conservation of very rare and threatened species should not only be focused on the conservation and management of their last remaining habitats, but should lead to the reinforcement of their populations by increasing the number of favourable sites.

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Trends in dragonfly occurrence in Belgium (Odonata)

Geert De Knijf, Anny Anselin & Philippe Goffart

Abstract

The group 'Gomphus' collected 65 000 records of 69 species of Odonata, more or less equally scattered over Belgium. The best-investigated areas are the northern part and some river valleys in the south. Most hot spots can be found in the northeastern part, with a maximum of 48 species for 25 km². Remarkable is the fact that 50% of the species occurs in less than 7% of the 5 km grid cells (UTM). We determined trends in occurrence by comparing three periods: before 1950, 1950-1989 and 1990-2000. Four species show a clear decline over the three periods, eight species give evidence of a historical decline but survive on a limited number of sites and eight species also display a historical decline but have been increasing during the last decade. Six species show a (very) clear increase over the three periods and two species display their increase only during the last ten years.

Key words: Odonata, dragonflies, Belgium, atlas, hot spot, abundance class shift, habitat.

Introduction

One of the aims of the Belgian Dragonfly Group 'Gomphus', a volunteer organisation founded in 1983, is to collect all distribution data of Odonata in Belgium with the intention to publish an atlas of the Belgium Odonata. For that reason we set up an Atlas Project and developed a network of more than 400 field-workers.

A special effort has been made to achieve a good coverage of the territory during the last ten years. Since 1990, all 10 km grid cells (UTM) and nearly 60% of the 5 km grid cells of Belgium have been visited at least once. In the Flemish region, little less than half the area of Belgium, more than 1700 localities were visited at least once since 1990. Nearly 65 000 records are available, two thirds of them collected since 1990, on 66 species (on a total of 69 species for Belgium). As early as in the 19th century, the Odonata fauna of Belgium was very well investigated. A first review by De Sélys-Longchamps (1888) already mentioned 65 species for Belgium. Figure 1 shows the coverage of all 1 km grid cells in which Odonata were observed since 1990. The northern part of Belgium (the Flemish region) and some river valleys in the south are very well investigated.

Species diversity

For each 5 km grid cell we calculated the number of observed species since 1990. The highest species diversity (fig. 2) is found on the poor sandy soils with heathlands and moors in the northeastern part, the Kempen and in some river valleys, peat moors and fens in the south. The maximum number for a single grid cell is 48 species or 73% of the actual Odonata fauna of Belgium. Even in a European perspective, with only 130 species (Wasscher & Bos 2000), this is a relatively high percentage of 37%. Fig. 3 gives the number of species for Log (2) of the number of the investigated 5 km grid cells (n = 908). We show that 33 (50 %) of the species occur in less than 7% of the grid cells and can be considered as rare in Belgium. On the other hand, 15 species (22%) occur in more than a quarter (28%) of the grid cells.

Trend analysis

To determine the change in occurrence of Odonata in Belgium, we make use of three major time periods: 1. before 1950, which we consider to be the historical species distribution; 2. 1950-1989, being the time of the great change in land use and the deterioration of the environment and the natural habitats and 3. 1990-2000, or the actual distribution. We calculate for each species the number of 10 km grid cells in which a certain species was observed. To compensate for the differences in recording effort, we made a correction for the total in recording effort per area. This means that the actual number of 10 km grid cells for each species is related to the total amount of

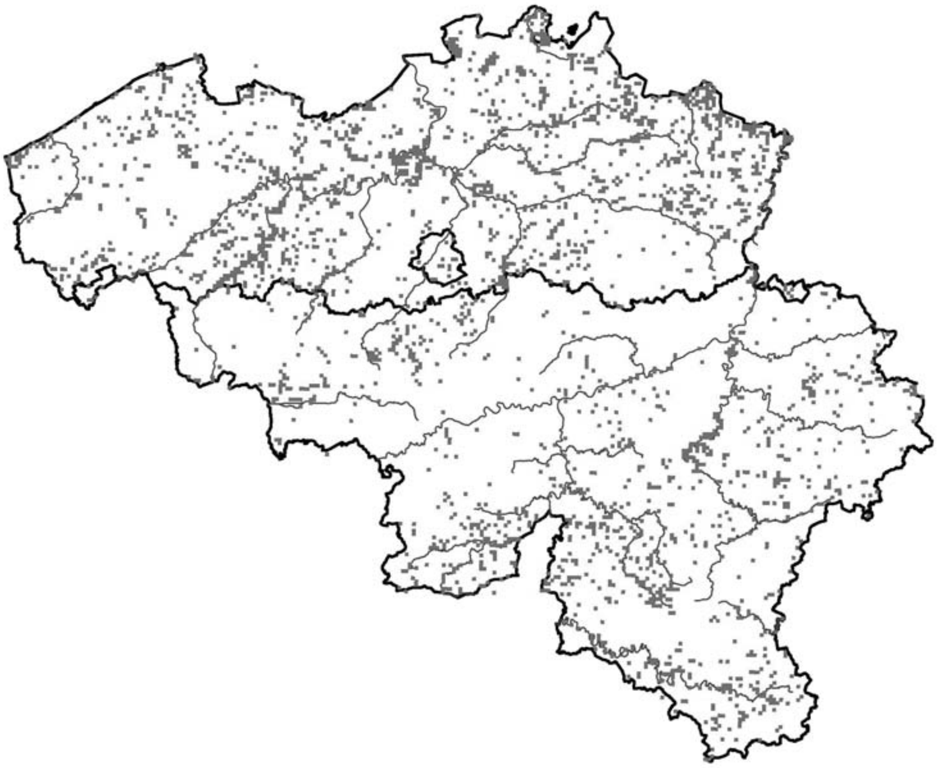

Figure 1
Geographic distribution of the localities with data since 1990, 1 km grid cells (UTM).

investigated 10 km grid cells for each period (before 1950: n = 178; 1950-1989: n = 327; 1990-2000: n = 339). By comparing the percentages of each period, we obtained a measurement of change (%) in the occurrence for each species in Belgium (table 1).

The Belgian Odonata

Out of a total of 69 species the indigenous status of eight is dubious. These are marked with an * in table 1. For four of them, *Aeshna affinis*, *Anax parthenope*, *Sympetrum fonscolombii* and *Sympetrum meridionale*, proof of reproduction in Belgium is available (Goffart 1999, Van den Berghe 1999, Versonnen et al. 2002), but there are no indications that populations exist already for at least ten consecutive years. For that reason we classify them as not indigenous. Despite the increased effort and the higher number of investigated 10 km grid cells, some species show an obvious decrease.

Extinct and declining species

Only two species, *Leucorrhinia caudalis* and *Nehalennia spesiosa*, are extinct in Belgium, the former already around 1900 and the latter since 1970. This is the lowest number in comparison with our surrounding countries: five extinct species in the Netherlands (Wasscher 1999), four in the former West-Germany (Clausnitzer et al. 1984), four in France (Dommanget 1987) and three in the United Kingdom and Ireland (Merritt et al. 1996). Four species show an obvious decline of more than 25% over the three periods: *Aeshna isoceles*, *A. subarctica*, *Coenagrion hastulatum* and *Leucorrhinia pectoralis*. This means that they not only display a historical decline but that their decrease has still been going on during

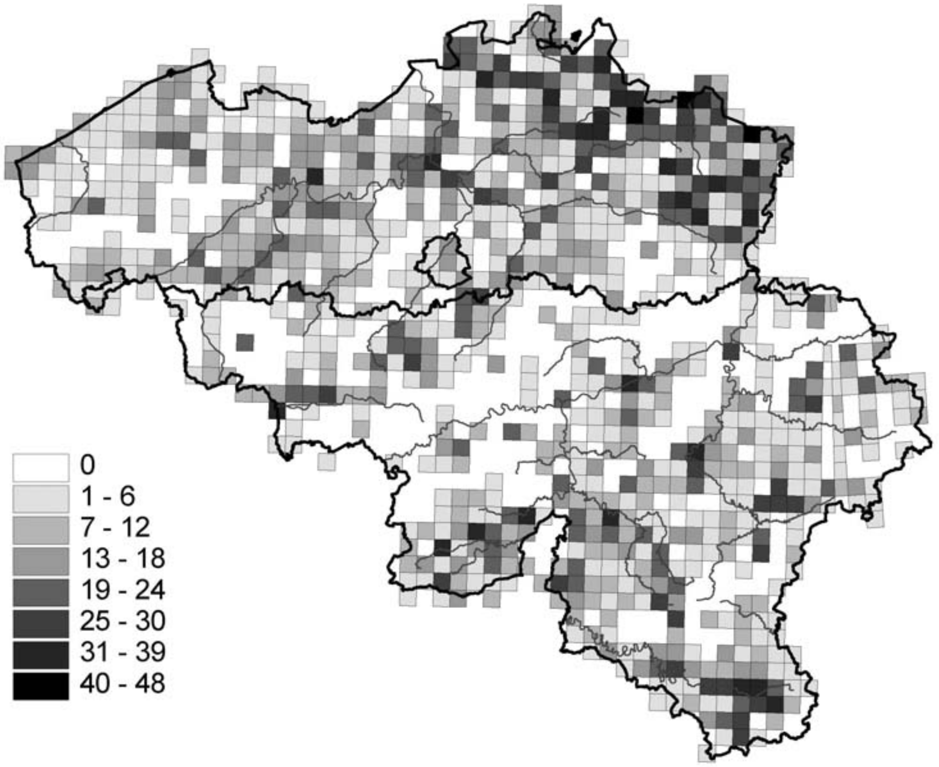

Figure 2
Total number of Odonata species in Belgium since 1990, 5 km grid cells (UTM).

the last decades. If the appropriate measures are not taken to protect and conserve the last populations and the habitats of these species, this will in a short term inevitably lead to the extinction of those four species in Belgium.

Comparing the periods before 1950 and 1950-1989, eight species (*Brachytron pratense*, *Epitheca bimaculata*, *Gomphus vulgatissimus*, *Leucorrhinia rubicunda*, *Libellula fulva Orthetrum coerulescens*, *Oxygastra curtisii*, and *Sympetrum depressiusculum*) show a historical decrease (>25%), but a stabilisation comparing the latter period with 1990-2000. This means that they can survive in a limited number of grid cells or that they were able to colonise new grid cells or formerly abandoned ones. Those species are here in the centre of their geographical distribution or have a more eastern range (Askew 1988).

Another group consists of species, which display a historical decrease of more than 25% (comparing the periods before 1950 and 1950-1989) but for which the number of 10 km grid cells the last ten years clearly augmented. This group contains seven species: *Cercion lindenii*, *Coenagrion mercuriale*, *C. scitulum*, *Lestes barbarus*, *L. dryas*, *Onychogopmphus forcipatus*, and *Sympecma fusca*. With the exception of *Lestes dryas*, they all have their main distribution in southern parts of Europe (Askew 1988). We suppose that recent changes in temperature in Europe favour the occurrence and distribution of these species, at the northern limits of their ranges.

Because of the differences in recording effort between the three periods, especially between on the one hand the first (before 1950) and on the other the second (1950-1989) and third period (1990-2000), it is expected that most species, with the exception of all the threatened ones, are

Table 1

Odonata species list of Belgium, ordered alphabetically. For each species the number of 10 km grid cells is given for three periods: P1= before 1950, P2 = 1950-1989 and P3 = 1990-2000. The percentage of occurrence (P1%, P2% and P3%) of all investigated grid cells is calculated by considering the total number of investigated grid cells per period: P1 (n = 178), P2 (n = 327) and P3 (n = 339). The measurement of change (%) in the occurrence for each species is obtained by comparing P2 with P1 (P21), P3 with P1 (P31) and P3 with P2 (P32).

Species		**P1**	**P1%**	**P2**	**P2%**	**P3**	**P3%**	**P21**	**P31**	**P32**
Aeshna affinis *	Vander Linden, 1820	3	1.7	2	0.6	23	6.8	-64	303	1009
Aeshna cyanea	(O.F.Müller, 1764)	45	25.3	208	63.6	238	70.2	152	178	10
Aeshna grandis	(Linnaeus, 1758)	18	10.1	91	27.8	115	33.9	175	235	22
Aeshna isoceles	(O.F.Müller, 1767)	13	7.3	15	4.6	9	2.7	-37	-64	-42
Aeshna juncea	(Linnaeus, 1758)	21	11.8	52	15.9	56	16.5	35	40	4
Aeshna mixta	Latreille, 1805	18	10.1	101	30.9	200	59.0	205	483	91
Aeshna subarctica	Walker, 1908	6	3.4	8	2.4	3	0.9	-27	-74	-64
Anax imperator	Leach, 1815	20	11.2	167	51.1	262	77.3	355	588	51
Anax parthenope *	(Sélys, 1839)	1	0.6	4	1.2	14	4.1	118	635	238
Brachytron pratense	(O.F.Müller, 1764)	25	14.0	19	5.8	24	7.1	-59	-50	22
Calopteryx splendens	(Harris, 1782)	47	26.4	114	34.9	151	44.5	32	69	28
Calopteryx virgo	(Linnaeus, 1758)	44	24.7	119	36.4	131	38.6	47	56	6
Cercion lindenii	(Sélys, 1840)	14	7.9	13	4.0	83	24.5	-49	211	516
Ceriagrion tenellum	(de Villers, 1789)	11	6.2	19	5.8	28	8.3	-6	34	42
Coenagrion hastulatum	(Charpentier, 1825)	18	10.1	21	6.4	10	2.9	-36	-71	-54
Coenagrion lunulatum	(Charpentier, 1840)	4	2.2	15	4.6	12	3.5	104	58	-23
Coenagrion mercuriale	(Charpentier, 1840)	10	5.6	3	0.9	5	1.5	-84	-74	61
Coenagrion puella	(Linnaeus, 1758)	43	24.2	210	64.2	252	74.3	166	208	16
Coenagrion pulchellum	(Vander Linden, 1825)	31	17.4	66	20.2	54	15.9	16	-9	-21
Coenagrion scitulum	Rambur, 1842	5	2.8	1	0.3	6	1.8	-89	-37	479
Cordulegaster bidentata	Sélys, 1843	2	1.1	7	2.1	8	2.4	91	110	10
Cordulegaster boltonii	(Donovan, 1807)	22	12.4	54	16.5	79	23.3	34	89	41
Cordulia aenea	(Linnaeus, 1758)	32	18.0	76	23.2	120	35.4	29	97	52
Crocothemis erythraea	(Brullé, 1832)	1	0.6	12	3.7	70	20.6	553	3576	463
Enallagma cyathigerum	(Charpentier, 1840)	30	16.9	195	59.6	253	74.6	254	343	25
Epitheca bimaculata	(Charpentier, 1825)	3	1.7	2	0.6	2	0.6	-64	-65	-4
Erythromma najas	(Hansemann, 1823)	14	7.9	90	27.5	126	37.2	250	373	35
Erythromma viridulum	(Charpentier, 1840)	14	7.9	71	21.7	159	46.9	176	496	116
Gomphus flavipes *	(Charpentier, 1825)	0	0.0	0	0.0	2	0.6	-	-	-
Gomphus pulchellus	Sélys, 1840	11	6.2	70	21.4	125	36.9	246	497	72
Gomphus simillimus *	Sélys, 1840	2	1.1	1	0.3	2	0.6	-73	-47	93
Gomphus vulgatissimus	(Linnaeus, 1758)	20	11.2	20	6.1	27	8.0	-46	-29	30
Hemianax ephippiger *	(Burmeister, 1839)	1	0.6	1	0.3	1	0.3	-46	-47	-4
Ischnura elegans	(Vander Linden, 1820)	41	23.0	253	77.4	300	88.5	236	284	14
Ischnura pumilio	(Charpentier, 1825)	11	6.2	31	9.5	50	14.7	53	139	56
Lestes barbarus	(Fabricius, 1798)	7	3.9	5	1.5	77	22.7	-61	478	1385
Lestes dryas	Kirby, 1890	16	9.0	22	6.7	33	9.7	-25	8	45
Lestes sponsa	(Hansemann, 1823)	38	21.3	130	39.8	156	46.0	86	116	16
Lestes virens	(Charpentier, 1825)	8	4.5	15	4.6	15	4.4	2	-2	-4
Lestes viridis	(Vander Linden, 1825)	18	10.1	122	37.3	199	58.7	269	480	57
Leucorrhinia caudalis	(Charpentier, 1840)	4	2.2	0	0.0	0	0.0	-100	-100	-
Leucorrhinia dubia	(Vander Linden, 1825)	22	12.4	46	14.1	48	14.2	14	15	1
Leucorrhinia pectoralis	(Charpentier, 1825)	14	7.9	13	4.0	5	1.5	-49	-81	-63
Leucorrhinia rubicunda	(Linnaeus, 1758)	17	9.6	16	4.9	17	5.0	-49	-47	2
Libellula depressa	Linnaeus, 1758	36	20.2	172	52.6	218	64.3	160	218	22
Libellula fulva	O.F.Müller, 1764	18	10.1	20	6.1	22	6.5	-40	-36	6
Libellula quadrimaculata	Linnaeus, 1758	32	18.0	104	31.8	146	43.1	77	140	35
Nehalennia speciosa	(Charpentier, 1840)	6	3.4	1	0.3	0	0.0	-91	-100	-100
Onychogomphus forcipatus	(Linnaeus, 1758)	19	10.7	13	4.0	35	10.3	-63	-3	160
Onychogomphus uncatus *	(Charpentier, 1840)	0	0.0	2	0.6	0	0.0	-	-	-100
Orthetrum brunneum	(Fonscolombe, 1837)	2	1.1	4	1.2	20	5.9	9	425	382
Orthetrum cancellatum	(Linnaeus, 1758)	25	14.0	179	54.7	256	75.5	290	438	38
Orthetrum coerulescens	(Fabricius, 1798)	24	13.5	23	7.0	28	8.3	-48	-39	17
Oxygastra curtisii	(Dale, 1834)	4	2.2	2	0.6	3	0.9	-73	-61	45
Platycnemis pennipes	(Pallas, 1771)	26	14.6	129	39.4	160	47.2	170	223	20
Pyrrhosoma nymphula	(Sulzer, 1776)	42	23.6	178	54.4	200	59.0	131	150	8
Somatochlora arctica	(Zetterstedt, 1840)	6	3.4	11	3.4	15	4.4	0	31	32
Somatochlora flavomaculata	(Vander Linden, 1825)	3	1.7	11	3.4	13	3.8	100	128	14
Somatochlora metallica	(Vander Linden, 1825)	20	11.2	79	24.2	118	34.8	115	210	44
Sympecma fusca	(Vander Linden, 1820)	20	11.2	19	5.8	54	15.9	-48	42	174
Sympetrum danae	(Sulzer, 1776)	30	16.9	119	36.4	139	41.0	116	143	13
Sympetrum depressiusculum	(Sélys, 1841)	14	7.9	17	5.2	23	6.8	-34	-14	31
Sympetrum flaveolum	(Linnaeus, 1758)	39	21.9	76	23.2	120	35.4	6	62	52
Sympetrum fonscolombii *	(Sélys, 1840)	9	5.1	9	2.8	49	14.5	-46	186	425
Sympetrum meridionale *	(Sélys, 1841)	7	3.9	0	0.0	3	0.9	-100	-77	-
Sympetrum pedemontanum	(Allioni, 1766)	4	2.2	8	2.4	24	7.1	9	215	189
Sympetrum sanguineum	(O.F.Müller, 1764)	27	15.2	135	41.3	221	65.2	172	330	58
Sympetrum striolatum	(Charpentier, 1840)	43	24.2	117	35.8	186	54.9	48	127	53
Sympetrum vulgatum	(Linnaeus, 1758)	16	9.0	100	30.6	139	41.0	240	356	34

going to demonstrate an increase in terms of percentage of occupied 10 km grid cells. Most records from the period before 1950 are based on collected specimens, which we suppose to give an overrepresentation of the rare species and an underestimation of the common species in this period. This means that the decrease of the species mentioned above is likely to be more severe than our analysis indicates.

Increasing species

We consider a species as increasing in case of a very obvious increase of more than 100% over the three periods or an increase of more than 200% between the periods before 1950 and 1950-1989 and an increase of at least 25% over the periods 1950-1989 and 1990-2000. Three species, *Aeshna mixta*, *Crocothemis erythraea* and *Erythromma viridulum*, show an increase in terms of percentage of occupied 10 km grid cells of nearly 100% or more for each period. The last two species are southern species that were able to shift their range of distribution to the north during the last decades (De Knijf 1995, Ott 1996, Wasscher 1999). Both have now become fairly common. Even a new species, *Gomphus flavipes*, was recently recorded in Belgium (Gubbels 2001).

Comparing the period before 1950 with the period 1950-1989, we note that ten species show an increase of more than 200% (table 1) and 13 more species display an increase of more than 100%. This is partly due to the factors mentioned above: differences in recording effort and old records based on voucher specimens. *Anax imperator*, *Gomphus pulchellus* and *Lestes viridis* are three species from which the number of 10 km grid cells not only increased with more than 200% over the first two periods but also with more than 50% over the periods 1950-1989 and 1990-2000, despite nearly the same number of investigated grid cells for both periods. We expect that their expansion is still going on and that they will be found at more and more sites.

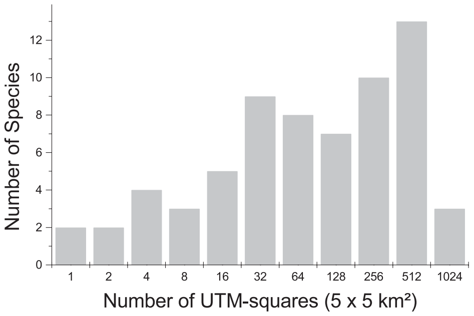

Figure 3

Number of species per 5 km grid cell (UTM).

Orthetrum brunneum and *Sympetrum pedemontanum* are two species that display an increase during the last decade. Both show an increase of 380% and 190%, respectively, over the last two periods and their absolute number of 10km grid cells multiplied by five or three. This change is not so conspicuous as between the periods before 1950 and 1950-1989, when their number of grid cells doubled but their relative frequencies don't differ much.

Habitats

Analysing the species composition and the distribution of some Odonata for several kinds of threatened habitat types in Belgium we notice that the species which inhabit rivers, rivulets and broks are *Calopteryx splendens*, *C. virgo*, *Coenagrion mercuriale*, *Cordulegaster bidentata*, *C. boltonii*, *Gomphus vulgatissimus*, *Onychogomphus forcipatus*, *Orthetrum coerulescens* and *Oxygastra curtisii*. Those species can be found along many rivers in the southern part of Belgium and in the northeastern part. Species of oligotrophic waters and bogs in Belgium are *Aeshna juncea*, *A. subarctica*, *Coenagrion hastulatum*, *C. lunulatum*, *Leucorrhinia dubia. L. rubicunda* and *Somatochlora arctica.* They are restricted to the northeast and the high altitudes of the Ardennes in Southeast-Belgium. Species of mesotrophic and natural eutrophic ponds and marshes occur in the whole northern part and in the very south of Belgium. They are *Aeshna isosceles*, *Brachytron pratense*, *Coenagrion pulchellum*, *Erythromma najas*, *Lestes dryas*, *Leucorrhinia pectoralis*, *Libellula fulva* and *Somatochlora flavomaculata.*

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Recent changes in the Dutch Heteroptera fauna (Insecta: Hemiptera)

Berend Aukema

Abstract

At present 610 species of Heteroptera are recorded from the Netherlands. The database of the Dutch bureau of the European Invertebrate Survey currently includes about 130 000 Dutch records (combinations of locality and species). The records, however, are strongly biased towards aquatic and semi-aquatic species (72 761 records of 64 species = 1137 records/species) in comparison with terrestrial species (55 375 records of 545 species = 101 records/species). Although since about 1850 there have always been Dutch heteropterists, collecting efforts show large differences in time and place and it is for instance easy to locate both residences and favourite holiday resorts of heteropterists from the distribution maps.

Local faunas are not static but dynamic and changes in the Dutch Heteroptera fauna were analysed for the period since 1960 and especially before and since 1980. A number of 571 species (93.6% of the Dutch species listed) have been recorded since 1960 and 510 of these (83.6%) have been recorded regularly since 1960 and are considered 'resident species'. The changes documented for the period 1980-2002 concern 61 species: 27 new arrivals, 27 species rediscovered after not having been recorded in the period 1960-1980, and 7 species not recorded since 1980.

From these data it is concluded that the turnover of species since 1980 (61 of 571 species) has been 10.7%. New arrivals (27) outnumber the extinctions (seven). Turnover of species of local faunas is considered a natural process (species come and go continuously), but it is also clear that habitat changes, international trade and global warming have contributed largely to the observed changes in the Dutch fauna. At least four of the 27 new arrivals are linked to international transport of plant material and the majority of the new arrivals are supposed to benefit from global warming.

Keywords: Heteroptera, Dutch fauna, turnover, extinctions, new arrivals, range changes, global warming.

Introduction

Knowledge about the Dutch Heteroptera fauna has been compiled since 1853 when De Graaf & Snellen van Vollenhoven published the first checklist of this group for the Netherlands, including 119 species. Updates were published by De Graaf et al. (1860, 1862), Snellen van Vollenhoven (1868-1879), Fokker (1883-1900), Reclaire (1932-1951) and Aukema (1989), respectively (table 1). The last list included 588 species. At present, with 22 additional species discovered since 1989 (table 1), 610 Heteroptera species are known from the Netherlands.

Data on Dutch Heteroptera records are compiled in the database of the working group Heteroptera of the Dutch bureau of the European Invertebrate Survey at the National Museum of Natural History, Leiden. Altogether nearly 130 000 records (combinations of locality and species) are included at present (fig. 1), showing a strong increase since the 1950s. The data, however, are strongly

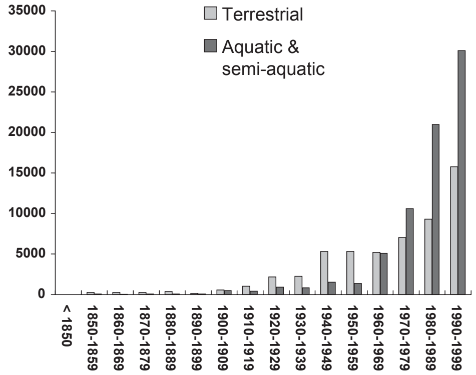

Figure 1
Number of records of Heteroptera per decade.

Table 1
Heteroptera known from The Netherlands: checklists and additional data. +: overlooked species.

	Source	
1.	De Graaf & Snellen van Vollenhoven (1853):	119 species
2.	De Graaf, Six & Snellen van Vollenhoven (1860, 1862):	200 species
3.	Snellen van Vollenhoven (1868-1878a, 1878b, 1879):	283 species
4.	Fokker (1883-1900):	410 species
5.	Reclaire (1932-1951):	488 species
6.	Aukema (1989):	588 species
7.	species added since 1989	**reference**
	Brachynotocoris puncticornis Reuter, 1880	Aukema 1990a
+	*Megalonotus emarginatus* (Rey, 1888)	Aukema & Woudstra 1990
	Dichrooscytus gustavi Josifov, 1981	Aukema 1990b
	Psallus punctulatus Puton, 1874	Aukema 1990b
	Phoenicocoris modestus (Meyer-Dür, 1843)	Aukema 1990b
	Coriomeris scabricornis (Panzer, 1809)	Aukema & Hermes 1992
	Nysius graminicola (Kolenati, 1845)	Aukema 1992
	Rhopalus tigrinus Schilling, 1829	Aukema 1993a
	Eurydema ornata (Linnaeus, 1758)	Aukema 1993a
	Cymatia rogenhoferi (Fieber, 1864)	Jansson 1995
	Stephanitis takeyai Drake & Maa, 1955	Aukema 1996a
	Emblethis denticollis Horváth, 1878	Aukema 1996b
+	*Nysius cymoides* (Spinola, 1837)	Aukema et al. 1997
+	*Rhyparochromus vulgaris* (Schilling, 1829)	Aukema et al. 1997
	Closterotomus trivialis (A. Costa, 1853)	Aukema 1999
	Micronecta griseola Horváth, 1899	Aukema et al. 2000
+	*Copium clavicorne* (Linnaeus, 1758)	Werner 2001
	Horvathiolus superbus (Pollich, 1781)	unpublished 2000
	Stagonomus pusillus (Herrich-Schaeffer, 1833)	unpublished 2000
	Rhaphigaster nebulosa (Poda, 1761)	Aukema & Steeghs 2002
	Holcocranum saturejae (Kolenati, 1845)	unpublished 2002
	Tritomegas sexmaculatus (Rambur, 1839)	unpublished 2002
	Total number of species (2002):	610

biased towards the aquatic and semiaquatic species (72 761 records of 64 species, i.e. 1137 records/species) in comparison to the terrestrial ones (55 375 records of 546 species, i.e. 101 records/species). This is mainly due to the fact that data on aquatic and semiaquatic species have been systematically collected for water quality assessment by different organisations/institutes involved in water management during the last decades. This means that although since about 1850 there have always been Dutch heteropterists, collecting efforts show large differences in time and place and especially the terrestrial species have not been sampled in a representative way, showing clusters of records (fig. 2) and numbers of species recorded (fig. 3) around residences of collectors and favoured holiday destinations like the coastal dune area, the West Frisian islands and the southern part of the province of Limburg. Therefore a general quantitative analysis of the data is not possible and a more or less qualitative approach had to be followed.

Faunal changes

Local faunas are not static, but dynamic: there are changes in time and space with respect to both species composition and species distribution. The following changes are considered:

- extinctions: species not longer recorded after a certain year (the pivot year);
- new arrivals: species not recorded before a certain year (the pivot year);
- range changes of resident species (species recorded both in the past and at present, showing increasing or decreasing ranges).

The pivot year selected here is 1980, because the

Figure 2
Number of records of terrestrial Heteroptera per 10 km square.

Figure 3
Number of species of terrestrial Heteroptera per 10 km square.

number of records of terrestrial species before and from this year onwards are more or less equal. Starting point is 1960.

Extinctions

Since 1960, 39 of the 610 species listed for the Dutch fauna have not been recorded anymore (table 2). Most of the species have been recorded only once or twice and 31 species have not been collected for at least 50 years or more. Of those *Arenocoris waltlii*, *Eurydema ventralis*, *Galeatus maculatus*, *Geocoris ater*, *Phymata crassipes* and *Spilostethus saxatilis* were not found for a century or more and probably have to be excluded from the list as truly extinct. The disappearance of some of the other species is clearly connected with the detoriation or disappearance of their habitat: *Salda morio* Zetterstedt, 1838 once lived in peat bogs, which largely disappeared, and *Brachycoleus pilicornis*, *Copium clavicorne* and *Cydnus aterrimus* disappeared together with the only locality where they once were found. *Brachycoleus pilicornis* and *C. aterrimus* are associated with *Euphorbia* species and the only

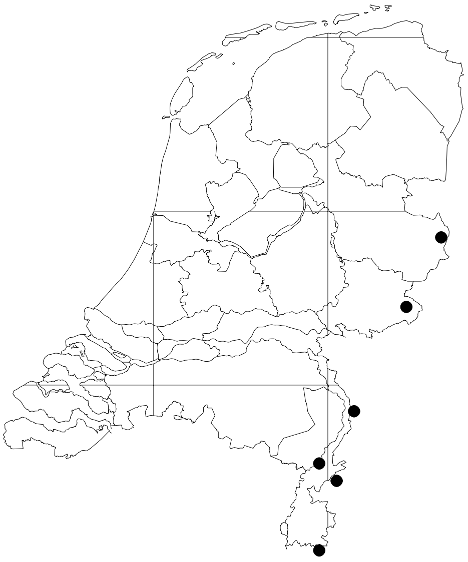

Figure 4
Dutch distribution of *Polymerus holosericeus* (not recorded since 1955).

Table 2
Heteroptera not recorded from The Netherlands since 1960 (see Aukema 1989): year of last record and number of 10 km squares occupied (N).

Family/species	**last record**	**N**
Saldidae (2)		
Chartoscirta elegantula (Fallén, 1807)	1958	3
Salda morio Zetterstedt, 1838	1918	2
Tingidae (4)		
Acalypta musci (Schrank, 1781)	<1943	1
Copium clavicorne (Linnaeus, 1758)	1913	1
Galeatus maculatus (Herrich-Schaeffer, 1838)	<1884	1
Physatocheila costata (Fabricius, 1794)	1951	3
Miridae (9)		
Brachycoleus pilicornis (Panzer, 1805)	1953	1
Capsodes gothicus (Linnaeus, 1758)	1911	1
Closterotomus biclavatus (Herrich-Schaeffer, 1835)	1948	1
Dicyphus constrictus (Boheman, 1852)	1910	1
Globiceps sphaegiformis (Rossi, 1790)	1924	2
Hadrodemus m-flavum (Goeze, 1778)	1949	6
Halticus saltator (Geoffroy, 1785)	1948	5
Pinalitus atomarius (Meyer-Dür, 1843)	1953	1
Polymerus holosericeus (Hahn, 1838)	1955	6
Anthocoridae (1)		
Dysepicritus rufescens (A. Costa, 1847)	1937	1
Cimicidae (2)		
Cimex columbarius Jenyns, 1839	1938	5
Cimex dissimilis (Horváth, 1910)	1940	5
Reduviidae (2)		
Phymata crassipes (Fabricius, 1775)	1890	1
Pygolampis bidentata (Goeze, 1778)	1958	6
Aradidae (1)		
Aradus corticalis (Linnaeus, 1758)	1910	2
Lygaeidae (10)		
Drymus pilicornis (Mulsant & Rey, 1852)	1942	2
Emblethis verbasci (Fabricius, 1803)	1944	2
Geocoris ater (Fabricius, 1787)	<1878	1
Geocoris megacephalus (Rossi, 1790)	1902	3
Lasiosomus enervis (Herrich-Schaeffer, 1835)	1956	3
Megalonotus emarginatus (Rey, 1888)	1951	4
Lygaeus equestris (Linnaeus, 1758)	1935	2
Raglius alboacuminatus (Goeze, 1778)	1951	2
Spilostethus saxatilis (Scopoli, 1763)	<1884	1
Tropidophlebia costalis (Herrich-Schaeffer, 1850)	1943	2
Stenocephalidae (1)		
Dicranocephalus agilis (Scopoli, 1763)	1955	4
Coreidae (2)		
Arenocoris waltlii (Herrich-Schaeffer, 1834)	1892	3
Gonocerus juniperi Herrich-Schaeffer, 1839	1951	7
Cydnidae (1)		
Cydnus aterrimus (Forster, 1771)	1951	1
Scutelleridae (2)		
Eurygaster austriaca (Schrank, 1776)	1935	9
Phimodera humeralis (Dalman, 1823)	1941	5
Pentatomidae (2)		
Eurydema ventralis Kolenati, 1846	1893	1
Palomena viridissima (Poda, 1761)	1952	26

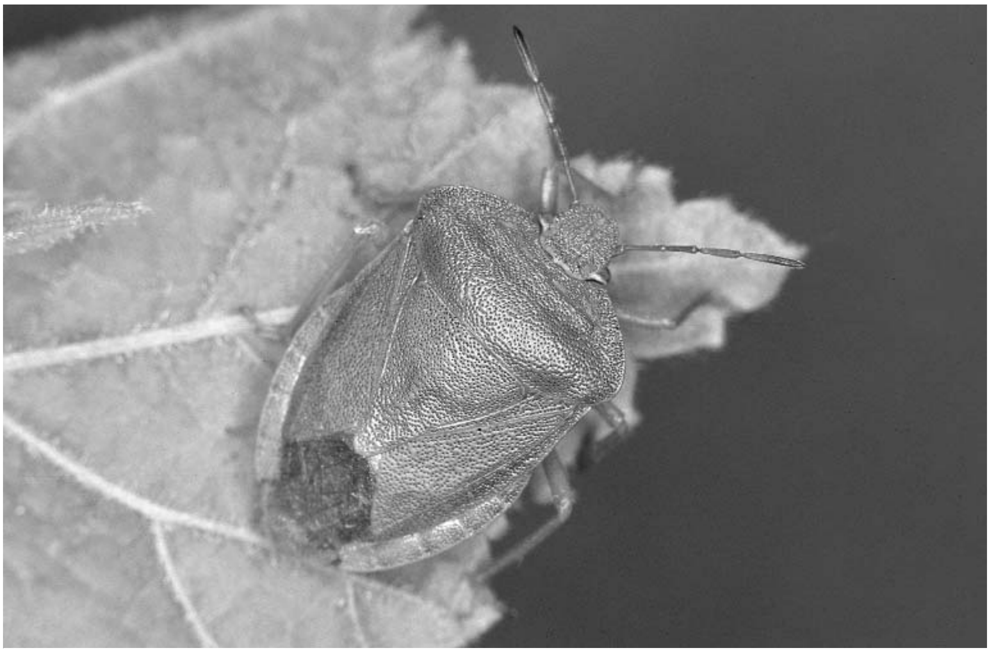

Figure 5
Palomena viridissima. Photo E. Wachmann, Berlin.

locality along the river Maas where they were found was destroyed by gravel winning activities (Aukema 1994). *Copium clavicorne* is only known from herbarium material of its foodplant *Teucrium chamaedrys* collected in 1913 on the former St. Pietersberg, dug down for cement production (Werner 2001). Many of the species

Table 3
Heteroptera not recorded since 1980. N: number of 10 km squares (see Aukema 1989).

Family/species	**Year**	**N**
Dipsocoridae (1)		
Cryptostemma waltli (Fieber, 1860)	<1967	6
Miridae (4)		
Amblytylus brevicollis Fieber, 1858	<1962	2
Bothynotus pilosus (Boheman, 1852)	<1966	5
Deraeocoris punctulatus (Fallén, 1807)	<1968	22
Stenodema virens (Linnaeus, 1767)	<1974	24
Anthocoridae (1)		
Anthocoris visci Douglas, 1889	<1973	4
Cimicidae (1)		
Cimex pipistrelli Jenyns, 1839	<1977	3

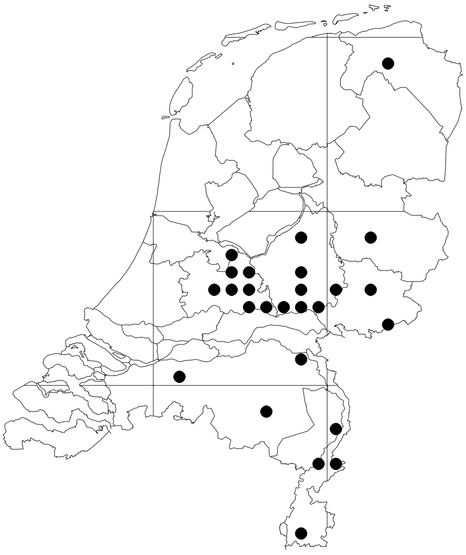

Figure 6
Dutch distribution of *Palomena viridissima* (not recorded since 1952).

Table 4
Heteroptera recorded in The Netherlands before 1960 and after 1980 only. N: number of 10 km squares.

Family/species	**before 1960**		**after 1980**		**reference(s)**
	Year	**N**	**Year**	**N**	
Saldidae (1)					
Saldula c-album (Fieber, 1859)	<1949	2	>1983	1	Aukema 1989
Tingidae (2)					
Lasiacantha capucina (Germar, 1837)	<1951	1	>1994	1	Aukema et al. 1997
Oncochila simplex (Herrich-Schaeffer, 1830)	<1955	2	>1981	3	Aukema 1989; unpubl.
Miridae (7)					
Acetropis gimmerthalii (Flor, 1860)	<1878	1	>1989	11	Aukema & Hermes 1990; unpubl.
Conostethus roseus (Fallén, 1807)	<1882	2	>1981	20	Aukema 1989; unpubl.
Heterocordylus leptocerus (Kirschbaum, 1856)	<1946	12	1985	1	Aukema 1989
Heterocordylus tumidicornis (Herrich-Schaeffer, 1835)	<1949	2	>2000	2	unpubl.
Hoplomachus thunbergii (Fallén, 1807)	<1951	19	>2001	2	unpubl.
Miridius quadrivirgatus (A. Costa, 1853)	<1956	2	>1992	3	Aukema 1993b; unpubl.
Psallus mollis (Mulsant & Rey, 1852)	1929	1	>1988	6	Aukema 1989; unpubl.
Microphysidae (1)					
Myrmedobia distinguenda Reuter, 1884	<1913	3	>1990	2	Aukema 1990c; unpubl.
Anthocoridae (1)					
Temnostethus longirostris (Horváth, 1909)	1951	1	>1987	11	Aukema 1989; unpubl.
Reduviidae (1)					
Empicoris baerensprungi (Dohrn, 1863)	<1926	2	>1987	4	Aukema 1989; unpubl.
Lygaeidae (6)					
Drymus pumilio Puton, 1877	<1960	3	2002	1	Aukema 1986; unpubl.
Emblethis griseus (Wolff, 1802)	<1951	1-2	>1983	1	Aukema 1989; unpubl.
Metopoplax ditomoides (A. Costa, 1847)	1948	1	>1994	27	Aukema et al. 1997; unpubl.
Pachybrachius luridus Hahn, 1826	<1951	8	>1983	7	Aukema 1989; unpubl.
Peritrechus lundii (Gmelin, 1790)	<1952	20	>1994	8	Hermes & Aukema 1998a; unpubl.
Scolopostethus grandis Horváth, 1880	1950	2	>1985	8	Aukema 2000
Berytidae (1)					
Berytinus montivagus (Meyer-Dür, 1841)	<1891	1	>1986	2	Aukema 1989; unpubl.
Coreidae (2)					
Bathysolen nubilus (Fallén, 1807)	<1953	7	>1982	4	Aukema 1989; unpubl.
Gonocerus acuteangulatus (Goeze, 1778)	<1950	3	>1998	6	unpubl.
Rhopalidae (1)					
Liorhyssus hyalinus (Fabricius, 1794)	1923	1	>1994	6	Aukema et al. 1997; unpubl.
Cydnidae (1)					
Sehirus morio (Linnaeus, 1761)	<1950	4	>1993	3	Hermes & Aukema 1998b; unpubl.
Pentatomidae (3)					
Carpocoris fuscispinus (Boheman, 1850)	<1951	5	>1996	2	Aukema et al. 1997; unpubl.
Chlorochroa pinicola (Mulsant & Rey, 1852)	<1953	13	>1983	17	Aukema 1989; unpubl.
Holcostethus sphacelatus (Fabricius, 1794)	<1909	2	1983	1	Aukema 1989

apparently reached the limits of their distribution, as for instance *Polymerus holosericeus* (fig. 4), a species only known from six squares along the eastern border.

The number of 'resident species' in 1960 was 545. Of these, seven species have not been recorded since 1980 (table 3), so altogether 46 species are not recorded since 1980. Some species of the lists probably are not extinct, but overlooked because they are very small (*Cryptostemma waltli*, living in wet moss), live in habitats that are sampled not frequently (*Anthocoris visci* on *Viscum album*) or

Figure 7
Deraeocoris flavilinea. Photo E. Wachmann, Berlin.

hardly ever (*Cimex columbarius* in dove-cotes, *C. dissimilis* and *C. pipistrelli* in bat roosts).

Most interesting are the three species that were once well established (recorded from more than 20 10 km squares) and disappeared without any obvious cause: the predatory mirid *Deraeocoris punctulatus*, the grass feeding mirid *Stenodema virens* and the polyphagous phytophagous pentatomid *Palomena viridissima* (figs. 5, 6).

On the other hand 27 species that were not recorded between 1960 and 1980 were rediscovered since 1980 (table 4). Most of these species remained rare, but five of them increased remarkably: *Acetropis gimmerthalii*, *Chlorochroa pinicola*, *Conostethus roseus*, *Metopoplax ditomoides* and *Temnostethus longirostris*. Species that obviously suffered significant losses, are *Heterocordylus leptocerus* and *Hoplomachus thunbergii*, and to a lesser degree *Peritrechus lundii*.

New arrivals

Since 1980, 27 species were discovered for the first time in the Netherlands (table 5). They can be classified as overlooked species, successful

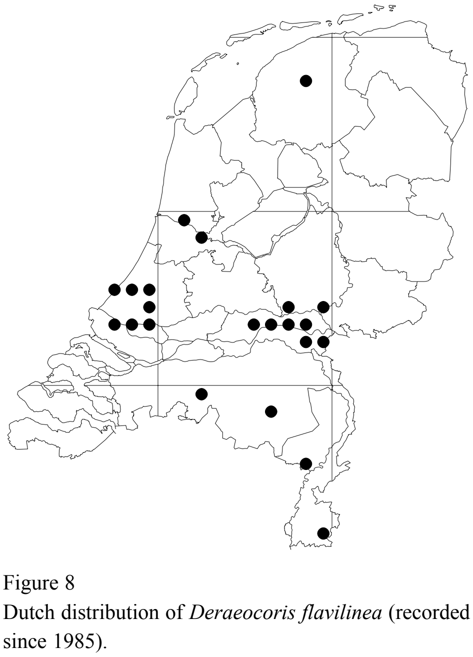

Figure 8
Dutch distribution of *Deraeocoris flavilinea* (recorded since 1985).

Figure 9
Metopoplax ditomoides. Photo E. Wachmann, Berlin.

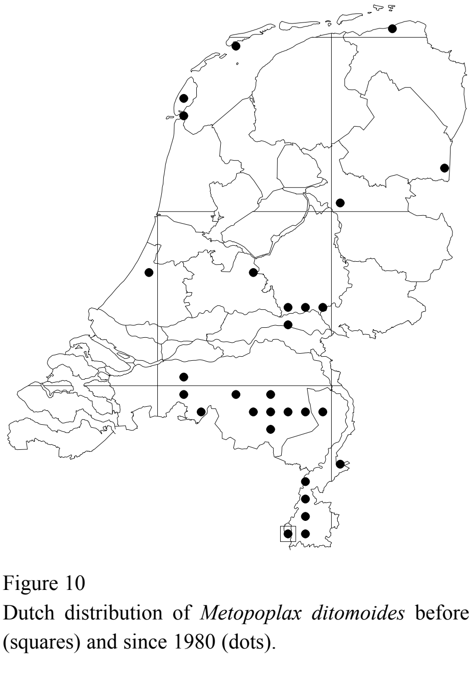

Figure 10
Dutch distribution of *Metopoplax ditomoides* before (squares) and since 1980 (dots).

incidental introductions related to international transport or trade in plant material (passive dispersal), or species extending their range in a natural way (active dispersal).

Kleidocerys privignis, *Phoenicocoris modestus*, *Psallus assimilis* and *P. pseudoplatani* represent clear cases of overlooked species. *Kleidocerys privignis* lives in wet biotopes and feeds on seeds of *Alnus glutinosa*, especially in the southern part of the country. *Phoenicocoris modestus* lives early in the season exclusively on *Pinus sylvestris* and may have been confused with the much more commoner *P. obscurellus* (Fallén, 1829). *Psallus assimilis* and *P. pseudoplatani* live monophagous on *Acer campestre* and *A. pseudoplatanus*, respectively. The first one is rare and only found in the southern part of the province of Limburg, but the second one is more common and found in a large part of the country, even in the north.

Closterotomus trivialis, *Dichrooscytus gustavi*, *Orsillus depressus* and *Stephanitis takeyai* are examples of species introduced with plant material. The strictly Mediterranean *Closterotomus trivialis* only occurs on ornamental shrubs and trees in the city of The Hague. *Dichrooscytus gustavi* thus far was only found on cultivated

Table 5
Heteroptera recorded from The Netherlands since 1980 only. A: natural pathway (active dispersal); O: overlooked T: transport related pathway (passive dispersal). NN: number of 10 km squares, northern provinces (Friesland, Groningen and Drenthe); NW: ibid, western provinces (Noord-Holland, Zuid-Holland and Zeeland); NR: ibid, remaining 'continental' provinces.

Family/species	**source**	**category**	**Year**	**NN**	**NW**	**NR**
Corixidae (2)						
Cymatia rogenhoferi (Fieber, 1864)	Jansson 1995	A	>1991	-	-	3
Micronecta griseola Horváth, 1899	Aukema et al. 2000	A	>1999	3	-	4
Tingidae (1)						
Stephanitis takeyai Drake & Maa, 1955	Aukema 1996a	T	>1994	1	5	3
Miridae (11)						
Brachyarthrum limitatum Fieber, 1858	Aukema 1989	A	>1980	-	-	7
Brachynotocoris puncticornis Reuter, 1880	Aukema 1990a	A	>1989	-	1	7
Closterotomus trivialis (A. Costa, 1853)	Aukema 1999	T	>1998	-	1	-
Conostethus venustus (Fieber, 1858)	Aukema 1989	A	>1980	1	13	22
Deraeocoris flavilinea (A. Costa, 1862)	Aukema 1989	?	>1985	2	7	15
Dichrooscytus gustavi Josifov, 1981	Aukema 1990b	T	>1990	-	1	4
Phoenicocoris modestus (Meyer-Dür, 1843)	Aukema 1990b	O	>1990	-	-	3
Psallus assimilis Stichel, 1956	Aukema 1989	O	>1985	-	-	3
Psallus pseudoplatani Reichling, 1984	Aukema 1989	O	>1985	2	4	6
Psallus punctulatus Puton, 1874	Aukema 1990b	A	>1990	-	-	2
Reuteria marqueti Puton, 1875	Aukema 1989	A	>1987	-	1	5
Aradidae (1)						
Aradus signaticornis R.F. Sahlberg, 1848	Aukema 1989	A	>1985	-	-	2
Lygaeidae (6)						
Emblethis denticollis Horváth, 1878	Aukema 1996b	A	>1992	-	4	3
Holcocranum saturejae (Kolenati, 1845)	unpublished 2002	?	2002	-	-	1
Horvathiolus superbus (Pollich, 1781)	unpublished 2000	A	2000	-	-	1
Kleidocerys privignus (Horváth, 1894)	Aukema 1989	O	>1982	-	3	16
Nysius graminicola (Kolenati, 1845)	Aukema 1992	A	>1990	-	1	-
Orsillus depressus (Mulsant & Rey, 1852)	Aukema 1989	T	>1986	1	3	6
Coreidae (1)						
Coriomeris scabricornis (Panzer, 1809)	Aukema & Hermes 1992	A	>1987	-	-	7
Rhopalidae (1)						
Rhopalus tigrinus Schilling, 1829	Aukema 1993	A	>1992	5	2	10
Cydnidae (1)						
Tritomegas sexmaculatus (Rambur, 1839)	unpublished 2002	A	2002	-	1	-
Pentatomidae (3)						
Eurydema ornata (Linnaeus, 1758)	Aukema 1993	A	>1992	-	1	1
Rhaphigaster nebulosa (Poda, 1761)	unpublished 2001	A	>1997	-	-	1
Stagonomus pusillus (Herrich-Schaeffer, 1833)	unpublished 2000	A	>2000	-	-	3

Juniperus species in parks and gardens but not in natural *Juniperus* stands. *Orsillus depressus* is found mainly in parks and gardens on cultivated conifers like *Chamaecyparis* and *Thuja*, but since 2002 it was also found twice in natural *Juniperus* stands. *Stephanitis takeyai* was imported with its foodplant *Pieris japonica* from Japan and is spreading in private gardens.

Many of the other species have a more southern distribution in Europe and their arrival in the Netherlands is supposed to have resulted from active dispersal, most likely stimulated by global warming. This assumption is supported by the fact that almost all recently arriving species (24 of 27) have been found in the 'continental' provinces (table 5). Besides, these provinces contain most of the total number of occupied squares by these species (135 of 198).

For some species, however, the pathway of their arrival is not clear at all. The predatory mirid *Deraeocoris flavilinea* (fig. 7), for instance, was considered an Italian endemic till the early 1980s,

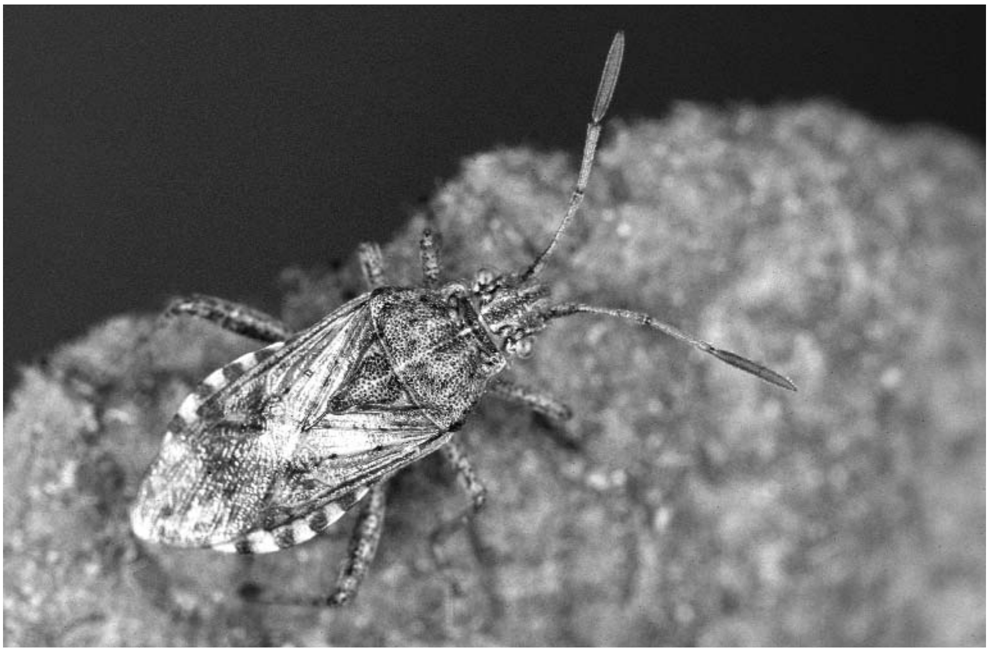

Figure 11
Stictopleurus punctatonervosus. Photo E. Wachmann, Berlin.

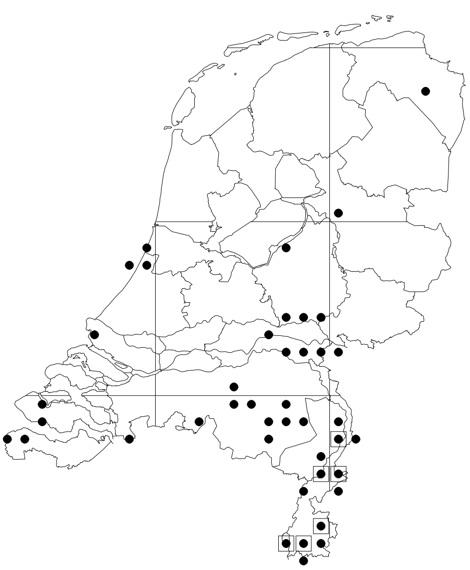

Figure 12
Dutch distribution of *Stictopleurus punctatonervosus* before (squares) and since 1980 (dots).

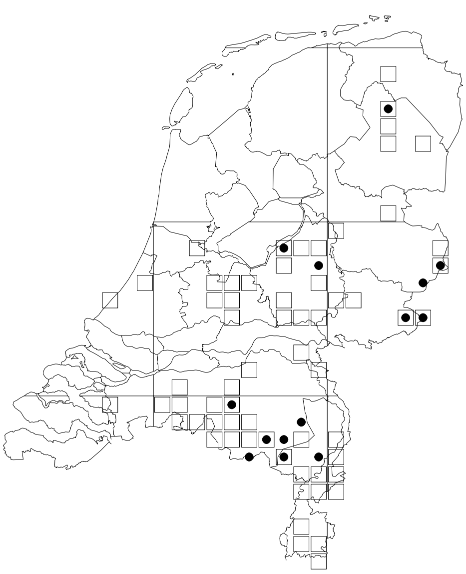

Figure 13
Dutch distribution of *Aquarius najas* before (squares) and since 1980 (dots).

when it appeared in France and successively showed up in more West-European countries, including England. It may have spread by flight, but the possibility that it was transported at least partly as eggs inserted in plant tissue cannot be ruled out. In the Netherlands it was recorded for the first time in 1985 and now there are 62 records from 20 squares (fig. 8). The lygaeid *Holcocranum saturejae* has a South European/Mediterranean distribution and feeds on *Phragmites australis*. So it may have been transported with thatch imported for roofing of houses. The Mediterranean mirid *Conostethus venustus*, usually found on *Matricaria*, most likely arrived by active dispersal along the coasts of the Atlantic and the English Channel and colonised Central-Europe along the river valleys from the northwest (Aukema 1988). It was recorded for the first time in 1980 and at present it was recorded 98 times from 34 squares distributed over a large part of the country.

Collection material of *Copium clavicorne*, *Megalonatus emarginatus*, *Nysius cymoides* and *Rhyparochromus vulgaris*, although discovered after 1989 (table 1), has been overlooked, and consequently these species are not included as new arrivals.

Range changes of resident species

Since a quantitative approach of range changes was not appropriate because of differences in sampling intensity in time and place, only some illustrative examples are given.

Increasing ranges since 1980

Micronecta scholtzi (Fieber, 1860) was recorded 19 times before 1980 (ten squares) and 129 times since 1980 (93 squares) and spread to the northeast with new records in the provinces of Drenthe, Friesland and Overijssel and even reaching the West-Frisian island Ameland. One of the possible causes of the increase of both the number of records and its range may be the increase of suitable biotopes (larger water bodies) during the last decades as a result of sand or gravel extraction for construction purposes.

Metopoplax ditomoides (fig. 9) was recorded once in 1948 from the province of Limburg. It was rediscovered in the same province in 1994 and recorded 46 times (29 squares) since (fig. 10). With the exception of Zeeland it reached all provinces and was even recorded from the West-Frisian islands Texel and Terschelling.

Stictopleurus abutilon (Rossi, 1790) was recorded 45 times before 1980 (15 squares) in the central and southern part of the country. Since 1980 there are 82 records (35 squares) and the species extended its range towards the north with records in the provinces of Drenthe, Friesland and Groningen, also reaching the West-Frisian Islands Texel and Terschelling.

Stictopleurus punctatonervosus Goeze, 1778 (fig. 11) was known before 1980 only from the province of Limburg (24 records, seven squares). Since 1980 139 records (42 squares) were listed and a considerable extension of its range towards the west and the north was registered (fig. 12) with records in the provinces of Noord-Brabant, Zeeland, Zuid-Holland, Noord-Holland, Gelderland, Overijssel en Groningen.

Declining ranges since 1980

Aquarius najas (De Geer, 1773) was a rather common species of small rivers and springs before 1980 (fig. 13: 124 records, 64 squares). Since 1980 it decreased considerably with only 24 records (12 squares) remaining (fig. 13). It disappeared completely from the western and central part of the country and in the north one population remained. Water pollution and a low dispersal power (macropters are very rare in Dutch populations) are thought to be responsible for this drastic decline.

Discussion

The vast majority of the changes since 1980 in the Dutch Heteroptera fauna known to have occurred consists of new arrivals or increasing species. This picture does not stand alone since, interestingly, the same trend was observed in British Heteroptera by Kirby et al. (2001) and not surprisingly a fair number of the same species is involved. Examples of species showing similar patterns and listed by Kirby et al. as ‘recently arrived, established and perhaps expanded in range’ are *Deraeocoris flavilinea*, *Dichrooscytus gustavi*, *Emblethis denticollis*, *Liorhyssus hyalinus*, *Metopoplax ditomoides*, *Nysius graminicola*, *Orsillus depressus*, *Stictopleurus abutilon* and *Stictopleurus punctatonervosus*. Not all Dutch new arrivals have reached Great Britain yet, but some certainly will, and *Stephanitis takeyai* already has. As in the Netherlands in Great Britain the number of new arrivals associated with introduced plants is relatively small: apart from *S. takeyai* only three species are listed by Kirby et al. (2001), of which only *Orsillus depresses* was added to the Dutch fauna as well.

The number of 27 species 'rediscovered' since 1980 after having not been recorded between at least 1960 and 1980 is rather large and shows that one has to be very careful using terms like 'extinct' or 'new arrival'. In a group like Heteroptera, with only a few active collectors at a time, species may be overlooked and thus remain 'rare' or 'obscure', especially when their habitat or foodplants are not or badly known. Good examples are *Acetropis gimmerthalii* and *Conostethus roseus*. *A. gimmerthalii* was collected only once in or before 1878 till its rediscovery in 1989, when it became clear that it lives early in the season exclusively on *Anthoxanthum odoratum*. Since then the species was taken at many localities (table 5). *Conostethus roseus* was collected twice in 1882 or earlier before its rediscovery on *Corynephorus canescens* on blowing sands and other sandy habitats in 1981, where it appeared to be not rare early in the season (table 5).

Conclusions

Since 1960, 571 (93.6%) of the Dutch Heteroptera species were recorded and 517 of them were recorded between 1960 and 1980. Since 1980, seven species were not recorded, 27 species were rediscovered and 27 new species were recorded. Consequently, the turnover of the Dutch Heteroptera fauna since 1980 can be estimated as 10.7% (61 out of 571 species). Moreover, the new arrivals (27) outnumber the extinctions (seven) by far. The possible causes of this turnover are not clear in all cases, but habitat changes, international trade and global warming are considered to be major causes. Turnover on a local scale, however, has to be considered a natural process as well, resulting from local extinctions and (re)colonisations.

Concerning changes in occurrences of resident species there is a need for better methods eliminating the influence of differences in collecting effort in time and space.

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Changes in ranges of hoverflies in the Netherlands in the 20th century (Diptera: Syrphidae)

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Abstract

In July 2001 the database of the Netherlands Syrphidae Recording Scheme contained approximately 200 000 records of Syrphidae. This database was used to examine changes in the hoverfly fauna of the Netherlands during the 20th century. The dataset was divided into two parts, before and since 1988, containing equal numbers of records. This revealed that there is a significant increase in the distribution of hoverfly species with saproxylic larvae. Probably this is a consequence of the changes in woodland management that have taken place in the past 20 years. Another result of the trend analysis is the conclusion that there is a high proportion of southern species among the increased species. A likely explanation for this is the change in climate in the past 20 years.

Of a total number of 317 species, 29% increased, 40% remained stable and 31% has decreased. Eight species have increased strongly and 22 species show a strong decline. The causes of the strong trends are often unclear, but seem to be very different from species to species.

Key words: Syrphidae, trends, Netherlands, saproxylic species, climate change.

Introduction

The Netherlands Syrphidae Recording Scheme has built up a database of approximately 200 000 records of Syrphidae (July 2001). These records cover all parts of the country and the oldest date back to the 19th century. This extensive database offers the possibility to acquire more knowledge of the changes in distribution and abundance of hoverfly-species in the Netherlands. Which species have decreased and which have increased? Is there a detectable general trend among different ecological species groups?

The construction of the database started in the 1980s. Aat Barendregt gathered all records of *Anasimyia* Schiner, 1864, *Helophilus* Meigen, 1822 and *Parhelophilus* Girschner, 1897 present in Dutch collections. In the 1980's and early 1990's *Brachyopa* Meigen, 1822, *Epistrophe* Walker, 1852, *Melangyna* Verrall, 1901 and *Platycheirus* Lepeletier & Serville, 1828 followed. In 1998 the Nederlandse Jeugdbond voor Natuurstudie, European Invertebrate Survey – The Netherlands and the Nederlandse Entomologische Vereniging started the Netherlands Syrphidae Recording Scheme. All digitally available records of private collectors were added to the database. This resulted in the publication of a provisional atlas of the Dutch Syrphidae, which was based on approximately 100 000 records (NJN 1998).

In July 2001 all the records in the Zoological Museum Amsterdam (ZMAN) and most of the smaller public collections were included in the database. Besides, many more records of private collectors were included (both collection and field data). The collection of the National Museum of Natural History Leiden (RMNH) had not yet been included in the database at that time. The contents of the database of July 2001 is summarized in table 1.

Methods

Calculation of trends

The data are divided into two periods: before 1988 and 1988-2000. Both the number of records and the number of investigated 5 km squares is approximately equal in both periods. Therefore it is not necessary to compensate for differences in recording intensity. Figure 1 shows that the spatial distribution of the records is similar in both periods.

Table 1
Summary of the contents of the Dutch Syrphidae database of July 2001.

	total	**before 1988**	**1988-2000**
number of records	194 942	93 505	101 437
number of investigated 5 km squares	1437	1239	1136
number of species	317	303	292

For each species, we calculated the relative abundance (RA) in both periods as follows:

$$RA = \frac{\text{(number of squares in which a species is recorded)}}{\text{number of investigated squares}} \times 100\ \%$$

The number of investigated squares is defined as the number of 5 km squares in which at least one hoverfly species is recorded.

The advantage of using the number of squares (instead of the number of records) is that this method is less sensitive for differences in the collecting behaviour of entomologists, for some of them collect almost every specimen they encounter, while others only take one or two. Besides, there is the effect of the considerably larger proportion of field observations in recent years, which results in a larger number of records of common species. This effect is very much reduced by basing the analysis on 5 km squares. According to their relative abundances, we assigned the species to 10 categories of abundance, both in the first and in the second period (table 2). The trend of each species was determined by assessing the shifts in categories between the periods (table 3).

Figure 1
Distribution of records of Syrphidae in the Netherlands before 1988 (squares) and in 1988-2000 (dots).

Statistics

The χ^2-tests were conducted by the computer program Microsoft Excel 97.

Ecological groups

The species are divided into four ecological groups: predatory species (Pr, n = 147), phytophagous species (Ph, n = 50), saprophagous species associated with wood (saproxylic species) (Sx, n = 55) and (semi-)aquatic saprophagous species (Aq, n = 61). This division is based on information in Rotheray (1993).

Northern and southern species

For each species, we determined the distributional borders in Europe. We did this by considering distributional data from the Netherlands and all surrounding countries (Ball & Morris 2000, NJN 1998, Speight 2001, Torp 1994, Verlinden 1991). Southern species are defined as species of which the northern limit of their range runs through the Netherlands. We calculated the proportion of northern and southern species among the increased species of all four ecological groups.

Results

Of a total number of 317 species, 29% increased, 40% remained stable and 31% has decreased, as shown in figure 2. The trends within the four recognized ecological groups are shown in figure 3a-d. To test whether the differences in the

Table 2
Categories of abundance (COA), indicating the percentage of investigated 5x5 km squares in which a species has been found.

COA	**maximum percentage of investigated 5x5 km squares**
0	0 %
1	0.39 %
2	0.78 %
3	1.56 %
4	3.13 %
5	6.25 %
6	12.5 %
7	25 %
8	50 %
9	100 %

Table 3
Explanation of trend categories, based on the shift in categories of abundance between the two considered periods.

trend category	**shift in category of abundance**
strong decrease	- 2 or more COA
decrease	- 1 COA
stable	no shift in COA
increase	+ 1 COA
strong increase	+ 2 or more COA

proportions of trend categories between these groups are statistically significant, χ^2-tests have been conducted (table 4). This revealed that only the observed increase of saproxylic species can not be attributed to coincidence ($p < 0.05$). The proportions of the trend categories within the other three ecological groups do not differ from the proportion among the total species group.

Several examples can be given of species belonging to the saproxylic species group that in recent years have appeared in regions where they had never been seen before, despite long term recording: *Brachyopa pilosa* Collin, 1939, *Brachypalpus laphriformis* Macquart, 1834, *Criorhina floccosa* (Meigen, 1822), *C. pachymera* Egger, 1858, *Temnostoma bombylans* (Fabricius, 1805), *T. vespiforme* (Linnaeus, 1758) and *Xylota sylvarum* (Linnaeus, 1758). Most of these are large, easily detectable and identifiable species, which must have been as conspicuous before 1988 as they are now. Besides, their forest habitat has always attracted hoverfly recorders, so a strong effect of differences in recording intensity seems improbable.

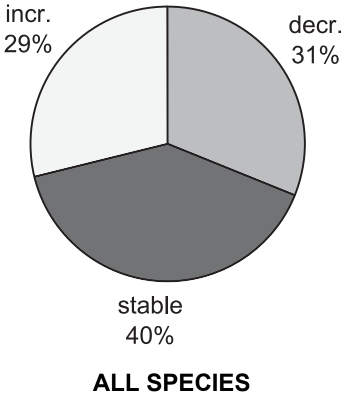

Figure 2
Proportions of trend categories among 317 species of Syrphidae.

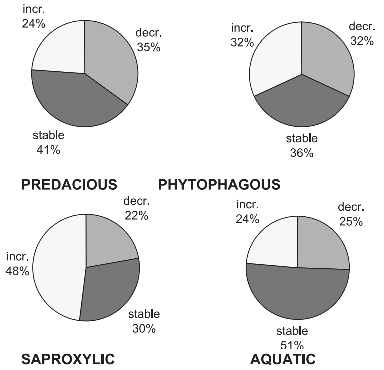

Figure 3
Proportions of trend categories among the four ecological groups of Syrphidae: predacious species (n = 146); phytophagous species (n = 50); saproxylic species (n = 54); (semi-)aquatic species (n = 59).

Table 4
Results of χ^2-tests of the observed proportions of trend categories within the four recognized ecological groups of hoverfly species (obs. = observed number, exp. = expected number). The only significant p-value ($p < 0,05$) is printed in bold.

	all n=317	predacious species n=146			phytophagous species n=50			saproxylic species n=54			(semi)aquatic species n=59		
		obs.	**exp.**	**p**	**obs.**	**exp.**	**p**	**obs.**	**exp.**	**p**	**obs.**	**exp.**	**p**
Increased species compared with stable and decreased species													
increased	92	35	42.4	0.179	16	14.5	0.643	26	15.7	**0.002**	14	17.1	0.370
stable / decreased	225	111	103.6		34	35.5		28	38.3		45	41.9	
Decreased species compared with stable and increased species													
decreased	99	51	45.6	0.335	16	15.6	0.907	12	16.9	0.153	15	18.4	0.336
stable / increased	218	95	100.4		34	34.4		42	37.1		44	40.6	
Stable species compared with decreased and increased species													
stable	126	60	58.0	0.739	18	19.9	0.588	16	21.5	0.129	30	23.5	0.081
decreased / increased	191	86	88.0		32	30.1		38	32.5		29	35.5	

Strongly increased species

A few species show a strong increase of two or more categories of abundance. These species are listed in table 5. This group of species is ecologically very heterogeneous. There seems to be no general factor which explains the increase of all species together. For some of them, the ‘increase’ might be explained by differences in recording effort. This could be true for *Sphegina verecunda*, a species with a specific habitat preference which is easily overlooked. In other species however, this is certainly no satisfactory explanation. *Cheilosia caerulescens*, for instance, is a species with phytophagous larvae which was first recorded in the Netherlands in 1986. Since then there have been numerous records, almost all of them from gardens. The increase of this easily identifiable species is probably caused by the increase in the use of its host plant, *Sempervivum*, in rooftop gardens in the Netherlands (Stuke 2000).

Strongly decreased species

A total number of 22 species has strongly decreased in the Netherlands (table 6), three of which have disappeared from the Netherlands. (Please note that there are several other species which have only been recorded before 1988 and probably have disappeared. However, these species are not considered as ‘strongly decreased’, because their number of records is too low.) Among these strongly decreased species some interesting groups of species which share certain ecological features can be recognized.

1. Coastal species (species which in the Netherlands seem to depend on areas with brackish water): *Lejops vittata*, *Platycheirus immarginatus*. The amount of suitable habitat has strongly declined in the Netherlands, especially since the former ‘Zuiderzee’ (now called ‘IJsselmeer’) was dammed in 1932. Another species belonging to this ecological group, *Eristalinus aeneus*, has remained stable in the Netherlands.
2. Bog species: *Anasimyia lunulata*, *Eristalis anthophorina*, *Parhelophilus consimilis*.
3. Fungus feeding species: *Cheilosia longula*, *C. scutellata*. These species presumably have decreased because the fungi in which they breed have decreased as well. In recent years both the fungi as the *Cheilosia*-species seem to recover from their decline.

Northern and southern species

Only three hoverfly species have been identified as ‘northern species’: *Eristalis anthophorina* (Fallén, 1817), *Eupeodes lundbecki* (Soot-Ryen, 1946) and *Neocnemodon verrucula* (Collin, 1931). All three species have decreased in the Netherlands.

The group of ‘southern species’ contains 58 species. A comparison with the non-southern species

Table 5
Strongly increased species.

species	**relative abundance before 1988**	**relative abundance 1988-2000**	**remarks**
Brachyopa pilosa Collin, 1939	2.3 %	7.0 %	this species now occurs in western parts of the Netherlands, where it has not been found before, despite many records of other *Brachyopa*-species
Cheilosia caerulescens (Meigen, 1822)	0.1 %	1.8 %	apparently this species rapidly colonized the gardens in which the host plant *Sempervivum* is growing (Stuke 2000)
Cheilosia illustrata (Harris, 1780)	2.6 %	10.2 %	cause of increase unclear
Epistrophe melanostoma (Zetterstedt, 1843)	2.7 %	8.9 %	southern species that benefits from climate change?
Eristalis picea (Fallén, 1817)	1.3 %	4.7 %	this is probably no real increase, but the result of specific recording efforts
Pipizella annulata (Macquart, 1829)	0.3 %	1.1 %	southern species that benefits from climate change?
Sphegina sibirica Stackelberg, 1953	0.0 %	1.4 %	increase all over Europe (Van der Ent & Jansen 1988)
Sphegina verecunda Collin, 1937	0.1 %	1.2 %	this is probably no real increase, but the result of specific recording efforts

(table 7) shows that the increase among southern species is 6 % larger than among non-southern species ($p = 0.04$).

Table 8 gives the proportion of southern species among the increased species of all four different ecological groups. None of these proportions is significantly different from the proportion of southern species in the total group of increased species. This suggests that climate change is not a more important factor in the increase of one ecological group than it is in the others.

Discussion

Conclusions

Two of the calculated results proved to be significant when tested with a χ^2–test. These results support the following conclusions:

- Hoverfly species with saproxylic larvae have become more widespread in the Netherlands after 1988.
- There is a relatively large group of southern species among the hoverflies that have increased after 1988.

The increase of saproxylic species

The most likely explanation for the increase of many saproxylic species is the change in woodland management in combination with the increased age of the Dutch forests. This has been suggested earlier by Barendregt (1992) and Reemer et al. (2000). In the management of

Table 6
Strongly declined species.

species	**relative abundance before 1988**	**relative abundance 1988-2000**	**disappeared**
Anasimyia lunulata (Meigen, 1822)	1.5 %	0.2 %	
Cheilosia longula (Zetterstedt, 1838)	3.8 %	1.3 %	
Cheilosia scutellata (Fallén, 1817)	7.1 %	2.9 %	
Chrysotoxum octomaculatum Curtis, 1837	3.4 %	0.4 %	
Dasysyrphus friuliensis (van der Goot, 1960)	1.6 %	0.3 %	
Eristalis anthophorina (Fallén, 1817)	4.3 %	1.1 %	
Eumerus flavitarsis Zetterstedt, 1843	0.9 %	0.1 %	
Eumerus sabulonum (Fallén, 1817)	1.1 %	0.1 %	
Leucozona glaucia (Linnaeus, 1758)	4.6 %	1.0 %	
Lejops vittata (Meigen, 1822)	1.7 %	0.2 %	
Mallota fuciformis (Fabricius, 1794)	1.1 %	0.0 %	yes
Melangyna barbifrons (Fallén, 1817)	1.5 %	0.2 %	
Neocnemodon verrucula (Collin, 1931)	1.0 %	0.2 %	
Parhelophilus consimilis (Malm, 1863)	1.7 %	0.7 %	
Paragus tibialis (Fallén, 1817)	0.8 %	0.0 %	yes
Parasyrphus vittiger (Zetterstedt, 1843)	6.5 %	1.9 %	
Platycheirus immarginatus (Staeger in Zett., 1849)	4.0 %	0.9 %	
Platycheirus parmatus Rondani, 1857	1.1 %	0.4 %	
Psarus abdominalis (Fabricius, 1794)	1.1 %	0.0 %	yes
Sphaerophoria fatarum Goeldlin de Tiefenau, 1974	3.2 %	0.9 %	
Sphaerophoria philanthus (Meigen, 1822)	3.2 %	1.0 %	
Sphaerophoria taeniata (Meigen, 1822)	3.8 %	1.1 %	

Table 7
Proportions of trend categories within the groups of southern and non-southern species.

	number of stable / decreased species	**number of increased species**	**expected number of increased species**	**p**
southern species	38 (18 %)	20 (24 %)	15.1	
non-southern species	173 (82 %)	64 (76 %)	52.5	
total	211	84		
				0.04

Table 8
The proportion of southern species among the increased species of the four ecological groups of hoverflies.

	total number	**number and proportion of southern species**	**expected number of southern species**	**p**
increased total	92	20 (22 %)		
increased predacious (Pr)	36	11 (31 %)	7.8	0.2
increased phytophagous (Ph)	16	4 (25 %)	3.5	0.8
increased saproxylic (Sx)	26	4 (15 %)	5.7	0.4
increased aquatic (Aq)	14	1 (7 %)	3.0	0.2

forests, the tendency to remove all dead wood and ill trees gave way for the recent policy (since 1973) of leaving it in the forests. Besides, an important part of the Dutch forests is no longer in use for forestry. This is of great benefit to saproxylic insects.

Another explanation for the increase of saproxylic hoverflies could be a larger proportion of southern species among them in comparison with the other ecological groups. However, the results in table 8 show that this is probably not the case.

The increase of southern species

Probably the warmer climate during the last 20 years is responsible for the high proportion of southern species among the increased species. Another indication for this is the recent addition of several southern species to the list of Dutch hoverflies, like *Cheilosia soror* (Zetterstedt, 1843), *Chrysotoxum intermedium* Meigen, 1822, *Paragus quadrifasciatus* Meigen, 1822 and *Scaeva dignota* (Rondani, 1857) (Lucas 1992, NJN 1998, Smit et al. 2001a, b).

Trend calculation

We have used categories of abundance to get a better overview of the changes in distribution. However, the use of categories has some disadvantages. The most important disadvantage is that it makes a big difference whether the relative abundance of a species lies on one side of the category border or on the other. For instance, a species with a pre-1988 distribution of 1.6 % (COA 4) and a post-1988 distribution of 6.0 % (COA 5) has ‘increased’, whereas a species with a pre-1988 distribution of 3.1 % (COA 4) and a post-1988 distribution of 6.3 % (COA 6) has ‘strongly increased’ (for explanations of these categories see table 2 and 3).

For future research on the changes in the Dutch syrphid fauna, it would be better to use a trend calculation which is not based on categories but on an assessment of the relative change. A good alternative would be the method that has been used for the calculations in several red lists in the Netherlands (Odé 1999, Wasscher 1999). In these reports, the trend is calculated as follows (RA= relative abundance):

$$\text{trend} = \frac{(\text{RA in recent period} - \text{RA in historical period})}{\text{relative abundance historical period}} \text{ x } 100\ \%$$

Because this paper is a comprehensive version of our lectures on the international colloquium of EIS, we decided not to use another method in this paper but to stick to the calculations we made for the lectures. In the atlas of the Dutch hoverflies (in prep.) we will publish new results of trend calculations.

Future analyses

The data in the database of the Netherlands Syrphid recording scheme have not been collected by a systematic, standardized method. This makes it hard to analyse and interprete the data. Because of this and because of the discussed disadvantages of the methods we used, the analysis in this paper should be regarded as a first attempt to present a view on the changes in ranges and abundances of the syrphid fauna in the Netherlands. Within a couple of years, the database will contain much more data and the methods we will use for the analysis will be more refined. We hope to present the results of the next trend analysis in the atlas of the Syrphidae of the Netherlands which will appear within a couple of years.

It would be interesting to compare the changes in the Netherlands with the changes in other northwestern European countries. At present several people in different countries are working on distributional databases. In the near future a better analysis of distributional changes of European Syrphidae will be possible.

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Status of Dolichopodidae of the Flemish Red Data Book in the Netherlands (Insecta: Diptera)

Marc Pollet, Henk Meuffels & Patrick Grootaert

Abstract

The distribution and status of threatened and rare Flemish dolichopodid species in the Netherlands is investigated. Rarity classes are based on the percentage of sampled UTM 10 km squares with species records, in combination with the most recent capture date. The Dutch fauna comprises 244 species, 22 of which have presumably become extinct. About 52% of the 224 shared species with Flanders seem to be more common in the latter region. Among the 23 species that are more widespread in the Netherlands, saltmarsh-, heathland-inhabiting and riparian species are better represented than in the entire shared fauna. The observed faunal discrepancies might be related to regional differences in both habitat availability, topography and management.

Key words: Diptera, Dolichopodidae, Red Data Book, Flanders, The Netherlands, biodiversity.

Introduction

Dolichopodidae or long-legged flies are usually metallic greenish to bronze coloured with a body size of 1-10 mm. Only a few species feature non-metallic yellow, brown or black bodies. Their body is either stout or slender, sometimes midge-like but always somewhat compressed laterally. In general, long-legged flies prefer humid areas and many species can be found in large numbers especially in humid forests, humid heathland, saltmarshes, dune slacks and on banks of water bodies. Other species like *Medetera* and *Sciapus* species occur mainly on tree trunks and other vertical structures, whereas *Aphrosylus* species are confined to littoral rocks and *Thinophilus* species prefer wet sand or decaying seaweeds on beaches. Except for the leafmining *Thrypticus* larvae, both adult flies and larvae are predacious and feed on soft-bodied invertebrates.

Dolichopodidae meet all criteria – taxonomical, biological, biogeographical and logistic – to make this dipteran family an excellent agent for bio-indication (Pollet & Grootaert 1994). In order to actually use this taxon in nature conservation, a Red Data Book was recently generated for Flanders (Pollet 2000). Indeed, Red Data Books and Red Lists are considered as one of the most important and scientifically best founded instruments in the modern, offensive nature conservation management (Maes et al. 1995). Pollet (2000) shows that at present 9% of the species that are recorded from Flanders can be considered extinct, another 15% is seriously threatened while 33% is currently rare. Especially communities of saltmarsh habitats are endangered in Flanders, largely because of the scarcity of this habitat type.

Since the early 1970s, the second author systematically compiled all distribution records on dolichopodids in the Netherlands. Data were retrieved from the literature, specimens in the major Dutch museum collections were checked and during the past 30 years a large amount of new material was collected by him, Van Aartsen and other fellow dipterists. However, after the work of Meuffels (1974, 1978, 1981), no overall analysis of this data set had been carried out yet. In the present contribution, the dolichopodid fauna of Flanders is compared to the Dutch fauna with a focus on the threatened and rare Flemish species.

Material and methods

Distribution data until July 1997 were kindly provided by the second author and were converted into an Microsoft Access database. Unfortunately, additional data from recently updated files could not be incorporated in time so the overall comparison of the faunas is based on a summary table prepared by the second author and not on the raw dataset. However, in order to

Table 1
Overview of Red Data Book categories as defined in Pollet (2000).

Rarity	**Extinct**	**Very rare**	**Rare**	**Fairly rare**	**Common**
% sampled UTM 5 km squares	**0%**	**> 0- < 2%**	**2- < 5%**	**5- < 10%**	**>= 10%**
Trend (extent of decline)					
76-100%	0. Extinct	1. Critically endangered	2. Endangered	3. Vulnerable	A. In decline
51-75%	-	2. Endangered	2. Endangered	3. Vulnerable	A. In decline
26-50%	-	3. Vulnerable	3. Vulnerable	3. Vulnerable	A. In decline
≤ 25%	-	zZ. Very rare	Z. Rare	vZ. Fairly rare	N. Safe/at low risk

give an up-to-date account on the status of the threatened, very rare and rare Flemish species in the Netherlands, post-1997 data on the latter species were actually added to the database. Each distribution record consists of the following information: species, sampling locality, number of males and females, sampling date or period, collector or literature reference, collection and relevant remarks. All further information on sampling localities (like locality, toponym, province, UTM 10 km square) and species (full name, systematic position, conservation status in Flanders, habitat affinity) was retrieved from other databases or tables. In order to include as many records as possible in the analysis, lacking or partly lacking collecting dates were completed following the procedure by Pollet (2000). Evidently, only records from localities with a valid 10 km square were used.

The conservation status of a species is unequivocally reflected by its Red Data Book category, which is the combination of a rarity and trend criterion:

1. Species rarity is expressed as the absolute or proportional number of geographical entities (sampling sites, localities, UTM squares) where the species has recently been found. The final choice of approach and entities largely depends on the amount of data and the distribution of these data in time;
2. The trend criterion reflects the evolution of geographical distribution (or rarity estimates) over time but for practical reasons, is mostly assessed by comparing distributions between two time periods separated by the so-called pivot year.

In the case of the Red Data Book of Flanders (Pollet 2000, see table 1), UTM 5 km squares were selected as geographical entities as they comprise sufficiently detailed information on the geographical distribution in this region and, moreover, are not affected by the results of intensive sampling activities within a restricted area (which might, in contrast, largely increase the number of localities or sampling sites). On the other hand, 1980 was selected as pivot year as 1. the distribution of sampled squares was nearly equal between 1850-1980 (n = 171) and 1981-1997 (n = 167) and 2. since the early eighties of the last century, new collecting techniques (e.g. Malaise traps, water traps, emergence traps) were introduced in sampling campaigns in Belgium and largely replaced the traditional net sweeping. Coincidently, also the number of collected species was largely comparable between both time periods (214 in 1850-1980 versus 226 in 1981-1997).

The selection of a reliable pivot year proved to be impossible for the Dutch dataset as the current database did not contain all distribution records (see above). Moreover, even 1975, which split the distribution data in two comparable sets (with 242 10 km squares sampled until and 221 squares after 1975) was considered too artificial and therefore not sufficiently reliable as it was situated within the peak collecting activities of the second author and Van Aartsen in particular (1967-2000) who gathered most of the recent data. As a result, rarity of the Dutch species was determined in a slightly different way. Species with no distribution records since 1967 (= start of large scale sampling activities by Van Aartsen) are considered extinct in the Netherlands. For the remaining species, an overall (and not current!) rarity was calculated as the proportional number of 10 km squares in which the species has thus far been discovered (1853-2000) to the total number of squares sampled, regardless of any decrease in distribution over time. Analogous to Pollet (2000), the following rarity classes were distinguished:

- zZ (very rare): species found in < 2% of the sampled squares;
- Z (rare): species found in 2% - < 5% of the sampled squares;
- vZ (fairly rare): species found in 5 - < 10% of the sampled squares;
- A (common): species found in ≥ 10% of the sampled squares.

For reasons of comparability, Belgian and Flemish data sets were analyzed in exactly the same way.

The Dutch dataset yielded 7562 records with a unique combination of species, 10 km square and sampling year, and 7773 records uniquely defined by species, locality and sampling year. In comparison, the Belgian database comprises 9527 and 10 214 of these records respectively, whereas the Flemish database contains 7156 records of unique combinations of species, 5 km square and sampling year, and 7217 entries of species, locality and sampling year.

The null hypothesis for the comparison of Flemish and Dutch dolichopodid faunas states that each species is equally rare or common in both regions. Comparisons with the Belgian fauna are limited as no Red Data Book of dolichopodid flies of Belgium is available, and the southern part of Belgium houses a large number of (Central European) species that do not occur in the Netherlands.

Results

Dolichopodid flies are known from 333 of 480 Dutch 10 km squares which represents 69.4% of the area. In Belgium, slightly fewer (66.9%) squares were investigated, but sampling yielded considerably more species and records (see above).

Since 1853, 244 dolichopodid species have been discovered in the Netherlands, as compared to 260 in Flanders and 295 in Belgium (Pollet 2000), while 224 species are shared with Flanders. Ten species are exclusively recorded from the Netherlands (see table 2). *Chrysosoma exsul* (Parent, 1932) is a Neotropical species which was apparently introduced in greenhouses

Table 2

Overview of the rarity status of dolichopodid species in the Netherlands ranked according to Flemish Red Data Book categories.

	Rarity classes (NL)					**not known from NL**	**Total no. of species**
Red Data Book category (Fl)	extinct	very rare	rare	fairly rare	common		
0. Extinct in the wild	3	6	3	-	1	9	22
1. Critically endangered	1	2	6	1	-	-	10
2. Endangered	-	6	2	5	1	-	14
3. Vulnerable	1	4	3	6	1	1	16
zZ. Very rare	5	11	4	1	-	4*	25
Z. Rare	2	13	9	4	-	1	29
vZ. Fairly rare	-	8	10	11	3	1	33
?. Insufficiently known	1	11	3	2	1	20	38
N. Safe/At low risk	-	1	11	22	39	-	73
Not known from Flanders	4	6	-	-	-	-	10
Not known from Belgium	5	3	2	-	-	-	10
Total no. of species	22	71	53	52	46	36	280

* including the recently discovered *Neurigona lineata*

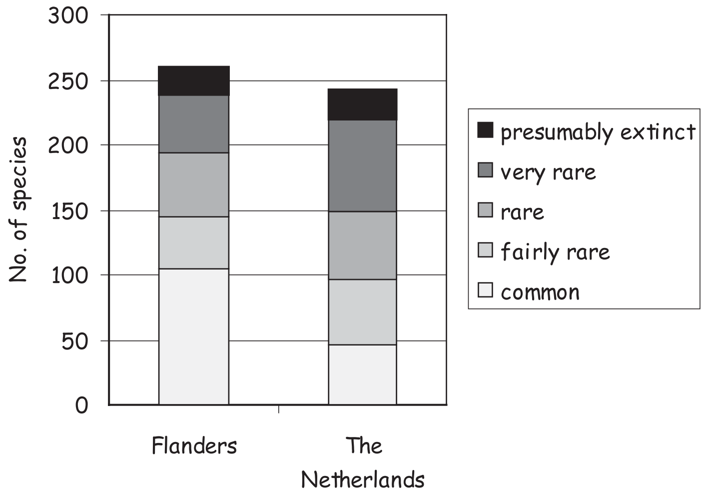

Figure 1
Species distribution over rarity classes.

in Amsterdam and Leiden and collected there during the late thirties and early forties of the last century. Of the other exclusively Dutch species, only *Medetera obscura* (Zetterstedt, 1838) and *Sciapus basilicus* Meuffels & Grootaert, 1990 were collected in fair numbers and in more than 2% of the sampled squares. All the remaining species are known from only one single or, at most, two specimens. Four species (*Acropsilus niger* (Loew, 1869), *Chrysosoma exsul*, *Dolichopus calinotus* Loew, 1871, *Medetera pinicola* Kowarz, 1877) have not been found since 1967 and must be considered extinct.

About 53% of all shared dolichopodid species seem to be significantly more widespread in Flanders than in the Netherlands (table 3). As can be seen in figure 1, about 40% of all Flemish species can be termed common, whereas the very rare, rare and fairly rare species occupy a comparable proportion of the fauna. The Dutch dataset shows a quite different composition in which very rare species with 29.1% (n = 71) are the major group. This discrepancy with the Flemish fauna is explained by a less productive sampling strategy and/or a strategy focused on rare species in special or protected habitats in the Netherlands. About 20% of the Dutch sampled squares have records of only one or two species as compared to 8.4% of the Flemish squares. Moreover, over half of the Flemish squares contain more than 20 species, whereas this species richness has been established in only about a quarter of the Dutch squares (fig. 2). Most Dutch species have been collected in Hilversum (n = 96) and Elsloo (n = 85) and adjacent localities, obviously favourite collecting sites of De Meijere and Meuffels, respectively.

Nine of the 22 currently extinct Flemish species have never been recorded from the Netherlands and of three other species, *Diaphorus winthemi* Meigen, 1824, *Dolichopus plumitarsis* Fallén, 1823 and *Tachytrechus ammobates* Haliday, 1851, only old Dutch records exist. The remaining species of RDB category ‘0’ still seem to occur in the Netherlands. Except for *Hercostomus germanus* (Wiedemann, 1817), all of these species are rare to very rare in the Netherlands, although some species can locally be abundant, like *Neurigona pallida* (Fallén, 1823) on the Sint-Pietersberg (province of Limburg) and *Hydrophorus balticus* (Meigen, 1824) on some of the Wadden Islands (Vlieland and Terschelling). In contrast to its apparent commonness (known of nine out of 12 Dutch provinces), *H. germanus* mainly occurs in dry inland habitats in the northern and central parts of the Netherlands. Despite the fact that suitable habitats seem to be present in the south as well, the

Table 3
Comparison of species rarity in Flanders and the Netherlands.

Relative distribution *	**No. of species**
Significantly more common in Flanders	118
Not significantly more common in Flanders	41
Equally common in Flanders and The Netherlands	41
Not significantly more common in The Netherlands	13
Significantly more common in The Netherlands	11
Total no. of shared species	224

* significant difference: χ^2 test, $p< 0.005$ or $p<0.010$; not significant difference: ≥ 1% of sampled UTM 10 km squares between both regions; equally common: difference of < 1% of sampled UTM 10 km squares.

species has been found only once after 1950 in the provinces of Noord-Brabant and Limburg. Both *H. germanus* and *Diaphorus hoffmannseggi* Meigen, 1830 are significantly more widespread in the Netherlands than in Flanders.

Only one 'Critically endangered' Flemish species, *Dolichopus latipennis* Fallén, 1823, seems to be currently extinct in the Netherlands despite the fact that during the first half of the 20th century this species was found in numbers in several localities in the province of Noord-Holland. Especially at Diemen, it seemed to be rather abundant. Five in Flanders critically endangered species seem to be more common in the Netherlands: *Dolichopus clavipes* Haliday, 1832, *Machaerium maritimae* Haliday, 1832, *Tachytrechus insignis* (Stannius, 1831), *Thinophilus flavipalpis* (Zetterstedt, 1843) and *T. ruficornis* (Haliday, 1838), the first two even significantly so. *Tachytrechus insignis* is mainly known from dune slacks whereas the other four species are strictly halophilous.

All 14 species of the RDB category 'Endangered' still occur in the Netherlands but the majority seems to be less common there except for *Sciapus longulus* (Fallén, 1823) and *S. laetus* (Meigen, 1838). Moreover, in contrast to its scattered distribution in Flanders, *S. longulus* has been sampled in 11 out of 12 provinces in the Netherlands and at some sites (e.g. Heerenveen,

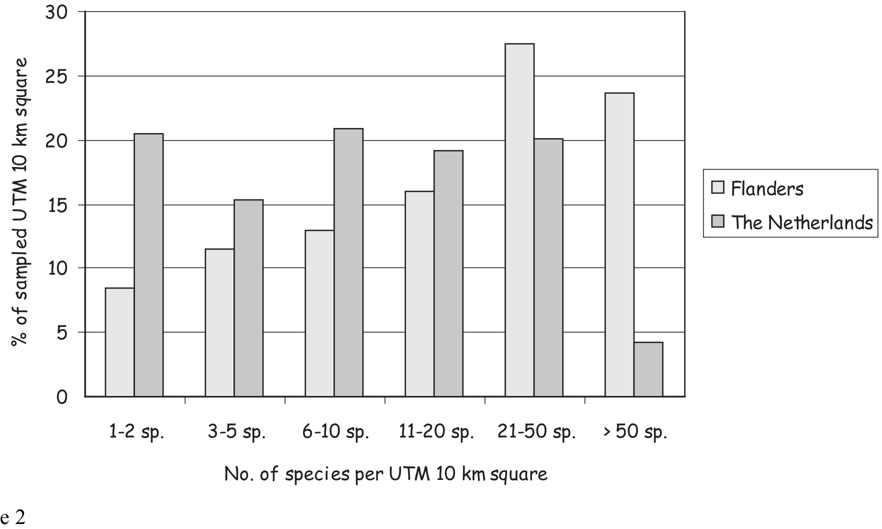

Figure 2
Distribution of species numbers over UTM 10 km squares in The Netherlands and Flanders.

province Limburg, and Pannerden, province Gelderland) even in fair numbers. Although less pronounced than in Flanders, in The Netherlands *Hercostomus nigripennis* (Fallén, 1823) also shows a recent, though not significant, decline of 30% since 1975 (χ^2= 2.05, n.s.).

Chrysotus monochaetus Kowarz, 1874 is the only 'Vulnerable' Flemish species which seems to be currently extinct in the Netherlands as its only capture dates from 1918 (Denekamp, province of Overijssel). *Syntormon aulicum* (Meigen, 1824) on the other hand has not yet been recorded from the Netherlands, although it has recently been detected in several reedmarsh sites close to the Dutch border. All other species are equally rare or even rarer in the Netherlands except for *Dolichopus migrans* Zetterstedt, 1843 and *Hydrophorus oceanus* (Macquart, 1838) which are confined to dry forests on sandy soils and saltmarshes, respectively.

Of the 24 'Very rare' Flemish species, three are unknown to the Netherlands (*Campsicnemus pusillus* (Meigen, 1824), *Dolichopus apicalis* Zetterstedt, 1849, *Hercostomus parvilamellatus* (Macquart, 1827)) while five have not been collected there since 1967 (*Lamprochromus strobli* Parent, 1925, *Syntormon metathesis* (Loew, 1850), *S. tarsatum* (Fallén, 1823), *Telmaturgus tumidulus* (Raddatz, 1873), *Thrypticus smaragdinus* Gerstäcker, 1864) and should be considered extinct. However, all are of modest size and might just have been overlooked. Moreover, they all have even been discovered only recently in Flanders (since 1981). Three species are more common in the Netherlands: *Dolichopus rupestris* Haliday, 1833, *Hydrophorus nebulosus* Fallén, 1823 and *Rhaphium nasutum* (Fallén, 1823).

Medetera muralis Meigen, 1824 and *Syntormon monile* (Haliday, 1851) are the only 'Rare' Flemish species with only old Dutch records: the former was most recently collected in 1939, the only record of the second species dates from 1896! No Dutch records are present for *Achalcus phragmitidis* Pollet, 1996 despite its occurrence in reedmarshes in 'Het Meetjeslandse Krekengebied' near the Dutch border. Only the saltmarsh-inhabiting *Dolichopus diadema* Haliday, 1832 appears to be more widespread in the Netherlands than in Flanders.

Figure 3 compares species that are shared by Flanders and the Netherlands with species that are more common in the Netherlands from an ecological point of view. Saltmarsh species and, to a lesser extent, riparian and heathland-inhabiting species are better represented in the Netherlands than in the shared fauna. In contrast, not a single

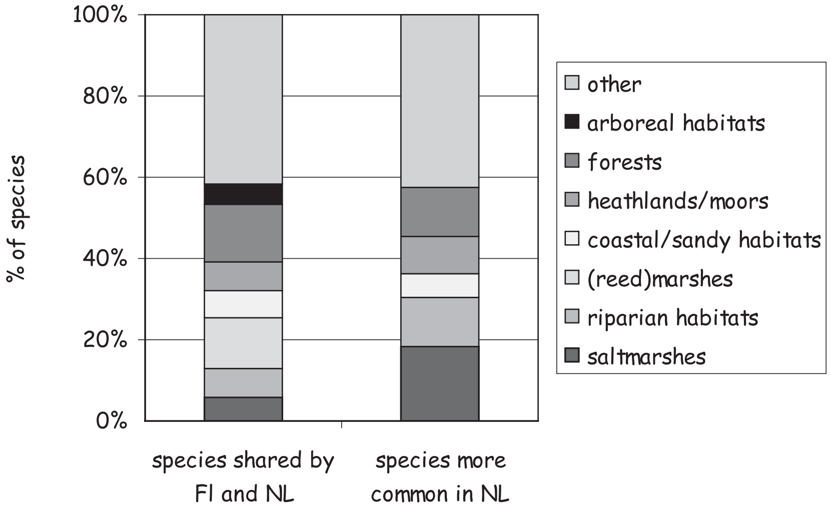

Figure 3
Comparison of species distribution over ecological groups.

marshland-inhabiting or arboreal species seems to be more common in the Netherlands.

The following ten species have not yet been collected in Flanders, but are shared by Wallony (southern Belgium) and The Netherlands: *Campsicnemus marginatus* Loew, 1857, *Dolichopus arbustorum* Stannius, 1831, *D. phaeopus* Haliday, 1851, *Hercostomus exarticulatus* Loew, 1857, *Neurigona erichsoni* (Zetterstedt, 1843), *N. suturalis* (Fallén, 1823), *Sciapus albifrons* (Meigen, 1830), *S. pallens* (Wiedemann, 1830), *Sympycnus aeneicoxa* (Meigen, 1824) and *Syntormon zelleri* (Loew, 1850). Both *Neurigona* species, *H. exarticulatus* and *S. zelleri* are confined to the southeastern Dutch province of Limburg.

Finally, another 47 Belgian species are unknown to the Netherlands (including the recently discovered *Neurigona lineata* (Oldenberg, 1904)), 25 of which are only recorded from Wallony.

Discussion

Comparing regional faunas is always a challenge because of the amount of factors that bias the different data sets. More than two thirds of shared species between Flanders and the Netherlands appear to be less common in the Netherlands (fig. 1), but this seems to be strongly affected by the applied collecting techniques. Even now, most Dutch dipterists usually use sweepnets to collect flies whereas white water traps and Malaise traps are the main sampling techniques in Flanders. It is evident that the latter collecting methods have considerable advantages to sweepnetting: 1. the sampling effort is much higher and continuous, 2. inaccessible habitats or habitats that hardly allow collecting by sweeping (e.g. reedmarshes) can easily be sampled and 3. the attractiveness of the traps and the activity and local abundances of the species are the main factors that influence the yields, regardless of the species size. Nevertheless, it is very hard to believe that common Flemish species like the woodland-inhabiting *Dolichopus wahlbergi* Zetterstedt, 1843, the eurytopic *Medetera saxatilis* Collin, 1941 and *Syntormon denticulatum* Zetterstedt, 1843 are actually rare in the Netherlands. The lack of records of *Achalcus phragmitidis* Pollet, 1996 (Z, rare), *Hercostomus pilifer* (Loew, 1859) (vZ, fairly rare) and *Syntormon aulicum* (Meigen, 1824) (3, vulnerable) is also surprising. *Syntormon aulicum* and *A. phragmitidis* occur in reedmarshes along creeks in northern East Flanders near the Dutch border and there is no reason to assume that they do not inhabit similar habitats in the southern part of Zeeuws Vlaanderen (province Zeeland) across the border.

On the other hand, rarity estimates as percentages of sampled squares should be interpreted with great caution as they are sometimes misleading. For instance, *Hercostomus gracilis* (Stannius, 1831) is known from 12 10 km squares or 9.2% of the sampled Flemish squares. In the Netherlands, it is only recorded from 6.0% which, however, represents nearly twice as many squares, indicating that this species is actually observed in a considerably larger area in the Netherlands.

Relatively more species of saltmarshes (*D. clavipes*, *D. diadema*, *H. oceanus*, *M. maritimae*, *T. flavipalpis*, *T. ruficornis*), humid heathlands and peatbogs (*D. simplex*, *D. vitripennis*, *H. nebulosus*) and riparian habitats (*D. hoffmannseggi*, *H. litoreus* Fallén, 1823, *R. nasutum*, *T. insignis*) than of any other ecological group prove to be more common in the Netherlands. This can undoubtedly be explained by the fact that these habitats are more widespread in the Netherlands and occupy larger surfaces. In this way, habitats can easily be recolonized when a local population becomes extinct. This is not the case in Flanders, especially in West Flanders, with only two saltmarshes present (De IJzermonding NR at Nieuwpoort and Het Zwin NR at Knokke) and only a few scattered heathland relicts.

On the other hand, not a single marshland or arboreal species seems to be more common in the Netherlands than in Flanders, which is particularly hard to believe for the reedmarsh faunas. It might, however, be related to the relatively little attention that has been drawn to these faunas thus far.

This faunal comparison clearly indicates that a Red Data Book of a certain region is not fully applicable for even an adjacent region. This is not only due to differences in the representation of habitat types or a different topography but also a result of a past and/or present management. Several species of springs or clean running water that have recently become extinct in Flanders, still occur in the Netherlands (*D. hoffmannseggi*, *Hercostomus chetifer* (Walker, 1849), *H. longi-*

ventris (Loew, 1857), *Liancalus virens* (Scopoli, 1763)). On the other hand, four out of eight *Hydrophorus* species shared by Flanders and the Netherlands seem to be more common in the Netherlands (*H. balticus*, *H. litoreus*, *H. nebulosus*, *H. oceanus*). Species of this genus are usually observed skating on the surface of shallow water bodies in search for mates or prey. As they are good indicators for (the condition of) this substrate, their wider distribution in the Netherlands might reflect the presence of more shallow water and/or a superior surface water quality than in Flanders. And this is not a local phenomenon as *Hydrophorus* species are highly stenotopic and restricted to strongly different habitat types like humid heathlands (*H. nebulosus*) and saltmarshes (*H. oceanus*).

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Biogeography and ecology of southern Portuguese butterflies and burnets (Lepidoptera)

Thomas Schmitt

Abstract

During several visits to the western part of the Algarve (southern Portugal), the author mapped the butterflies and burnets of this region. In total, I observed 58 butterfly species (51 Papilionoidea, 7 Hesperiidae) and 6 Zygaenidae during my observations in spring and summer.

More than 80% of the species are Palaearctic faunal elements, three species are considered Holarctic, three are Nearctic and four are Palaeotropic. Around 75% of the Palaearctic species are Mediterranean faunal elements. Within the Palaearctic group, the 23 species belonging uniquely to the Atlanto-Mediterranean faunal type are by far the largest group. Siberian elements are lacking. Thus, the observed species composition is characteristic for the Atlanto-Mediterranean region.

Some of the observed species can be found all over the study area, often in a variety of habitats. Other species are more or less geographically restricted. Their regional distribution patterns depend on geomorphological and ecological constraints. Several species are restricted to the limestone areas, others are limited to the acid schist and granite areas. Several species were only observed in the western coastal dunes. Some species occur exclusively in the mountain areas. Some species were not recorded along the windy western and south-western coastal areas. Several species become rare or even disappear in suitable habitats that show little diversity of the vegetation. The occurrence of many species is directly linked to one or few distinct types of vegetation like cork oak forests, deciduous forests and natural hedges along water courses, *Cistus* macchias, garigues on limestone, dry grasslands or hot rocky places with little vegetation.

Key words: Algarve, Lepidoptera, Hesperiidae, Papilionidae, Pieridae, Lycaenidae, Nymphalidae, Zygaenidae, Atlanto-Mediterranean region, faunal elements, glacial refugia, climatic compensation.

Introduction

For more than 100 years, the general inventory of species has been an important subject in biology. This is also true for butterflies as can be demonstrated by the work of Seitz (1909). More detailed publications on the regional distributions of butterflies in Europe combined with maps were mainly published in the last two decades of the 20th century (Bink 1992, Buszko 1997, Delmas & Maechler 1999, Ebert & Rennwald 1991, Emmet & Heath 1990, Fernández-Rubio 1991a, b, Goffart & de Bast 2000, Gonseth 1987, Henriksen & Kreutzer 1982, Huemer & Tarmann 1993, Jacsić 1988, Pamperis 1997, Schaider & Jacsić 1989).

Nevertheless, the knowledge of the distribution of butterflies is unequally distributed over Europe: While the data basis in the northern part of Europe with comparatively small species numbers is quite strong, the distribution patterns in the species rich south of Europe are scarcely known. This also applies for the Iberian Peninsula whose butterfly and burnet fauna is by far not exhaustively investigated (compare Fernández-Rubio 1990, 1991a, b).

For Iberia's most western part, Portugal, the actual knowledge about butterflies has been compiled recently (Maravalhas et al. 2003). Even so, there is no doubt that Portuguese butterflies are still not studied exhaustively. While several publications deal with the regions north of the Tejo (Carneiro-Mendes 1950, Montalvão et al. 1985, Silva Cruz 1967, Silva Cruz & Wattison 1929), large areas of the southern part are faunistically unexplored.

In the south of Portugal, the Algarve occupies an exceptional position: in this holiday region, some faunistical work has been done by Portuguese

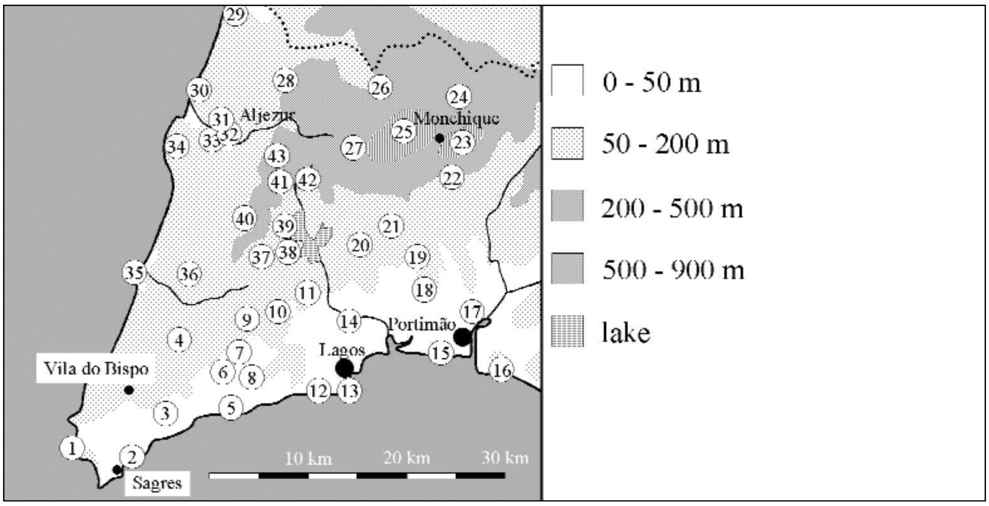

Figure 1
Map of the study area with indication of elevations (see legend). Study sites are numbered from 1 to 43. 1: Cabo de São Vicente, 2: Sagres, 3: between Raposeira and Hortas de Tabual, 4: Pedralva, 5: east of Salema, 6: south-west of Barão de São Miguel, 7: east of Barão de São Miguel, 8: Almádena, 9: Barão de São João, 10: Bensafrim, 11: Colinas Verdes, 12: Porto de Mós, 13: Ponte da Piedade, 14: Odiaxere, 15: Praia do Vau, 16: Ferragudo, 17: around 3 km north of Portimão, 18: Torre, 19: north of Alcalá, 20: Pereira, 21: Montes de Cima, 22: south of Caldas de Monchique, 23: Picota, 24: around 5 km north of Monchique, 25: Foia, 26: Foz do Farelo, 27: Marmelete, 28: Moinhos do Sogro, 29: Odeceixe, 30: Praia das Amoreiras, 31: north of Aljezur, 32: west of Aljezur, 33: castle of Aljezur, 34: Monte Clerigo, 35: Carrapateira, 36: around 2 km east of Bordeira, 37: Pincho, 38: western bank of Barragem da Bravura, 39: Corsino, 40: Peso, 41: Três Figos, 42: Romeiras, 43: Mosqueiro.

and foreign scientists (Corley et al. 2000, Passos de Carvalho & Corley 1995, Teodoro Monteiro 1969, Teodoro Monteiro & Passos de Carvalho 1984). Yet the distribution patterns are still incompletely known for many species in the Algarve. Especially the interactions between distribution, natural preconditions and human impact as well as the ecology and biogeography of species have hardly been investigated.

Therefore, I intensively studied the meso-scale distribution of the butterflies and burnets in the western part of the Algarve. Based on these data, I give an overview of their biogeographic status in the first part of this article. In a second part, I relate the obtained regional distribution patterns to the physico-geographical preconditions (such as geology, soils, relief), the intensity and way of land use as well as to the observed ecological demands of the different species.

Material and methods

During several stays in the western part of the Algarve, I made excursions to 43 different places (fig. 1); most of these places were visited at least twice. The excursions were made from March to May and from July to September from 1986 to 2000 with increasing intensity. However, the studies were more intensive in spring than in summer. During the excursions, I took note of all butterfly and burnet species, their estimated number of individuals, their habitats and their behaviour. For some species, I searched also for their pre-imaginal stages.

Based on the results of these excursions, I generated preliminary distribution maps for the observed species.

The nomenclature is according to Karsholt & Razowski (1996).

Description of the studied area

The western part of the Algarve has a striking

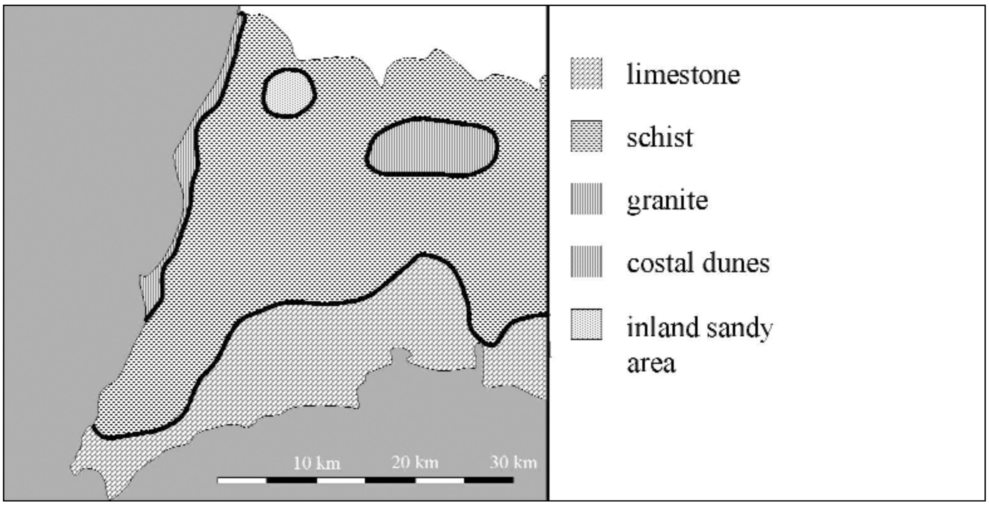

Figure 2
Geology of the study area.

geomorphological (fig. 1, 2) and ecological diversity. Along the southern coast, we find a plain or slightly hilly limestone area with basic soils. Large parts of this area are covered with fig tree and almond plantations. Especially along the coastline, the pressure of urbanisation is constantly increasing. However, also areas with garigue and macchia vegetation exist (often with *Quercus coccifera*, *Cistus albidus*, *C. monspeliensis*, *Thymus* species, several *Ophrys* species and other orchids). An extended hilly area of schist with rather acid soils flanks the limestone area in the north. In its southern part, we find mostly degraded macchias (composed of *Cistus ladanifer*, *Lavandula stoechas*) and dry pastures and grasslands. Further north, the hilly character of the landscape is more pronounced, and we find more species rich macchias (often with *Cistus crispus*, *C. ladanifer*, *C. salvifolius*, *Lavandula stoechas*), cork oak forests (often with *Arbutus unedo*, *Erica arborea*), hedge complexes along river courses (composed of *Rubus fruticosus* agg., *Salix* species) and small pastured patches. All over this schist area, more and more places are forested with *Eucalyptus* trees. Between the limestone and the schist areas, we find a narrow stripe of sandstone (rarely more than 500 m width). A large granite block tops the northern part of the schist area and reaches 900 m above sea level at the Foia mountain. This area is covered by cork oak and *Eucalyptus* forests, *Cistus* garigues and macchias as well as pastures. In the granite area, the plant species composition of the different habitats is similar to the schist area. A narrow strip of coastal dunes with their typical vegetation (often with *Halimium halimifolium*, *Corema alba*, *Thymus camphoratus*, *Armeria* species) extends along the western coastline. In the north-western part of the study area, we find a larger area with sandy soils covered by dry grasslands, some monocultural forests, species poor *Cistus* macchias and garigues.

Results

Faunal elements

I found a total number of 58 butterfly species (51 Papilionoidea and 7 Hesperiidae) and 6 Zygaenidae. The total list of recorded species is given in table 1. Using the classification of Varga (1977; modified for *I. feisthamelii*), the Papilionoidea are grouped into the following faunal element types:

I) Holarctic or Palaeartic (14 species)
  I.1) Holartic polycentric (3 species: *Celastrina argiolus*, *Lycaena phlaeas*, *Papilio machaon*)

Figure 3
Euphydryas aurinia beckeri. Photo Thomas Schmitt.

  - I.2) Holopalaearctic polycentric (10 species: *Callophrys rubi*, *Coenonympha pamphilus*, *Euphydryas aurinia*, *Gonepteryx rhamni*, *Melitaea phoebe*, *Pieris brassicae*, *P. rapae*, *Polyommatus icarus*, *P. semiargus*, *Pontia daplidice*)
  - I.3) Holomediterranean-Holarctic (1 species: *Euchloe crameri*)
- II) Western Palaearctic (30 species)
  - II.1) Holomediterranean-Turkestanic (2 species: *Nymphalis polychloros*, *Pararge aegeria*)
  - II.2) Holomediterranean-Iranic (6 species: *Argynnis pandora*, *Lasiommata megera*, *Maniola jurtina*, *Polyommatus bellargus*, *Satyrium spini*, *Vanessa atalanta*)
  - II.3) Mediterranean (22 species)
    - II.3.a) Holomediterranean s.str. (4 species: *Gonepteryx cleopatra*, *Hipparchia statilinus*, *Leptotes pirithous*, *Pyronia cecilia*)
    - II.3.b) Northern Mediterranean (2 species: *Leptidea sinapis*, *Pyronia tithonus*)
    - II.3.c) Atlanto-Mediterranean (16 species: *Aricia cramera*, *Coenonympha dorus*, *Cupido lorquinii*, *Euchloe belemia*, *Euphydryas desfontainii*, *Glaucopsyche melanops*, *Hipparchia fidia*, *Iphiclides feisthamelii*, *Melanargia ines*, *M. occitanica*, *Melitaea aetherie*, *M. deione*, *Pyronia bathseba*, *Satyrium esculi*, *Tomares ballus*)
- III) Palaeotropic (4 species: *Charaxes jasius*, *Colias crocea*, *Lampides boeticus*, *Zizeeria knysna*)
- IV) Nearctic (3 species: *Danaus plexippus*, *Vanessa cardui*, *V. virginiensis*)

Siberian and other eastern Palaearctic faunal elements were lacking.

After the classification of Naumann et al. (1984), all five *Zygaena* species belong to the Atlanto-Mediterranean faunal element (*Zygaena fausta*, *Z. lavandulae*, *Z. rhadamantus*, *Z. sarpedon*, *Z. trifolii*). According to its distribution (Naumann et al. 1999), *Aglaope infausta* has also to be considered an Atlanto-Mediterranean faunal element. For the Hesperiidae, a classification is not available for all species. Using the work of de Lattin (1957) on the Lepidoptera of the Palatinate, one of the species is of the Atlanto-Mediterranean faunal type (*Spialia sertorius*) and four of the Holomediterranean faunal type (*Carcharodus alceae*, *Thymelicus acteon*, *T. lineolus*, *T. sylvestris*). The distribution patterns of *Gegenes nos-*

Table 1
List of butterfly and burnet species found in the western Algarve during the study. The species are listed according to their phylogenetic classification.

Zygaenidae
Aglaope infausta (Linnaeus, 1767)
Zygaena sarpedon (Hübner, 1790)
Zygaena fausta (Linnaeus, 1767)
Zygaena rhadamantus (Esper, 1793)
Zygaena lavandulae (Esper, 1783)
Zygaena trifolii (Esper, 1783)

Hesperiidae
Carcharodus alceae (Esper, 1780)
Spialia sertorius (Hoffmannsegg, 1804)
Muschampia proto (Ochsenheimer, 1808)
Thymelicus lineola (Ochsenheimer, 1808)
Thymelicus sylvestris (Poda, 1761)
Thymelicus acteon (Rottemburg, 1775)
Gegenes nostrodamus (Fabricius, 1793)

Papilionidae
Zerynthia rumina (Linnaeus, 1758)
Iphiclides feisthamelii (Duponchel, 1832)
Papilio machaon (Linnaeus, 1758)

Pieridae
Leptidea sinapis (Linnaeus, 1758)
Pieris brassicae (Linnaeus, 1758)
Pieris rapae (Linnaeus, 1758)
Pontia daplidice (Linnaeus, 1758)
Euchloe crameri (Butler, 1869)
Euchloe belemia (Esper, 1800)
Colias crocea (Fourcroy, 1785)
Gonepteryx cleopatra (Linnaeus, 1767)
Gonepteryx rhamni (Linnaeus, 1758)

Lycaenidae
Lycaena phlaeas (Linnaeus, 1761)
Tomares ballus (Fabricius, 1787)
Callophrys rubi (Linnaeus, 1758)
Satyrium esculi (Hübner, 1804)
Satyrium spini ([Denis & Schiffermüller], 1775)
Lampides boeticus (Linnaeus, 1767)
Leptotes pirithous (Linnaeus, 1767)
Zizeeria knysna (Trimen, 1862)
Cupido lorquinii (Herrich-Schäffer, 1847)
Celastrina argiolus (Linnaeus, 1758)
Glaucopsyche melanops (Boisduval, 1828)
Aricia cramera (Eschscholtz, 1821)
Polyommatus semiargus (Rottemburg, 1775)
Polyommatus icarus (Rottemburg, 1775)
Polyommatus bellargus (Rottemburg, 1775)

Nymphalidae
Argynnis pandora ([Denis & Schiffermüller], 1775)
Vanessa atalanta (Linnaeus, 1758)
Vanessa cardui (Linnaeus, 1758)
Vanessa virginiensis (Drury, 1773)
Nymphalis polychloros (Linnaeus, 1758)
Euphydryas aurinia (Rottemburg, 1775)
Euphydryas desfontainii (Godart, 1819)
Melitaea phoebe ([Denis & Schiffermüller], 1775)
Melitaea aetherie (Hübner, 1826)
Melitaea deione (Geyer, 1832)
Charaxes jasius (Linnaeus, 1767)
Pararge aegeria (Linnaeus, 1758)
Lasiommata megera (Linnaeus, 1758)
Coenonympha dorus (Esper, 1782)
Coenonympha pamphilus (Linnaeus, 1758)
Pyronia tithonus (Linnaeus, 1771)
Pyronia cecilia (Vallantin, 1894)
Pyronia bathseba (Fabricius, 1793)
Maniola jurtina (Linnaeus, 1758)
Melanargia occitanica (Esper, 1793)
Melanargia ines (Hoffmannsegg, 1804)
Hipparchia statilinus (Hufnagel, 1766)
Hipparchia fidia (Linnaeus, 1767)
Danaus plexippus (Linnaeus, 1758)

trodamus and *Muschampia proto* make the Holomediterranean type of dispersal likely for these two species.

Regional distribution patterns

Several geomorphological and ecological constraints influence the regional geographic distribution of the butterfly and burnet species in the western part of the Algarve. In the following, I give examples for geology, altitude, wind exposure, diversity and type of vegetation.

Geology: Several species were mostly restricted to the limestone areas (*Aglaope infausta*, *Satyrium esculi*, *S. spini*, *Zygaena fausta*, *Z. sarpedon*). Other species were only found in the granite and schist areas (*Callophys rubi*, *Charaxes jasius*, *Gonepteryx rhamni*, *Hipparchia fidia*, *H. statilinus*, *Leptidea sinapis*, *Nymphalis polychloros*, *Polyommatus bellargus*, *Pyronia tithonus*, *Zerynthia rumina*).

Altitude: Some species apparently are restricted to the mountain range of the Serra de Monchique and their foothills (*Gonepteryx rhamni*, *Hipparchia statilinus*, *Leptidea sinapis*, *Nymphalis polychloros*, *Pyronia tithonus*).

Wind exposure: A number of species were not

Figure 4
Polyommatus bellargus. Photo Thomas Schmitt.

found in the windy area along the western coastline and the south-western tip of the Algarve (*Aricia cramera*, *Celastrina argiolus*, *Euphydryas aurinia*, *Gonepteryx cleopatra*, *Leptotes pirithous*, *Muschampia proto*, *Pararge aegeria*, *Polyommatus bellargus*, *Satyrium esculi*, *Thymelicus acteon*, *T. sylvestris*).

Diversity of vegetation: The southern parts of the schist area have a high proportion of macchias that are poor in plant species diversity and *Eucalyptus* monocultures. These habitats are relatively poor in butterfly and burnet species. Species often missing in these habitats (although being generally widely distributed) are: *Charaxes jasius*, *Gonepteryx cleopatra*, *Iphiclides feisthamelii*, *Muschapia proto*, *Papilio machaon.*

Type of vegetation: The existence of many butterfly and burnet species is more or less linked to the existence of one or a few vegetation types such as deciduous and cork oak forests (*Charaxes jasius*, *Gonepteryx rhamni*, *Nymphalis polychloros*), natural hedges (especially *Rubus*) (*Celastrina argiolus*, *Euphydryas aurinia*, *Pyronia tithonus*), *Cistus* macchias (*Leptidea sinapis*, *Thymelicus sylvestris*, *Zerynthia rumina*), garigues and macchias on limestone (*Satyrium esculi*, *S. spini*, *Zygaena fausta Z. sarpedon*), dune vegetation (*Melitaea phoebe*, *Polyommatus semiargus*, *Zygaena lavandulae*, *Z. rhadamantus*), dry grassland (*Carcharodus alceae*, *Coenonympha pamphilus*, *Colias crocea*, *Muschampia proto*, *Polyommatus bellargus*, *Pyronia cecilia*), wet grassland (*Euphydryas desfontainii*) or rocky places with little vegetation (*Hipparchia fidia*, *H. statilinus*, *Lasiommata megera*, *Lycaena phlaeas*).

Some highly opportunistic and/or migrating species were found nearly at all study sites (*Colias crocea*, *Euchloe belemia*, *E. crameri*, *Lampides boeticus*, *Lasiommata megera*, *Lycaena phlaeas*, *Maniola jurtina*, *Melanargia ines*, *Pieris rapae*, *Polyommatus icarus*, *Pyronia bathseba*). For opportunistic and/or migrating species, which occur at comparatively low densities in the study region, I obtained seemingly confusing distribution patterns (*Carcharodus alceae*, *Coenonympha pamphilus*, *Papilio machaon*, *Pieris brassicae*, *Pontia daplidice*, *Vanessa atalanta*, *V. cardui*). Other species were found so rarely that their distribution patterns are still poorly understood (*Argynnis pandora*, *Coenonympha dorus*, *Cupido lorquinii*, *Gegenes nostrodamus*, *Glaucopsyche melanops*, *Melanargia occitanica*, *Melitaea aetherie*, *M. deione*, *Thymelicus lineola*, *Tomares ballus*, *Vanessa virginiensis*, *Zizeeria knysna*, *Zygaena trifolii*).

Discussion

What are the origins of the southern Portuguese butterflies and burnets?

The butterfly and burnet species observed in the study region resemble a typical Atlanto-Mediterranean fauna. Thus, 23 of the 64 butterfly and burnet species (35.9%) belong to the Atlanto-Mediterranean faunal element which had its single centre of dispersal in the Iberian Peninsula. It is very likely for these species that they occurred in the study region also during the last glaciation.

Several dispersal centres in the Mediterranean region are suggested for 20 species (31.3%) which belong to the western Palaearctic-Mediterranean element (s.l.). Like the Atlanto-

Mediterranean species, the majority of these Mediterranean species (s.l.) is widely distributed in Spain (Fernández-Rubio 1991a, b) and Portugal (Maravalhas et al. 2003). Therefore, it is also likely that they existed in the Atlanto-Mediterranean core area and occurred in the study region during the last glaciation. This suggestion is supported by genetic studies of *Maniola jurtina* and *Polyommatus bellargus* (Schmitt & Seitz 2001).

Also in the group of polycentric species of the Holopalaearctic, Holomediterranean-Palaeartic and Holarctic faunal type (14 species, 21.9%), many representatives (if not all of them) probably were distributed in the Iberian Peninsula during the last glaciation as has been proved for *Euphydryas aurinia* (Joyce & Pullin 2001) and *Polyommatus icarus* (Schmitt & Seitz 2001) by genetic studies (for a review of these studies see Schmitt 2003a)

Thus, up to 89.1% of the butterfly and burnet species have persisted in the study region for at least 100 000 years. Maybe this percentage is even higher because the four species classified by Varga (1977) as Palaeotropical faunal elements and *Vanessa cardui* classified as a Nearctic element might have immigrated into Europe prior to the last glaciation. If so, they might have had expansion centres in the Atlanto-Mediterranean region too.

Therefore, postglacial immigration to the study region is only sure for two of the observed butterfly species: *Vanessa virginiensis* and *Danaus plexippus*. While *V. virginiensis* seems to have become established in Portugal during the last century (for an overview see Schmitt 2003b), *D. plexippus* is still a rare migrant along the western European coasts (Emmet & Heath 1990, Fernández-Rubio 1991b, Tolman & Lewington 1998).

A characteristic feature of the studied Lepidoptera fauna is the complete lack of Siberian or other eastern Palaearctic faunal elements. As shown by de Lattin (1967), these species are mostly absent from the Iberian Peninsula and most of the Mediterranean region. Only few species out of this group were able to colonise the northern most regions of Spain (Fernández-Rubio 1991a, b).

Habitat preferences and climatic compensation

For many species, their preferred habitat type in the western Algarve is quite similar to their ecological demands observed elsewhere in Europe (Asher et al. 2001, Bink 1992, Ebert & Rennwald 1991, Hofmann 1994, Maravalhas et al. 2003, Naumann et al. 1999, Settele et al. 1999, Tolman & Lewington 1998, Weidemann 1986, 1988). Only some species differ remarkably from their habitat demands in Central Europe. For instance, *Euphydryas aurinia* (flying in the Algarve exclusively with its subspecies *beckeri*) occurs in the western Algarve preferably along the edges of small watercourses and on small pastures along these watercourses. In the northern parts of Europe, this species occurs at swampy or even semidry meadows (Asher et al. 2001, Emmet & Heath 1990, Ebert & Rennwald 1991). *Thymelicus sylvestris*, which is most characteristic of macchias in the western Algarve, has to be considered a species of meadows more in the north of Europe. *Polyommatus semiargus*, which is restricted to some humid places in the dunes near Aljezur, is a species of meadows in Central Europe, and *Melitaea phoebe* is restricted to the warmest semidry meadows in Central Europe (Ebert & Rennwald 1991).

These ecological differences seem to be a strategy to compensate for the rather different climatic regimes over a large area of distribution. So the species prefer warm, sunny and dry habitats in the cooler north and cooler and wetter, shady habitats in the south (Erhardt & Thomas 1991).

The absence of several species in the lowland region of the western Algarve might indicate climatic compensation too, especially because several of these species (*Gonepteryx rhamni*, *Pyronia tithonus*, *Nymphalis polychloros*) prefer woody habitats in Central Europe (Asher et al. 2001, Ebert & Rennwald 1991, Emmet & Heath 1990). Such species have no other possibility than to climb up mountains for climatic compensation, a general feature observed in southern Europe (Tolman & Lewington 1998, Zahm 1999).

In the western Algarve, the preference of geological structures deviates from the findings elsewhere for some species. Thus, *P. bellargus*, in the western Algarve found only in habitats with acid soils, clearly prefers limestone regions further north (Bink 1992, Ebert & Rennwald 1991, Emmet & Heath 1990). Furthermore, the great majority of species (if not all), restricted in the western Algarve to the schist and granite areas, can also be found in other regions in limestone areas (Asher et al. 2001, Bink 1992, Ebert & Rennwald 1991, Emmet & Heath 1990, Settele et al. 1999, Weidemann 1986, 1988). While limestone regions and especially south facing slopes within these regions are often remarkably warm, the restriction to non-limestone regions of the western Algarve might also be a strategy for climatic compensation.

Ecological demands and distribution patterns

As shown above, many of the ecological constraints seem to be responses to the necessity of climatic compensation, making climate a predominant factor in the shaping of regional distribution patterns. Apparently, some distribution constraints are not dependent on climate itself.

Thus, species occurring in forests or in habitats with hedges are missing or much less abundant along the western coast and in the south-western tip of the Algarve. These regions, strongly exposed to the wind, only have few wind-protected places, thus not offering suitable conditions for the existence of this ecological group of butterflies.

Human land-use locally reduced the diversity in plant species by exhaustive agriculture and the plantation of monocultural forests (especially of *Eucalyptus* trees). While lepidopteran diversity is linked with plant diversity (Steffan-Dewenter & Tscharntke 2000), this human impact also caused local reductions in butterfly and burnet species numbers.

Concluding remarks

Summing up, the distribution patterns revealed for the western part of the Algarve seem to be shaped by the ecological demands of the respective species. Thus, the distribution patterns of the different habitat types are of enormous importance for the local distribution of the butterfly and burnet species. While these habitat types directly depend on natural preconditions (geology, soils, altitude, wind exposure) and human activities (intensity and type of land use), the study of these constraints is of great importance for an understanding of the meso-scale distribution patterns.

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Butterflies for the new millennium: mapping butterfly distributions in Britain (Lepidoptera)

Richard Fox, Martin Warren, Paul Harding, Jim Asher, Gail Jeffcoate & Stephen Jeffcoate

Abstract

Butterflies for the New Millennium is the largest and most comprehensive survey of butterfly distribution ever undertaken in Britain and Ireland. The number of contributing recorders, the coverage achieved and the number and quality of distribution records generated far exceed those available for any other invertebrate taxon. The data thus provide a unique insight into the effects of habitat degradation and climate change on a high profile insect group.

The results of the first five years of the survey (1995-1999) have been analysed to assess broad-scale distribution changes over the past two decades and the past two centuries. In both time periods, the British distributions of most butterfly species have shown substantial change. The trends affecting habitat specialist and habitat generalist (wider countryside) species differ significantly. The distributions of half of the habitat generalists have increased (consistent with an expected positive response to observed climate change), whereas most habitat specialists declined (consistent with habitat degradation). The opposing forces of climate change and habitat degradation are thought to be the main driving forces. The decline of specialist species indicates a reduction in overall biodiversity, whilst mobile and widespread generalists increasingly dominate biological communities. These patterns of change are thought to be representative of many other invertebrate groups in Britain and demonstrate the use of butterflies as indicators of environmental change.

Key words: Lepidoptera, butterfly recording, butterfly distribution, habitat degradation, climate change, biodiversity, conservation, indicator species.

Introduction

Butterflies have a special place in people's experience and vision of the countryside. No other invertebrates have the same popular appeal. This popularity, together with the ease with which most species can be identified and recorded, accounts for a long history of butterfly recording in Britain and Ireland (Harding et al. 1995).

The Butterflies for the New Millennium (BNM) project was launched in 1995 by Butterfly Conservation and the Biological Records Centre at the Centre for Ecology and Hydrology, because it was clear that the distributions of many butterflies had changed substantially since the only previous national survey (1970-1982).

Up-to-date distribution information is essential to inform decisions in nature conservation. The main aims of the BNM project were to provide such data to support conservation and land-use policy, inform the development planning system and guide direct conservation efforts. Since the survey was to be an inclusive project, utilizing members of the public and volunteers from a wide range of organisations, other aims were to develop the numbers and expertise of people recording butterflies and to promote the conservation of butterflies to a wider audience. Data from the first five years of the survey (1995-1999) have been analysed and published in a major new book, The Millennium Atlas of Butterflies in Britain and Ireland (Asher et al. 2001).

The BNM survey

The survey was achieved by mobilizing volunteers across Britain and Ireland. Participants were issued with standard recording forms and instructions, but records were not gathered systematically (with respect to geography or time). However, considerable efforts were made to target recording to ensure the best possible coverage of the survey area with the available resources. Records were collected, verified and computerised by volunteer county co-ordinators and local data sets then collated annually in a central database.

After five years of recording, the success of the survey was clear. Between 1995 and 1999, over

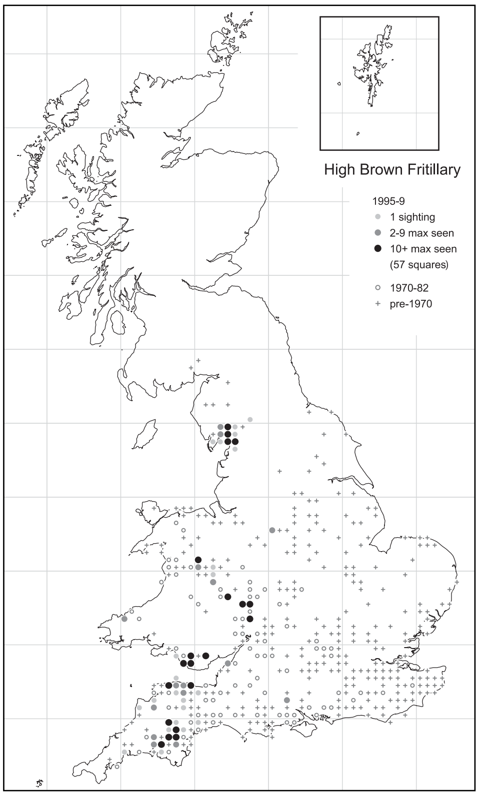


Figure 1
The high brown fritillary was once widespread in England and Wales in coppiced woodlands and bracken habitats. It has declined severely since the 1950s due to habitat deterioration, and is now one of the rarest and most threatened butterflies in Britain.

10 000 participants had generated more than 1.6 million butterfly records. This represents a twelvefold increase over the number of records compiled by the previous survey (Heath et al. 1984) and in less than half the survey time period. Coverage was also more comprehensive with 99% coverage achieved at the 10 km square level in Britain (and 98% in Ireland). The precision and detail of the records gathered also represented a great improvement over the previous survey. For example, over 90% of the BNM records had a 1 km square or 100 m square grid reference, compared to 51% of 1970-1982 records.

The current distribution of each species, determined by the BNM survey, has been compared with that recorded in 1970-1982 and historical information dating back to 1800. Recording effort bias complicates the interpretation of distribution change in Ireland. Therefore, this paper considers only the changes that have occurred in Britain.

Patterns of change since 1970-1982

Many resident butterflies continued to decline in the final decades of the 20th century. The pattern of change among different species has been considered using the ecological concept of island and matrix species (Pollard & Eversham 1995). This concept has been modified using the terms habitat specialist and wider countryside species.

British butterflies can be divided relatively easily into these two groups based on their ecological attributes. Habitat specialists have 'narrow' niches and tend to be sedentary, univoltine and use only one or two species of larval foodplant. Wider countryside species tend to have 'wide' niches and many are mobile, bivoltine or trivoltine and polyphagous. The British butterfly fauna consists of approximately equal numbers of habitat specialists and wider countryside species, yet there are clear differences between the distribution changes of the two groups over the last 20 years.

Most habitat specialists have suffered substantial decreases in their distributions at the 10 km square scale. The high brown fritillary *Argynnis adippe* (Denis & Schiffermüller, 1775), for example, was once widespread in woodlands across England and Wales, where the traditional practice of coppicing created a regular supply of sunny clearings. These provided a warm, sheltered microclimate essential for the larvae. Each clearing would remain suitable for only a few years before the trees regrew, but the butterfly was able to persist by colonising new clearings nearby. However, the high brown fritillary has undergone the most severe decline of any extant species and has been lost from 77% of the 10 km squares in which it was recorded in the 1970-1982 survey (fig. 1, 2). It is now restricted to only 50 sites, mainly in bracken (*Pteridium aquilinum*) dominated habitats.

Other butterflies have suffered similarly spectacular declines in Britain. The distributions of the wood white *Leptidea sinapis* (Linnaeus, 1758) and pearl-bordered fritillary *Boloria euphrosyne*

Figure 2
The high brown fritillary *Argynnis adippe*.

(Linnaeus, 1758), both specialist butterflies of woodland clearings, have decreased by 62% and 60%, respectively, in Britain since 1970-1982. The marsh fritillary *Euphydryas aurinia* (Rottemburg, 1775), a habitat specialist of unimproved damp or chalk grasslands that is classified as vulnerable in Europe (van Swaay & Warren 1999), has undergone a 55% decrease in Britain in the last two decades. The recent declines of several other species are causing concern. Examples include the large heath *Coenonympha tullia* (Müller, 1764), silver-studded blue *Plebeius argus* (Linnaeus, 1758), duke of burgundy *Hamearis lucina* (Linnaeus, 1758), dingy skipper *Erynnis tages* (Linnaeus, 1758) and small pearl-bordered fritillary *Boloria selene* (Denis and Schiffermüller, 1775). Only one habitat specialist species (the white admiral *Limenitis camilla* (Linnaeus, 1764) has undergone a substantial expansion of its distribution at the 10 km grid square scale.

It is recognised that the comparison of distributions at coarse geographical scales (e.g. 10 km grid squares) greatly under-estimates population level declines (Thomas & Abery 1995). High rates of population decline and colony extinction may exist within a 10 km square, but only the final loss from the square will be registered on distribution maps at this resolution. Therefore, the national distribution declines measured by the BNM survey are minimum estimates of population loss and many species have probably declined even more severely at the local level (Cowley et al. 1999).

In contrast, the distributions of many wider countryside species have expanded or remained stable. The comma *Polygonia c-album* (Linnaeus, 1758) is one of a group of 14 wider countryside species that have undergone substantial range expansions in Britain. Since the 1970-1982 survey, its range margin has moved 220 km northwards (fig. 3, 4). In addition, vagrant commas have been recorded recently in Scotland, where the species became extinct in the 19th century, and on the Isle of Man and in Northern Ireland, where the species has never been resident.

Some of these expansions represent the continuation of trends that began many decades earlier (as is the case for the comma, which has been expanding sporadically since the 1920s), while others are recent events. An extreme case is the brown argus *Aricia agestis* (Denis & Schiffermüller, 1775). At the time of the 1970-1982 survey its distribution was decreasing, but recently the butterfly has

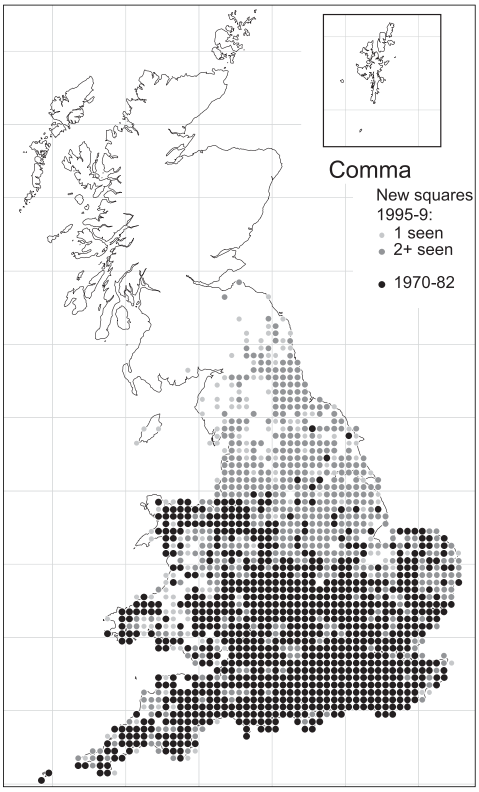


Figure 3
Since the 1970s, improving climatic conditions have allowed the comma to colonise much of northern England. Its distribution has increased by almost 80% at the 10 km square scale.

increased the range of habitat types in which it can breed and has spread into many new areas (C.D. Thomas et al. 2001). This decline has since been reversed and its distribution has more than doubled (108% increase in recorded 10 km squares).

Many of these wider countryside species are re-expanding following previous declines in the late 19th and early 20th centuries. Examples include the orange-tip *Anthocharis cardamines* (Linnaeus, 1758), peacock *Inachis io* (Linnaeus, 1758), comma and speckled wood *Pararge aegeria* (Linnaeus, 1758). The distributions of these butterflies have increased by 43%, 34%, 79% and 54% respectively. The main direction of all distribution expansions has been northwards.

At the 10 km square scale, only one wider countryside species, the wall *Lasiommata megera* (Linnaeus 1767), has undergone a substantial decline.

Patterns of change since 1800

Historical records dating back over 200 years, show that more than half of the 59 resident butterflies in the British fauna have disappeared from over 20% of their range. This includes five species that have become extinct during the period (the black-veined white *Aporia crataegi* (Linnaeus, 1758), large copper *Lycaena dispar* (Haworth, 1802), mazarine blue *Polyommatus semiargus* (Rottemburg, 1775), large blue *Maculinea arion* (Linnaeus, 1758), and large tortoiseshell *Nymphalis polychloros* (Linnaeus, 1758). A number of 15 species (25% of the total fauna) have suffered decreases in distribution of greater than 50% at the 10 km square scale (fig. 5).

The causes of distribution change

Human activities caused massive changes in the landscape of Britain during the 20th century. These changes have been largely detrimental to wildlife and three main factors have led to the historical and recent declines of butterflies. First is the destruction of semi-natural habitats. Huge amounts of butterfly habitat have been lost to intensive agriculture and forestry and to urban and infrastructure development. For example, 80% of chalk and limestone grassland has been destroyed in Britain since the 1940s (see Asher et al. 2001 for references and further examples of habitat loss). This is a key habitat for butterflies, providing conditions for 12 habitat specialist species and the sole habitat for four: the lulworth skipper *Thymelicus acteon* (Rottemburg, 1775), silver-spotted skipper *Hesperia comma* (Linnaeus, 1758), chalkhill blue *Polyommatus coridon* (Poda, 1761) and adonis blue *Polyommatus bellargus* (Rottemburg, 1775).

The rapid intensification of farming and forestry has had a profound effect on the way that the remaining semi-natural habitats are managed, as these generally represent small, economically marginal fragments of land. Most habitat specialist butterflies are sensitive to subtle changes in their habitats and can decline rapidly if management regimes become unsuitable. Many are also adapted to early successional habitats, which have been maintained (unwittingly) for centuries by

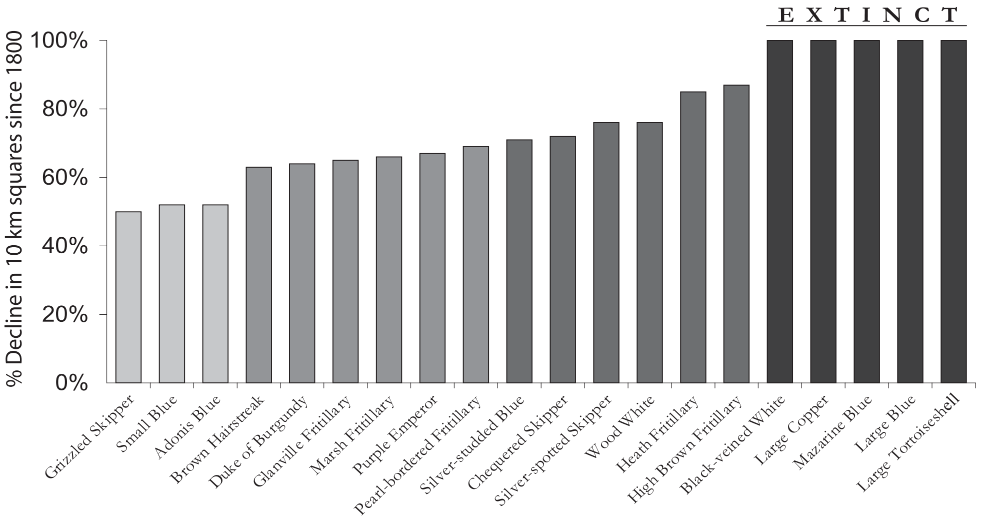
Figure 4
The comma *Polygonia c-album*.

practices such as low intensity livestock grazing on grasslands and coppicing in woods. The decline of such traditional forms of land management during the 20th century is the second major factor that has led to the severe declines of butterflies. For example, semi-natural grasslands in some lowland areas have been abandoned by farmers and graziers, leading to an immediate loss of the short turf conditions (and very warm microclimates) needed by specialist butterflies such as the large blue, silver-spotted skipper, silver-studded blue, adonis blue and grayling *Hipparchia semele* (Linnaeus, 1758). A few species that require longer grass may have benefited in the short-term (e.g. the lulworth skipper) but eventually decline as scrub invades the grassland. At the other extreme, overgrazing has adversely affected some butterfly habitats, particularly in upland areas. Subsidies available under the EU Common Agricultural Policy have encouraged a substantial increase in numbers of livestock, especially sheep, and specialist butterflies such as the pearl-bordered fritillary and marsh fritillary have declined as a result of increased grazing pressure.

Many woodland specialist butterflies have suffered declines, as their habitats have become more shaded and overgrown following the abandonment of coppicing in most broad-leaved woodlands. On the other hand, this reduced level of management has facilitated the spread of the white admiral, a specialist butterfly of shady woodland.

The third major cause of butterfly declines is the fragmentation of remaining habitat. Although fragmentation is a consequence of habitat destruction and deterioration due to changing management, it places surviving butterfly populations at further risk as patches of semi-natural habitats become smaller and more isolated from each other. Small habitat patches tend to support small populations of butterflies that are susceptible to extinction because of stochastic events, like fire or disease, or demographic and genetic effects. Increasing isolation reduces the probability of a habitat patch being recolonised by butterflies (Thomas et al. 1992, 1998). The relative importance of habitat quality and fragmentation effects on butterfly declines has recently been described empirically by J.A. Thomas et al. (2001).

All three of these factors have combined to cause an overall degradation of semi-natural habitats and consequent decline of resident butterfly species. This habitat degradation has had a disproportional-



Adonis Blue	52%	Pearl-bordered Fritillary	69%	High Brown Fritillary	87%	Large Tortoiseshell	100%
Small Blue	52%	Purple Emperor	67%	Heath Fritillary	85%	Large Blue	100%
Grizzled Skipper	50%	Marsh Fritillary	66%	Wood White	76%	Mazarine Blue	100%
		Glanville Fritillary	65%	Silver-spotted Skipper	76%	Large Copper	100%
		Duke of Burgundy	64%	Chequered Skipper	72%	Black-veined White	100%
		Brown Hairstreak	63%	Silver-studded Blue	71%		

Figure 5
The most serious losses of range amongst British butterflies since 1800.

ly large negative effect on habitat specialist butterflies in Britain relative to wider countryside species. The main factor causing wider countryside species to expand their distributions appears to be climate change. Average spring and summer temperatures in central England have increased by 1.5 and 1°C respectively in the past 25 years (Roy & Sparks 2001), a substantial increase for climatically-sensitive insects such as butterflies, many of which reach their European range margin in Britain. The evidence for the role of climate change in range expansions comes from the simultaneous spread of species, counter to the downward trend in extent of most butterfly habitats, and also from northward range shifts elsewhere in Europe (Parmesan et al. 1999). Most of these expanding species use habitats that are still relatively common, such as hedgerows, roadside verges and woodland edges. They are relatively mobile butterflies and have been able to move through the modern landscape, tracking climatic change and capitalising on recent favourable weather.

BNM and nature conservation

The BNM survey has generated an unprecedented amount of data with many potential applications. Of particular importance in nature conservation is the opportunity to reassess UK Biodiversity Action Plan (BAP) priorities and targets for butterflies (UK Biodiversity Group 1998). The severity of declines recorded for some BAP species, such as the wood white and duke of burgundy, was unexpected and suggests that they require increased priority. Other rapidly declining species, including the dingy skipper, grizzled skipper *Pyrgus malvae* (Linnaeus, 1758) and dark green fritillary *Argynnis aglaja* (Linnaeus, 1758) now warrant consideration for inclusion in the UK BAP (Fox et al. 2001).

The BNM data give the precise locations of key butterfly populations. This is vital in local nature conservation, feeding into local government policies (such as Local Biodiversity Action Plans), informing the planning process and allowing direct conservation action through, for example, habitat management and site designation. Moreover, because recording effort has increased, many thousands of new sites for declining species have been identified. This has been particularly notable in Scotland, where many previously unknown colonies of species such as the chequered skipper *Carterocephalus palaemon* (Pallas, 1771), northern brown argus *Aricia artaxerxes* (Fabricius, 1793) and pearl-bordered fritillary have been discovered.

BNM and research

The data set provides a powerful tool for a wide range of ecological and biogeographic research. It is clear that the distributions of butterflies are changing rapidly, perhaps more rapidly than other well studied taxa such as birds and higher plants. This speed of response (a consequence of short life-cycles, close dependence on climate and, in many cases, specific habitat and microclimate requirements) coupled with ease of recording and popularity amongst the public make butterflies good potential indicator species for studying and assessing environmental change.

BNM data are already being used in research to predict the responses of British butterflies to climate change. Climate response surface models have been developed to assess the extent of climatically suitable habitat potentially available to butterflies under various scenarios of climate change. Most butterfly species might be expected to benefit from rising temperatures, at least in the short- or medium-term. However, when measures of habitat availability were incorporated into the models, they indicated that the range expansions of even wider countryside species (such as speckled wood and ringlet *Aphantopus hyperantus* (Linnaeus, 1758)) have lagged behind climatic changes because of habitat fragmentation (Hill et al. 2001a). This finding has been reinforced by further work using a spatially explicit model to simulate the migration of butterflies within areas of range expansion. This also strongly suggested that landscape structure (i.e. habitat fragmentation) accounted for different rates of expansion of the speckled wood in different parts of Britain (Hill et al. 2001b).

These findings have implications for the long-term conservation of the British butterfly fauna. Many populations of habitat specialists already appear to be isolated on remaining (often small) patches of suitable habitat, and will be unable to track shifting patterns of climate and vegetation. The fact that habitat fragmentation is also limiting the responses of wider countryside species to climate change is of great concern.

Conclusions

In summary, the BNM survey has been a great success in assessing the recent and long-term trends in the distribution of resident butterfly species. The data provide a unique insight into the effects of habitat degradation and climate change on a high profile insect group. Most butterflies should have responded positively to climate change over recent decades and yet many species have declined. Certainly for habitat specialist butterflies, the detrimental effects of habitat loss have outweighed the beneficial impacts of a warming climate. Therefore, without substantial conservation intervention, butterfly communities will be driven towards lower species richness and increasing dominance by widespread generalist species.

The data set generated by the survey will form a vital tool for nature conservation and research and a new baseline against which to measure future change, including the success of conservation initiatives such as the BAP. British butterflies constitute a very small group – there are ten times as many butterfly species in continental Europe and nearly 500 times as many other invertebrate species in Britain. Nevertheless it is almost certainly the best studied insect fauna in the world and the BNM project has shown how butterflies can and should be used as flagship species, not only to raise the profile of insect conservation but also to involve members of the public in biological recording.

Acknowledgements

The Butterflies for the New Millennium survey would not have been possible without the enthusiastic participation and support of many conservation and land-management organisations, statutory agencies, local record centres and individual recorders. Generous sponsorship was provided by the Vincent Wildlife Trust, the Esmée Fairbairn Foundation, ICI, The Heritage Council and the Joint Nature Conservation Committee. Butterfly images are reproduced with the kind permission of Robert Thompson.

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Changing distributions of Cantharidae and Buprestidae within Great Britain (Coleoptera)

Keith Alexander

Abstract

Data are presented on the distribution of selected species from two coleopteran families chosen to represent a random slice of the British fauna. The species have been chosen as exhibiting extremes of range changes, from declining species, through stable distributions, to expanding species. Examination of this small group of beetles already reveals significant changes, some of which may be related to global climate change. Predictions can be made about which others of these beetle families are likely to show detectable changes in range in the near future.

Key words: biological recording, changing distributions, Cantharidae, Buprestidae, Coleoptera.

Introduction

The Cantharoidea and Buprestoidea Recording Scheme has been in operation since 1984 and is one of a series of recording schemes operated through the UK Biological Records Centre. This particular Scheme covers both Great Britain and Ireland (Alexander 1992, 1994, 1999, 2000). A provisional atlas is due out soon and the data set is very new and not yet published.

This data set is presented here as a ‘random’ slice of our fauna, and examined to see if any large-scale changes in distribution are apparent. This taxonomic grouping comprises about 60 species of beetle, with the Cantharidae primarily predatory species and the Buprestidae phytophagous. Their conservation status varies from British Red Data Book (Shirt 1987) – six species – right through to more or less ubiquitous species.

The coverage of Great Britain achieved during the operation of the Scheme has been reasonably good. Figure 1 shows the distribution of a fairly ubiquitous species *Cantharis cryptica* Ashe, 1947. However, older records are of variable quality and quantity making assessment of change difficult. Detection of gross change is possible, but gradual declines or increases may not be detectable.

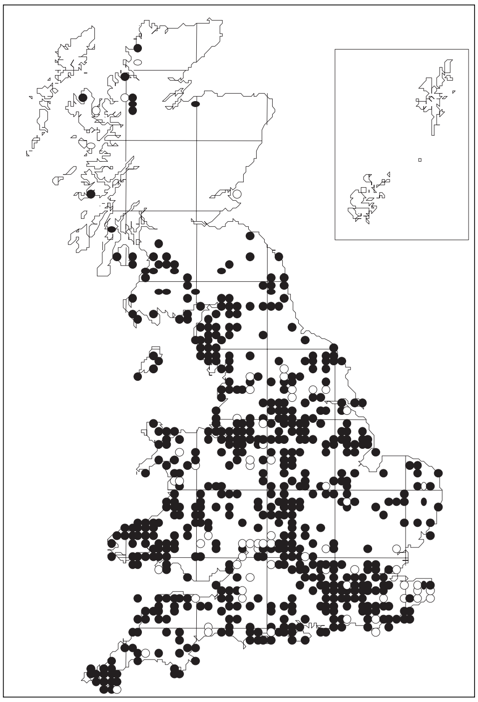

Figure 1
Distribution map for *Cantharis cryptica*. Each circle represents a 10 km square of the Great Britain and Irish National Grids – open circles represent record dates only pre 1980, closed circles for records 1980-2000.

Changes within past 100 years

Many distributions appear relatively stable, even with highly localised species, like *Ancistronycha abdominalis* (Fabricius, 1798) (fig. 2, 3), which is a species of open woodlands in the uplands. *Cantharis obscura* Linnaeus, 1758 shows a similar pattern.

Others show gross declines and range contractions which reflect the well-documented destruc-

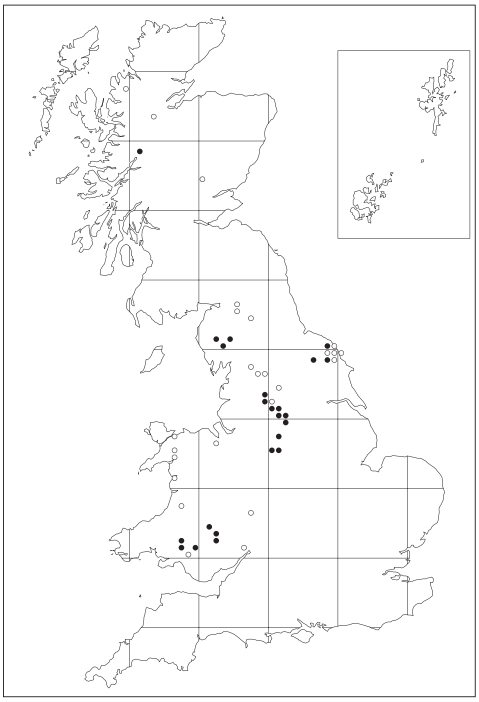

Figure 2
Distribution map for *Ancistronycha abdominalis*. Each circle represents a 10 km square of the Great Britain and Irish National Grids – open circles represent record dates only pre 1980, closed circles for records 1980-2000.

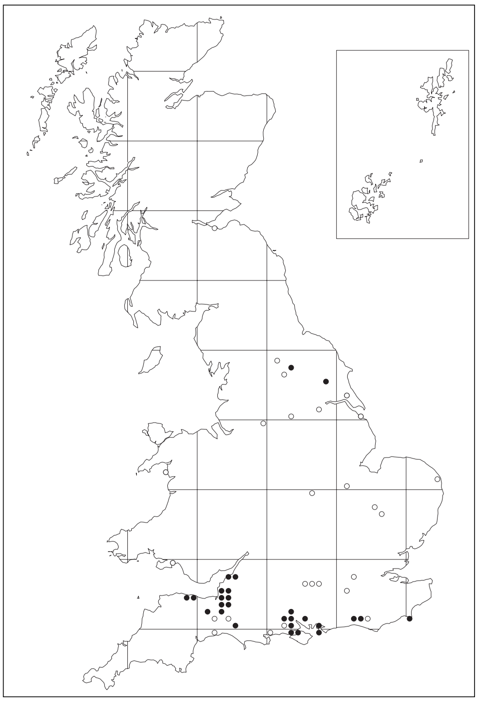

Figure 4
Distribution map for *Cantharis fusca*. Each circle represents a 10 km square of the Great Britain and Irish National Grids – open circles represent record dates only pre 1980, closed circles for records 1980-2000.

tion of semi-natural habitats through intensification of agriculture etc., like *Cantharis fusca* Linnaeus, 1758 (fig. 4), a speciality of damp hay meadows and marshy grasslands. Other species characteristic of these habitats, such as *Cantharis figurata* Mannerheim, 1843, *C. pallida* Goeze, 1777 and *C. thoracica* (Olivier, 1790) show no obvious large scale changes in range but undoubtedly have been lost from many localities within their ranges. Despite its dramatic decline across Britain, *C. fusca* does not feature in the British Red Data Book and has not been picked out as a Species of Conservation Concern during current Biodiversity Action Plan initiatives in Britain.

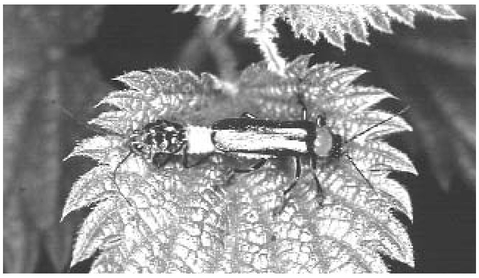

Figure 3
Ancistronycha abdominalis, adult beetles in copulation. Photo R. Thomas.

Other species similarly show declines through habitat loss:

- the ancient tree specialists *Malthinus frontalis* (Marsham, 1802) and *Malthodes crassicornis* (Mäklin, 1846);
- the coppice woodland species *Agrilus angustulus* (Illiger, 1803);
- open woodland species *Agrilus laticornis* (Illiger, 1803), *Rhagonycha lutea* (Müller, 1764) and *R. translucida* (Krynicki, 1832).

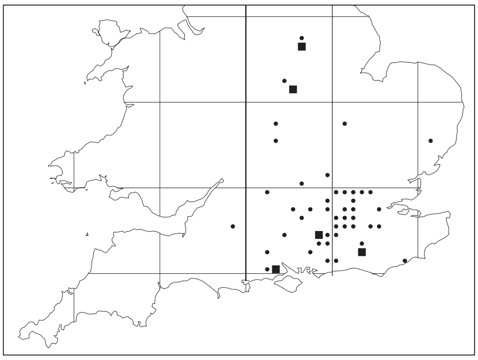

Figure 5
Distribution map for *Agrilus pannonicus*. Squares represent areas with records prior to 1980, with circles more recent records.

Figure 6
Agrilus pannonicus, adult beetle. Photo: R. S. Key.

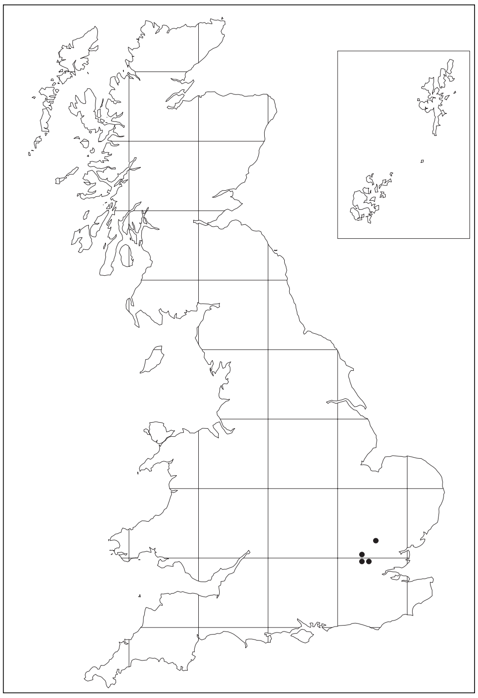

Figure 7
Distribution map for *Agrilus sulcicollis*. Each circle represents a 10 km square of the Great Britain and Irish National Grids – open circles represent record dates only pre 1980, closed circles for records 1980-2000.

Even a few of the more generally widespread species appear to be showing early signs of countrywide decline, like *Cantharis livida* Linnaeus, 1758 and *C. rufa* Linnaeus, 1758 (Alexander 1999).

Changes within past 20 years

In contrast, two Buprestidae have shown dramatic changes in range during the 20 years of the Recording Scheme. *Agrilus pannonicus* (Piller & Mitterpacher, 1783) = *A. biguttatus* (Fabricius, 1777) (fig. 5, 6), develops in dying and freshly dead thick bark on oak trees (*Quercus robur*). It is widespread across central Europe, within the main range of the host tree, but has a very localised relict distribution in the northern parts of its range, e.g. in the oak forest areas of southern Norway and Sweden (Bílý 1982). Until recently its distribution in Britain was very stable. It was regarded as a classic relict old forest species. Its known localities were the medieval old forests, such as Sherwood, Windsor, the New Forest, and a very small number of other sites.

It began to be found more widely from the early 1980s, so the population was at a strong point when the south-east of England received some severe storms, especially in 1987. At the time this event was claimed to be part of a ‘natural’ cycle, but, with hindsight, it seems more likely to be a manifestation of predicted effects of global climate change brought about through the activities of mankind.

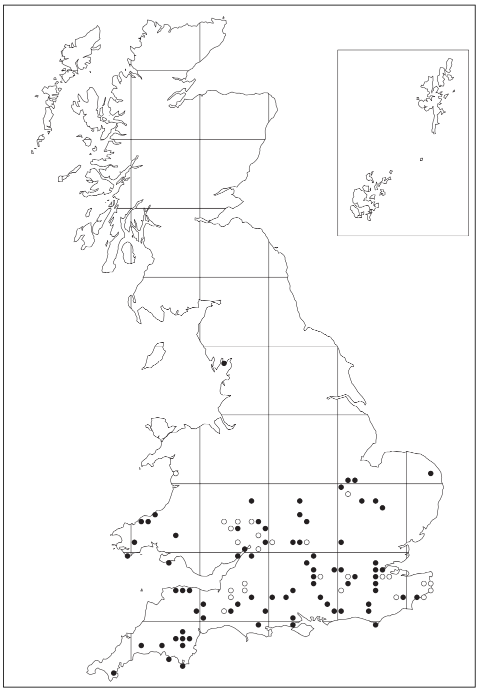

Figure 8
Distribution map for *Malthinus balteatus*. Each circle represents a 10 km square of the Great Britain and Irish National Grids – open circles represent record dates only pre 1980, closed circles for records 1980-2000.

A previously unknown fungal disease on oak also appeared during the 1990s and continues to provide a steady supply of suitable host trees – probably another manifestation of the undesirable effects of globalisation!

Agrilus sulcicollis Lacordaire, 1835 (fig. 7) is a species unknown in Britain when the Scheme was launched in 1984. It is another oak *Quercus* bark species. It was first detected in the British Isles in 1992 in Hertfordshire, and has subsequently been found in a wide arc of country across the north of London: Middlesex (1998), and Bedfordshire and Essex (2000). It is assumed that it was first introduced accidentally with imported timber.

A third species, *Agrilus sinuatus* (Olivier, 1790), appears to have been expanding locally in response to increased extent of its larval habitat in agricultural land – old hawthorns *Crataegus monogyna* which have developed along field boundaries where they are no longer maintained by cutting and on rough hillsides which are no longer grazed.

Predictions for future changes

If the local climate continues to warm then it should be possible to predict which species will begin to show noticeable change.

Interestingly *Agrilus sulcicollis* is one of three species which Levey (1977) predicted might become established in Britain on the basis of their known distribution in northwestern Europe. We await the arrival of the other two species: *Agrilus cyanescens* Ratzeburg, 1837 (develops in woody growth of *Lonicera* species) and *Anthaxia quadripunctata* (Linnaeus, 1758) (develops under bark on spruce *Picea* and pine *Pinus*) – the latter has been brought in with imported timber in the past but has never established itself in the wild.

Other species which currently show a southern distribution in Britain may be expected to expand northwards. *Malthinus balteatus* Suffrian, 1851 (fig. 8) is a species of moist woodlands across southern Britain and appears to be a relatively mobile species within its range. *Malthinus seriepunctatus* Kiesenwetter, 1851 is more catholic in its choice of woodland habitats and is similarly southern and relatively mobile.

It is very difficult to offer predictions beyond these simple approaches as climate change models suggest a wide range of effects which will vary in different areas of the country. Species presently with a northerly distribution may be expected to retreat northwards if the climate warms, but it has been suggested that these upland areas will also become wetter and so the impact on the local insects will be very complex.

Conclusions

Examination of this small group of beetles – selected as a random slice of the British fauna – reveals significant changes.

The main changes currently detectable are of declines which reflect the loss and degradation of semi-natural habitats directly through human land-use. A high percentage of the 60 species have declined significantly during the 20th century – 12 (20%) of the species give serious cause for conservation concern (Alexander, 1999). Others also show signs of extensive decline.

Only two or three species are currently showing expanded distributions within Britain. These are variously thought to be due partly to global climate change, partly to globalisation, and partly to changing land-use patterns.

To some extent, predictions can be made about which other of these beetle families are likely to show detectable changes in range in the near future, although this is a very complex area.

The overarching conclusion is that habitat loss and degradation remain the main issues for conservation attention. Global climate change will merely exacerbate the problems. Changing distributions of species may just be a distraction.

Acknowledgements

The data presented here have been collected by a large number of entomologists throughout Great Britain, acting in a voluntary capacity, and have been processed by the UK Biological Records Centre.

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Post-glacial dispersal strategies of Orthoptera and Lepidoptera in Europe and in the Carpathian basin

Zoltan Varga

Abstract

Ecologically transitional regions are characterised by high species diversity due to the overlap of species with different geographical origins caused by dispersal processes along gradients, e.g. the overlap of species belonging to different zonobiomes. The overlap of azonal communities along short-distance gradients results in the organisation of community-complexes and landscape mosaics connected by habitat ecotones characterised by overlap of several faunal types, like Mediterranean, Balkanic, Siberian, Ponto-Caspian, Ponto-Pannonian, Turano-Eremic and Xeromontane elements in the Pannonian forest-steppe complexes.

For some invertebrate groups, such as the land gastropods or some soil arthropods, the Carpathian basin contains a considerable proportion of endemic species. The eastern and southern Carpathians, together with the mountains of western Transsylvania, can be considered as core areas of survival and autochtonous evolution in some invertebrate groups with limited mobility. In mobile insect groups only peripherically isolated sibling (sub)species have evolved, which display manifold biogeographic connections, for instance to the Balkan peninsula, Asia minor or southern Russia. The distribution of Mediterranean-Manchurian bicentric faunal elements, connected to the Ponto-Caspian waterway-system, shows long-distance disjunctions from the eastern Asiatic taxa. Gallery forests of the Illyrian and Pannonian types and wetlands accompanying the large rivers of the Pannonian lowland have served as corridors of the northward expansion of these species.

The post-glacial repopulation of the Carpathian basin from different directions has been supported by Illyrian versus Dacian vicarious pairs of sister (sub)species. Cases of vicarious 'Siberian'-Mediterranean sibling taxa have also been established. Recent results confirm that the montane part of the range of several 'Siberian' boreo-montane species does not have its origin in post-glacial 'Siberian' invasion.

Populations of some butterfly species have been studied in different geographical scales. Patterns of metapopulation structure and of genetic differentiation have been established.

Key words: biogeography, Lepidoptera, Orthoptera, dispersal, Carpathian basin.

Introduction: biodiversity and phylogeography

The continuity of life is maintained by distinct biological individuals of limited life-span. Similarly, the continuity of changing genetic information, called evolution, is carried by species of limited life-span. Species diversity is generated by *branching processes* called *speciation*: by partition of the genetic variation into distinct breeding systems with specific mate recognition signals (SMRS) and separated by reproductive isolation. The subdivision of the formerly at least potentially coherent gene-pool results in the genealogical diversity (Eldredge 1985, Eldredge & Salthe 1984). *Genealogical diversity* is usually connected with some *core areas* which can be outlined by areographical methods and tested by tools of the phylogenetic analysis (Cracraft 1983, Cracraft & Prum 1988). The other aspect of the biological diversity is the *compositional* one. Due to dispersal, overlap and survival of species belonging to different biogeographical types some regions can be characterised by the accumulated presence of floristic and faunistic elements of diverse age and different geographical origin.

The study of the structure and dynamics of ranges by genetic markers, called 'phylogeography' (Avise 1989, 1994, 1999, Avise & Hamrick 1996, Roderick 1996) has become to one of the most rapidly evolving fields of population biology. Phylogeny means the topology of the process of evolution at different hierarchical levels of organisation (Avise 1994): the level of genetic identity versus non-identity, the level of kinship in sexually reproducing organisms, the level of differentiation into ecotypes, geographical races and species (the level of emerging reproductive barriers) and the level of phylogenetic lineages separated by reproductive isolation (monophyletic supraspecific units). The study of genetic differentiation of genealogical lineages and the analysis of the processes governing their geographical distribution (phylogeography) has demonstrated that the cladograms of groups of related species (supraspecific taxa) should match the historical 'area-cladograms' of the geographical ranges occupied by them (Enghoff 1993, 1995, Oosterbroek & Arntzen 1992). The processes which generate spatial patterns of diversity, exhibit some basic features:

- The genetic differentiation of populations results in 'elementary' branching processes which form a reticulating network of populations connected by more or less regular, or restricted gene-flow, as a consequence of full or limited exchangeability of individuals.
- There are 'hot spots' (core areas of diversity), characterised by the occurrence of numerous strictly endemic species. These areas appear to be repeated more or less regularly in the different taxonomical groups. The 'hot spots' are considered to have a long-term ecological stability (Fjeldså & Lovett 1997, Fjeldså et al. 1997), which cause the accumulation of the genetic information ('gene-centres'). The genealogical connections of endemic taxa, belonging to well-defined core areas, can be analysed by phylogenetic methods ('areas of endemism', Harold & Mooi 1994).
- There are ecologically transitional regions with high numbers of species, but without high proportions of endemism (Williams et al. 1999, 2000). They are characterised by the overlap of ranges of species of different geographical origins caused by dispersal processes along gradients. An example is the overlap of species belonging to different zonobiomes and azonal communities in forest-steppe areas of the Carpathian basin (Varga 1995).

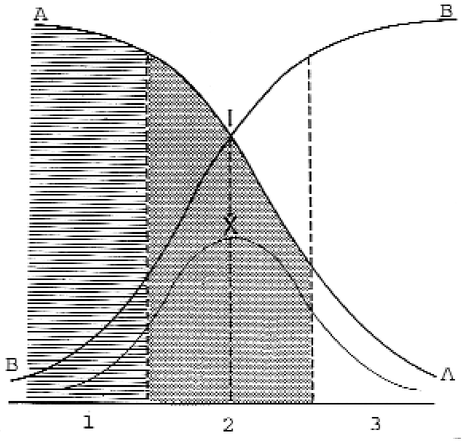

Figure 1
The graph and sectors of the 'centrifugally' decreasing species number of a faunal type under ideal conditions. A. centrifugal decrease of the species number, B. cumulative curve of the normal type of distribution, X. arithmetic mean of the normal distribution (Gauss curve), I. point of inflexion, 1. section of the zonal distribution of the faunal type, 2. section of the disaggregation (fluctuation) of the faunal type (with peripheric subspeciation), 3. section of the biogeographical extinction of the faunal type.

In this paper, the biogeographical terminology is adopted from Natura 2000 (Council of Europe 1998).

Overlaps by dispersal along gradients

In the Palaearctic region, the most important possibility of long-distance extension is the east-west dispersal along geographical latitudes, north to the chains of the Eurasiatic mountain system. A large number of 'trans-Palaearctic', Euro-Siberian areas has been established by this mechanism, which resulted in the formation of several peripherically isolated and often taxonomically differentiated populations at the zone of 'disaggregation' of the distribution at the mountain regions of Central and South Europe (Varga 1977). Supposed the normal distribution of area sizes belonging to the same core area (to the same faunal type), the graph of the centrifugally decreasing species number represents the inverse of the cumulative graph of the normal distribution, which can be subdivided into three sectors by tangents of maximal convexity and concavity of the graph (fig. 1): the sector of 1. zonal distribution, 2. disaggregation and 3. the extinction of the faunal type in question. The normal distribution of the area sizes will be performed only under ideal conditions. Under real circumstances it is strongly influenced by climatic, orographical and other conditions. For instance, the Pyrenees and the Carpathians have served as effective barriers of dispersal in numerous atlanto-mediterranean (including Lusitanian) and ponto-mediterranean (including Balkanic) species, respectively. Thus, in these faunal types the number of species with restricted areas is relatively high, as illustrated by the numerous Iberian and Balkanic endemics.

In the Palaearctic region there are two main consequences of dispersal along gradients:

1. The overlap of zonobiomes along long-distance gradients: formation of transitions with overlaps of ‘zonal’ sectors of several faunal types, e.g. the overlap of Mediterranean (s.l.), Ponto-Caspian and Siberian (West-Siberian, Mandzhurian, East-Siberian) faunal types in the East European forest-steppe, with gradual decrease of the Mediterranean component and increase of the Siberian component along a west-eastern gradient (De Lattin 1957, 1967). This appears to be typical for the orographically less varied eastern European (Boreal, Continental and Steppic) regions.
2. The overlap of azonal communities along short-distance gradients resulting in the organisation of community-complexes (‘sigmeta’ of German phytosociological tradition) and landscape mosaics connected by habitat ecotones. These community-complexes are characterised by the overlap of several faunal types, both in zonal sectors and in sectors of disaggregation, e.g. the overlap of Mediterranean, Balkanic, Siberian, Ponto-Caspian, Ponto-Pannonian, Turano-Eremic and Xeromontane faunal elements in the Pannonian forest-steppe complexes (Varga 1989a, 1992, 1995, 1996, 1997). They have been proved to be rather dynamic overlaps, often with short-term fluctuation dynamics, especially in the boundary regions of lowland and hilly areas, with a variety of relatively stable versus mobile ecotones.

The orographically varied landscapes of Central Europe and the Carpathian basin display several different cases of short-distance overlaps. Southern parts of Central Europe, North of the Alps and Balkans (like southern France, southern Germany, hilly parts of the Carpathian basin, Williams et al. 1999, 2000) belong to the regions of Europe having the highest number of species in vascular plants, in some groups of insects and vertebrates, without a significant fraction of point-endemics. This clearly demonstrates the importance of the overlap of different floral and faunal elements populated this region post-glacially from different core areas.

The mosaic-like structure of the traditional Central European cultural landscape with a variety of managed open habitats and their ecotones (hedges, ridges, lines of trees, forest fringes etc.) in a forested matrix proved to be rather suitable to preserve the connectivity of habitats and also a high level of *compositional* diversity. A large number of species has been successfully adapted to moderate perturbations (extensive grazing, mowing by hand, coppicing), typical for traditional land use (fig. 2).

Endemism and autochtonous evolution in the Carpathian basin

Core areas are characterised by numerous endemic taxa. The level of endemism is generally correlated with the geological age of the refugia where relict-like taxa have been evolved and/or could survive (Fjeldså & Lovett 1997). From a geological point of view, the Carpathian basin belongs to the youngest areas of Europe. Its relief has developed under the influence of the Alpine orogenesis and by retreat of the Pannonian inland sea. There are, however, some taxonomical groups which show considerable proportion of endemic species, such as the land gastropods (Soós 1943), or some soil arthropods, like Opiliones and Diplopoda (Korsós 1994).

Most endemics are narrow specialists, inhabiting extreme habitats: thermal springs (Gastropoda: *Melanopsis parreysi* Philippi, *Theodoxus prevostianus* C. Pfeiffer), karstic caves (Gastropoda: Paladilhia hungarica Soós, *Paladilhiopsis* spe-

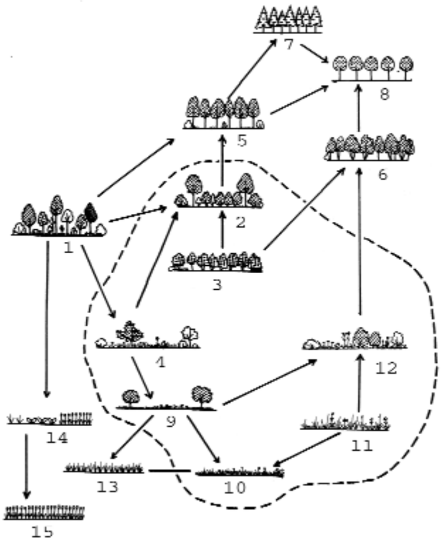

Figure 2
Habitat types and species diversity in the European cultural landscape. 1. virgin forest, 2. nature-like mixed forest after logging and abandoning, 3. young forest after coppicing ('Niederwald'), 4. grazed steppe forest ('Hudewald'), 5. homogenous managed forest ('Hochwald'), 6. dense medium-aged forest after repeated coppicing, 7. coniferous plantation, 8. deciduous, intensively used plantation, 9. wooded pasture, 10. extensively managed greenland (hayfield), 11. abandoned, semi-natural grassland with tall-forbs ('Versaumung'), 12. abandoned, semi-natural grassland with tall-forbs and scrubs, 13. intensive greenland, 14. traditional agricultural land, 15. intensively used, monoculture-like agricultural land. Area surrounded with broken line: habitat types with high species diversity.

cies; Palpigradi: *Eukoenenia vagvoelgyii* Szalay; Amphipoda: *Niphargus* species; Isopoda: *Mesoniscus graniger* I. Frivaldszky; Diplopoda: *Brachydesmus troglobius* Daday, *Haasea hungarica* Verhoeff, *Hungarosoma bokori* Verhoeff; Carabidae: *Anophthalmus*, *Duvalius*, *Typhlotrechus* species) and karst springs (Gastropoda: *Sadleriana pannonica* Frauenfeld; Trichoptera: *Drusus*, *Rhyacophila* species, mostly in the Apuşeni mountains and the eastern and southern Carpathians).

The endemic insects of the Carpathians are, as a rule, short-winged, flightless forms which have been isolated in 'massifs de refuge' (Orthoptera: *Isophya*, *Odontopodisma*, *Poecilimon* species; the relict-like species: *Capraiuscola ebneri* Galvagni, *Podismopsis transsylvanica* Ramme, *Uvarovitettix transsylvanica* Bazyluk & Kis, *Zubovskia banatica* Kis; Kis 1962a,b, 1965, 1980; Coleoptera, Carabidae: *Duvalius*, *Morphocarabus*, *Patrobus*, *Trechus* species; Curculionidae: *Otiorrhynchus* species) (some of these species have been suggested for inclusion into the Annex II-IV of the Natura 2000). The bulk of these endemic taxa is confined to the Eastern and Southern Carpathians, to the Apuseni mountains and to the mountains of Banat, which could preserve relict species (such as the Tertiary relict gastropods *Chilostoma banaticum* Rossmaessler, *Pomatias rivulare* Eichwald) or point-endemics (Orthoptera: *Capraiuscola ebneri* Galvagni, *Podismopsis transsylvanica* Ramme, *Uvarovitettix transsylvanica* Bazyluk & Kis, *Zubovskia banatica* Kis; Isopoda: *Hyloniscus transsylvanicus* Verhoeff, *Protracheoniscus politus* C.L. Koch; Diplopoda: *Entomobielzia gaetica* Verhoeff, *Karpathophilon dacicus* Verhoeff) in refugia of deciduous forests, in areas with not frozen soil during the younger glaciations (Bennett et al. 1991, Krolopp & Sümegi 1995, Willis et al. 1995).

In the more mobile insect groups, the proportion of endemism lies rather low. For instance, in Odonata no endemic taxa occur in the Carpathian basin. Most endemic Lepidoptera of the Carpathian basin belong to Microlepidoptera, which are strictly specialised to some food-plants and the females are flightless, for instance species of Coleophoridae: *Coleophora hungariae* Gozmány (*Camphorosma annua*), *C. peisoniella* Kasy (*Artemisia santonicum*), Gelechiidae: *Ilseopsis hungariae* Staudinger, *I. salinella salicorniae* E. Hering (*Salicornia prostrata*), living on halophytic plants in the saline grasslands of the Fertő-Neusiedlersee area and of the Great Hungarian plain (Kasy 1965, 1981). Endemic subspecies of Geometridae and Noctuidae have evolved in the same habitats, as peripheric isolates of turano-eremic species from the late-glacial, kryoxerotic periods, like *Narraga tessularia kasyi* Moucha & Povolny, *Saragossa porosa kenderesensis* Kovács (*Artemisia santonicum*, *A. pontica*) and *Discestra dianthi hungarica*

Wagner (*Gypsophila muralis*). Some endemic taxa of the sandy areas of the Pannonian lowland are specialised predators or parasitoids, such as the spider *Dictyna szaboi* Chyzer and the pompilid wasp *Cryptocheilus szabopatayi* Móczár. Further species described as endemics later proved to be widespread steppicolous species.

In majority the endemics of the lower, hilly parts of the Carpathian basin, however, represent thermophilous post-(inter?-)glacial relicts with connections to the Balkan peninsula, Asia minor or southern Russia (for instance, in warm-humid alluvial areas: *Apamea sicula tallosi* Kovács & Varga, in Pannonian xerothermic oak forests: *Dioszeghyana s. schmidtii* Diószeghy, *Asteroscopus syriacus decipulae* Kovács, in the Villány mountains: *Polymixis rufocincta isolata* Ronkay & Uherkovich; in the dolomitic areas of the Transdanubian Middle Range: *Chersotis f. fimbriola* Esper, *Euxoa v. vitta* Esper, *E. hastifera pomazensis* Kovács, *Cucullia mixta lorica* Ronkay & Ronkay; in the Aggtelek Karst: *Chersotis fimbriola baloghi* Hacker & Varga). Similar connections can be observed in butterfly species, restricted to special, Pontic-Pannonian food plants, like *Plebeius sephirus* I. Frivaldszky (*Astragalus dasyanthus*, *A. exscapus*), *Melitaea telona kovacsi* Varga (*Cirsium pannonicum*).

Some endemic Macrolepidoptera subspecies of the Carpathians belong to the genera *Erebia* (*E. epiphron transsylvanica* Rebel, *E. pharte belaensis* Goltz, *E. manto traianus* Hormuzachi, *E. gorge fridericikoenigi* Varga, *E. pandrose roberti* Peschke, *E. pronoe regalis* Hormuzachi) and Glacies (*G. coracina dioszeghyi* Schmidt, *G. noricana carpathica* Schwingenschuss, *G. canaliculata schwingenschussi* Wehrli). Some endemic taxa are widespread in the Carpathians and in the neighbouring mountainous areas, like *Aricia artaxerxes issekutzi* I. Balogh and *Photedes captiuncula delattini* Varga, others are confined to the southern Carpathians, often with balkanic connections: *Erebia cassioides neleus* Freyer, *Coenonympha rhodopensis schmidtii* Diószeghy. The subspecies of *Erebia melas* inhabit island-like, calcareous mountain stocks, *Erebia m. melas* Herbst in Cernei mountain, *E. melas carpathicola* P. Gorj & Alexinschi in the eastern Carpathians and *E. melas runcensis* König in Apuşeni mountain). All these data clearly demonstrate that the Carpathians, especially the eastern and southern parts, together with the mountains of western Transsylvania (Apuºeni and Banat mountains) can be considered as core areas of survival and autochtonous evolution in many invertebrate groups of limited mobility. On the other hand, in the mobile insect groups, only peripherically isolated subspecies have been evolved, which display manifold biogeographic connections.

Relict species with long-distance disjunctions in the Carpathian basin

Several Mediterranean-Manchurian bicentric faunal elements with disjunct ranges occur in the Carpathian basin. The distribution of this species group is connected to the Ponto-Caspian waterway-system, and displays long-distance disjunctions from the eastern Asiatic vicariant taxa, which are often only subspecifically differentiated (Lepidoptera: *Apatura m. metis* Freyer – *Apatura metis substituta* Butler, *Chariaspilates formosarius hungaricus* Vojnits – *Chariaspilates f. formosarius* Eversmann, *Rhyparioides m. metelkanus* Lederer – *Rhyparioides metelkanus flavidus* Bremer, *Arytrura musculus* subspecies – *Arytrura m. musculus* Ménétries). Some species of this group occur at the lower course of the Danube and Drava and also in swampy-boggy areas of the lowlands in Transdanubia, in the Banat and eastern Hungary (*Polypogon gryphalis* Herrich-Schaeffer, *Herminia tenuialis* Rebel, *Diachrysia nadeja* Oberthur and also the species mentioned above). The refugia of these faunal elements had probably been at the lower course of the Danube and its tributaries. Gallery forests of the Illyrian and Pannonian type and alluvial wetlands accompanying the large rivers of the Pannonian lowland have served as corridors of the northward expansion of these species.

Different types of long-distance disjunctions have been observed in the relict-like steppe and semi-desert species. The polytypic butterfly *Melanargia russiae* Esper, widespread in West and Central Asia, South Siberia and in mountains of Italy and Balkan peninsula, had locally occurred – as *M. russiae clotho* Herbst – on tall-grass clearings of birch gallery forests of the sandy lowland in Kiskunság. Its extinction was partly the consequence of overcollecting, but mostly of destroying of the habitats (re-forestation with black locust *Robinia pseudoacacia*). The habitats of *Chondrosoma fiduciarium* Anker (Kasy 1965, 1981) are also tall-grass lowland and hilly steppes, often mixed with slightly saline patches. Other species are confined to open dolomitic rocky swards (*Phyllometra culminaria* Eversmann, *Lignyoptera fumidaria* Hübner, *Cucullia mixta lorica* Ronkay & Ronkay) or to open sandy and rupicolous grasslands (*Oxytripia orbiculosa* Esper, also vanishing). The rapidly growing garden suburbs of the Buda hills and the metastasis-like expansion of 'green-field' investments around the capital are the most recent threatening factors, often with considerable political and economical interests in the 'background'.

There are numerous halophytic food-plant specialists of the alkaline habitats, mentioned above, which are specifically or subspecifically differentiated. They represent marginal isolates of turano-eremic species, widespread in Transcaspia and Central Asia. The common characteristic feature of the area structure of these species is the large-scale disjunction between the Carpathian basin and the Eastern Ucranian-South Russian steppes.

Polycentric postglacial repopulation patterns in the Carpathian basin: areography and phylogeography

The Carpathian basin belongs to the regions of Europe, which have the highest biodiversity (Williams et al. 1999, 2000). Due to its transitional position during the Quaternary climatic fluctuations, the overlap and accumulation of the floristic and faunistic elements of contrasting habitats took place here. The overlapping of different climatic provinces, enhanced by the varied relief, edaphic and hydrographic conditions, has resulted in suitable conditions to survive for a large number of species, belonging to different core areas and displaying various patterns of long-distance and short-distance re-populations.

The 'molecular toolbox' of phylogeography (Roderick 1996) have facilitated the recent re-visitation of many taxonomical and biogeographical problems. 'Hard' evidences gained by molecular studies could support, complete or correct some of the previous biogeographical hypotheses. For instance, numerous genetic analyses could verify the existence of different glacial refugia within the Mediterranean region (Assmann et al. 1994; Cooper et al. 1995, Demesure et al. 1996, Dumoulin-Lapègue et al. 1997, Hewitt 1996, 2000, Lagercrantz & Ryman 1990, Schmitt & Seitz 2001a, Schmitt et al. 2001, Taberlet & Bouvet 1994, Taberlet et al. 1994, 1998, Wallis & Arntzen 1989) and demonstrated, that several species have repopulated Central Europe in the post-glacial period from different refugia in more waves. The 'secondary subdivision' (De Lattin 1957, 1967, Reinig 1950) of the Mediterranean refugium has also been repeatedly demonstrated, for instance in *Chorthippus parallelus* Zetterstedt, in the European hedgehog (Santucci et al. 1998) or by the comparative area analysis of several plant and mammalian species (Cooper et al. 1995, Hewitt 1996, Taberlet et al. 1998). The importance of the Siberian refugium (s.l.) has been pointed out (Nève 1996, Taberlet & Bouvet 1994, 1998) and evidence has been found supporting some kinds of the Mediterranean-Siberian polycentry in several cases (Nève 1996, Schmitt 1999, Schmitt et al. 2000, Schmitt & Seitz 2001b). In contrast with the opinion of De Lattin (1957, 1967), these results confirm the statement of the author (Varga 1975, 1977, 1989b) that the montane part of the ranges of several boreo-montane species has not been established by post-glacial 'Siberian' invasion, but has been formed by South European montane refugia. Results of selected lepidopterological studies are summarized here.

The Illyrian-Dacian vicariant taxa: the importance of the southwest-southeast 'pincer'

Because the Carpathian basin had occupied a transitional position between the Balkanic refugia and the cold-continental periglacial loess steppe zone during the glacial periods, the postglacial repopulation of the Carpathian basin has proceded both 1. by long-distance dispersal from the more remote (atlanto- and ponto-) Mediterranean and southern continental refugia, and 2. from some adjacent local survival areas, for instance from Northwest Balkanic ('Illyrian') versus South Transylvanian ('Dacian') Arboreal refugia. In such cases the 'arrows' of the northward dispersal of the southwestern and southeastern populations surround the mostly arid central part of the basin. These components of the flora and fauna extend northwards on the one hand through the foothills of the eastern Alps and Southwest-Pannonian hilly regions, and through the hilly regions of the Banat area and the western foothill of the Transylvanian 'Island' mountains (Apuşeni mountain), on the other. These areas are also characterised by some secondary precipitation maxima of sub-Mediterranean type during the 'aequinoctial' periods of the year.

In some cases the populations of the southwestern and southeastern 'strains' do not display any significant taxonomical differentiation, for instance in the silver lime (*Tilia tomentosa*) or some butterflies and moths (*Pyronia tithonus* Linnaeus, *Maculinea arion ligurica* Wagner, *Aplasta ononaria* Fuessly, *Idaea nitidata* Herrich-Schaeffer, *Zanclognatha tenuialis* Rebel). Much more evident is the repopulation of the Carpathian basin from different directions in the cases of vicarious pairs of closely related species or in subspecies of polycentric species. Such cases can be mentioned mostly for land gastropods, like *Pomatias elegans* O.F. Müller – *P. rivulare* Eichwald, *Chilostoma illyricum* – *C. banaticum* Rossmaessler, or in flighless insect groups, like short-winged Orthoptera: *Odontopodisma schmidti* Fieber – *O. rubripes* Ramme, *Isophya modestior* Brunner von Wattenwyl – *I. stysi* Cejchan. In the latter pair of species, a clear differentiation in the stridulation and in allozyme pattern has been observed (Orci et al. 2001, Pecsenye et al. in prep.). In addition, some vicariant atlanto- versus ponto-Mediterranean sibling pairs can also be observed in the more mobile insect groups, as in the butterflies *Spialia sertorius* Hoffmannsegg and *S. orbifer* Hübner.

The Mediterranean-Siberian polycentricity in the Carpathian basin

There are numerous cases of vicarious 'Siberian' (s.l.) – Mediterranean/arboreal and 'Siberian' (s.l.) – Mediterranean/oreal sibling taxa. By 'Siberian' we understand all continental arboreal species dispersed north of the steppe zone and which did not pass into the Mediterranean region. They have formed the ultimate peripheric isolates in the high mountains of this area, which represent a 'fluctuation belt' of Siberian faunal type (Varga 1977). The 'Siberian' species are widespread in temperate Eurasia ('Euro-Siberian' or trans-palaearctic type of area), and usually exhibit a wide range of morphological variation and ecological valence (e.g. the butterfly species *Maculinea arion* Linnaeus, *Melitaea phoebe* Denis & Schiffermüller, *Mellicta athalia* Rottemburg, *Euphydryas aurinia* Rottemburg). Their Mediterranean vicarious taxa (sibling species or semispecies) are usually confined to one of the Mediterranean 'secondary refugia' (De Lattin 1957, 1967): *M. a. ligurica* Wagner to the Adriato-Mediterranean, *M. ph. telona* Fruhstorfer to the ponto-Mediterranean, *P. m. malvoides* Elwes & Edwards, *M. a. celadussa* Fruhstorfer and *E. a. desfontainei* Boisduval to the atlanto-Mediterranean refugia.

They also often have a considerable range of variation, in some cases due to the incomplete reproductive isolation and hybridisation with the 'Siberian' taxa. Habitats, food-plants and phenological traits of the Siberian-Mediterranean vicarious pairs are often different. *Maculinea a. arion*, for instance, is connected to short-grass swards with cushions of *Thymus* species (Thomas 1995), which is the initial larval foodplant (exceptionally also *Origanum vulgare*). On the contrary, the initial foodplant of *Maculinea a. ligurica* is exclusively *Origanum vulgare*. The imaginal period is synchronised with the flowering period of *Thymus* and *Origanum*, respectively, because the females usually deposit the eggs on flower capitula of the initial food-plant. Thus, sympatric populations of both are ecologically and seasonally isolated. The Siberian species, *Melitaea phoebe* is euryoecious, polyphagous (with food-plants: *Centaurea*, *Carduus*, *Cirsium* species etc.) and widespread in the Carpathian basin. In contrast, the Ponto-Mediterranean sister (semi-) species *M. telona* is restricted to forest-steppe mosaics with semi-dry swards, where its larval food-plant, *Cirsium pannonicum* is abundant. *Melitaea phoebe* is regularly bivoltinous, while *M. telona* only exceptionally produces a very scarce second brood in the Carpathian basin.

In the case of the Siberian – Ponto-Mediterranean oreal pair of heath butterflies *Coenonympha tullia* Müller and *C. rhodopensis* Elwes the isolation is complete, as the vicarious taxa occupy only topographically, but not ecologically overlapping

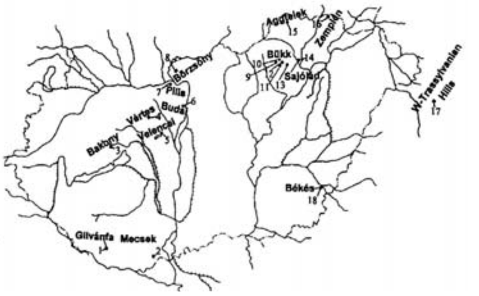

Figure 3
Sampling localities of *Parnassius mnemosyne* populations. 1. Gilvánfa, 2. Misina (Mecsek mountains), 3. Hárskút (Bakony mountains), 4. Vérteskozma (Vértes mountains), 5. Nadap (Velencei mountains), Nagyszénás (Budai mountains), 7. Pilisszentkereszt (Pilis mountains), 8. Magas-Tax (Börzsöny mountains), 9. Bányahegy (Bükk mountains), 10. Lusta valley (Bükk mountains), 11. Gyertyán valley (Bükk mountains), 12. Hollóstetö (Bükk mountains), 13. Kékmezö (Bükk mountains), 14. Sajólád, 15. Nagyoldal (Aggtelek karst), 16. Nagy-Milic (Zemplén mountains), 17. Szokácsi forest (West-Transsylvanian hills), 18. Békés.

areas in the Dinaric karst area. Similar trends have also been observed in the polymorphic lycaenid *Aricia artaxerxes* Fabricius – *inhonora* Jachontov – *allous* Geyer – *montensis* Verity superspecies, consisting of Siberian, European (sub-)alpine and Mediterranean-oreal taxa. The phylogeographical analysis of such supraspecific groups can explain some basic trends of the Quaternary faunal history in the Palaearctic.

In this context, the results of Schmitt (Schmitt 1999; Schmitt & Seitz 2001b) proved to be especially relevant. He subdivided the European populations of *Erebia medusa* Denis & Schiffermüller into five main groups, based on the study of 19 enzyme loci in 53 samples. The 'West-Central European' group (*E. medusa brigobanna* Fruhstorfer) consists of populations from France and Germany and one single sample from the Czech Erz mountains. The large 'East-Central European' group (*E. m. medusa* Denis & Schiffermüller) includes all populations from Czechia, Slovakia and North Hungary. The third group of populations is formed by those of West Hungary (and probably also West Balkans; *E. medusa narona* Fruhstorfer), while the isolated deme from Monte Baldo (southern Alps; *E. medusa hippomedusa* Ochsenheimer) shows the most extreme differences. *Erebia medusa psodea* Hübner, which is externally the most different subspecies, occurring in the South Carpathians and East Balkans, was not studied electrophoretically. The highest level of genetic variation has been found in the East-Central European group, which can probably be derived from a large, extended East European (and Siberian?) refugial population of the last glacial period. The observed genetic differences strongly support the hypothesis, that all subspecies have survived at least the last glaciation in different refugia.

Genetic differentiation and metapopulation structures in some butterflies in the Carpathian basin

Populations of some butterfly species have been studied in the Carpathian basin at different geographical scales. Populations of *Parnassius mnemosyne* Linnaeus and *Euphydryas maturna* Linnaeus have been compared both in larger and smaller regional scales, while populations of *Aricia artaxerxes* Fabricius and *Maculinea alcon* Denis & Schiffermüller – *M. rebeli* Hirschke have only been studied in a smaller region.

Parnassius mnemosyne: Populations from 11 geographical regions (Transdanubian Middle Range: Bakony, Vértes, Velencei, Budai and Pilis mountains; Mecsek mountains; Northern Middle

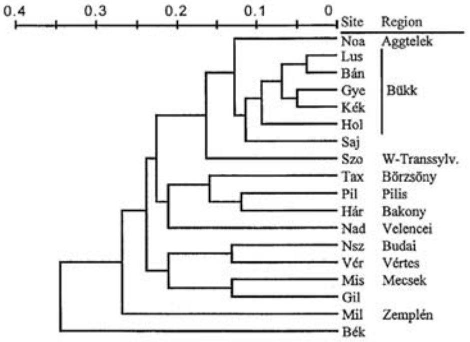

Figure 4
UPGMA dendrogram of *Parnassius mnemosyne* in Hungary, constructed on the basis of Cavalli-Sforza and Edwards chord genetic distances.

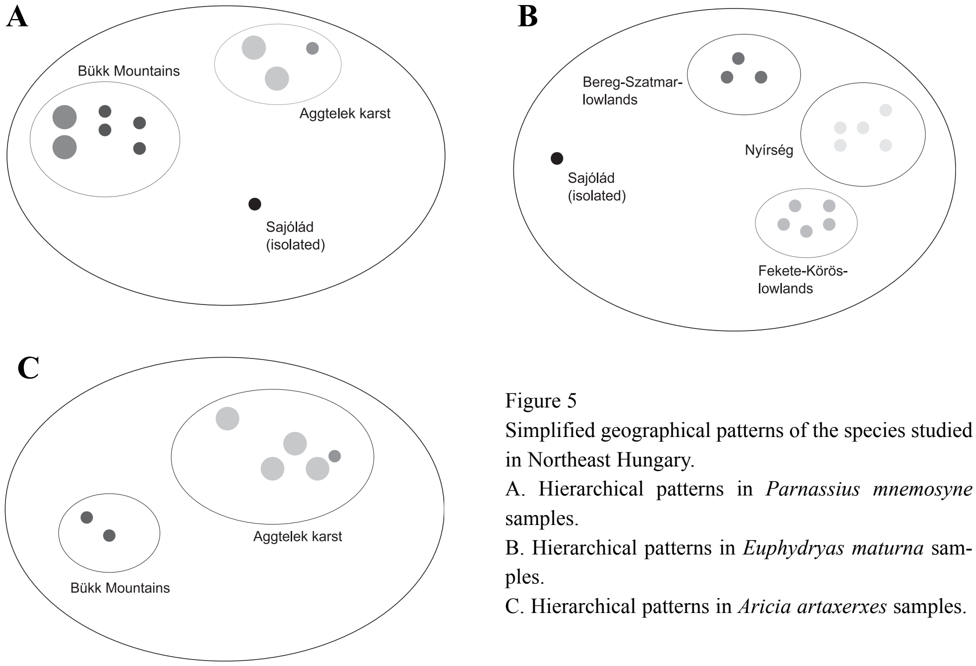

Figure 5
Simplified geographical patterns of the species studied in Northeast Hungary.
A. Hierarchical patterns in *Parnassius mnemosyne* samples.
B. Hierarchical patterns in *Euphydryas maturna* samples.
C. Hierarchical patterns in *Aricia artaxerxes* samples.

Range: Börzsöny, Bükk, Aggtelek karst, Zemplén mountains; lower foothills of the West-Transylvanian mountains) and three lowland isolates (Sajolád, Dráva valley, Black Körös valley) were sampled in Hungary and the neighbouring part of Rumania (fig. 3). The UPGMA dendrogram constructed on the basis of Cavalli-Sforza and Edwards genetic distances did not indicate a clear geographic pattern (fig. 3, 4, 5). The branching pattern among the populations from the Börzsöny mountains and Transdanubia did not correlate with the geographical distances between sampling localities. Populations of the Bükk mountains were clustered together, and they also showed genetic similarity to the Sajolád isolate, which is only separated by 15 km of unsuitable habitat from the Bükk mountains. These results support Eisner's statement (1954) who grouped most of the Transdanubian populations into one subspecies (*P. m. litavia*). When populations from Northeast Hungary (except for the Zemplen population) were also added to the Transdanubian data set, the F_{st} value hardly increased. If we accept that the populations of the Vértes, Budai, Bakony and Velencei mountains are all members of one subspecies, almost all the other investigated populations (except for Zemplén mountains and the Körös valley) should be also grouped to the same subspecies. The Zemplén and Körös valley populations proved to be genetically distinct. Meglécz et al. (1997) demonstrated that the Bükk populations exhibit metapopulation structure. Only occasional differentiation was observed between Bükk populations, while significant genetic differentiation was found between almost all pairs of populations from different regions. Even the small, recently isolated Sajolad population was found to be genetically different from the Bükk region.

Euphydryas maturna: Most of our samples originated from three regions of the eastern part of the Pannonian lowland (Bereg-Szatmár lowland, Nyírség and Black Körös valley), but also from some populations in southern Transdanubia and the North Hungarian middle range. The isolated population of the Sajólád forest was considered as a distinct region in this case as well. The UPGMA dendrogram constructed on the basis of Cavalli-Sforza and Edwards genetic distances shows that – as opposed to *P. mnemosyne* – most of the genetic variation could be observed among the populations within the regions, while the differentiation according to regions merely shows a lower level. Within all regions, all populations showed significantly different F_{st} values. Thus, no evident geographical differentiation has been established (fig. 5).

Aricia artaxerxes: Two larger isolates of this species, described as *A. artaxerxes issekutzi* I. Balogh occur in the North Hungarian-Slovakian karst region and in the Bükk mountains. The number of alleles pro loci was higher in the Karst region than in the Bükk mountains. Some rare alleles (e.g. *Est*, *Got*, *Mdh*, *Pgi*, *Pgm*) observed in the 'Karst' populations were lacking from the samples of the Bükk mountains. On the other hand, the frequency of the heterozygotes was not significantly lower in the Bükk mountains. In addition, the genetic differentiation of all samples proved to be significant. It means that the level of genetic differentiation shows a stronger correlation with the frequency distribution of the more frequent alleles than with the presence/absence of rare alleles.

Significant deviations from the Hardy-Weinberg equilibrium were found at several loci (*Adh-1*, *Adh-2*, *Aldox*, *Est*, *Idh*). The Fisher's exact test has shown a significant heterozygote deficiency in both regions, which was mostly expressed in the *Aldox*, *Est* and *Me* loci. These results are confirmed also by the F-statistics. The populations showed a considerable level of genetic variance (F_{it}), in which the 'within populations' fraction proved to be larger than the 'between populations' fraction (F_{is}>F_{st}). The F_{is} values were significant at the *LDH*, *EST*, *ME* loci, while the F_{st} values at the *PGM*, *GOT*, *EST*, *ME*, *ADH*, *ACON*, *GDH* loci, and the F_{it} values at the *GOT*, *LDH*, *EST*, *ME*, *ADH*, *GDH* loci.

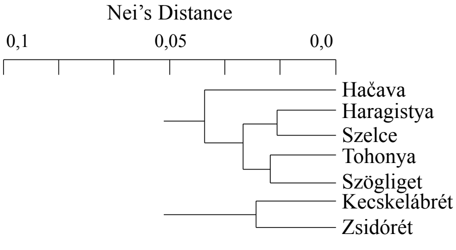

Figure 6

UPGMA dendrogram of the North Hungarian / South Slovakian populations of *Aricia artaxerxes*.

The UPGMA dendrogram constructed on the basis of Nei genetic distances, for both years 1999 and 2000, showed a peculiar geographical pattern also within the Karst region populations. The sample from the higher Zadielska planina (Hačava) was clearly separated from the other ones, and the pattern of differentiation of populations essentially reflected the vertical subdivision (higher versus lower karst plateaux) of the region (fig. 5, 6).

Summarizing conclusions: biodiversity and conservation priorities in the Carpathian basin

The Carpathian basin, and within it Hungary, shows a high level of biodiversity, despite the fact that in Hungary there are no high mountains nor any littoral habitats. As an explanation of this richness, the transitional biogeographical position of the Carpathian basin can be mentioned (see paragraph 2). The highest level of biodiversity has been observed in some marginal areas where the overlapping of several different faunal components has taken place, like the western and southwestern parts of Transdanubia with the overlap of Pannonian, Illyrean and Alpine influences and also the northeastern edges of the country with the overlap of Pannonian, Carpathian and Dacian influences. Accumulation of diverse faunal elements also took place at the colline altitudes of the Hungarian middle range, where the overlapping of Mediterranean (Holo- and Ponto-Mediterranean, Balkanic and Anatolian) elements has succeeded. Conservation centres of relict species – often as endemic species/subspecies – are typical for the edaphically extreme habitats which could resist against the postglacial re-forestation and could preserve the elements of earlier climatic periods under special ecological constraints. These patterns of species diversity are well demonstrated by the manifold composition of insect assemblages of vegetation complexes consisting of mosaic-like patterns of forest, skirt and grassland compartments. A nested hierarchy of diversity is present at levels of populations, communities, community-complexes (sigmata) and landscapes.

Recently, the biogeographical division of Europe has been completed by the addition of five further biogeographical regions: Arctic, Pannonian, Steppic, Black Sea and Anatolian (Natura 2000, directive 92/43/CEE, 1997). It means, that due to its peculiar biogeographical character, the Pannonian region has been recognized as equivalent to the further 11 large regions of Europe. The 'Areas of Special Conservation Interests' was completed with the list of threatened types of natural habitats which require special conservation measures (1998). In the Pannonian region at least 36 of these habitat types occur, and some of the most significant European stands of them can be preserved in this region. Studies on the biogeographical composition of the flora and fauna of the Carpathian basin exhibit also some important applied aspects.

The indicative value of species largely depends on their biogeographical character. Thus, the habitat lists and the species lists of the European nature conservation information systems and conventions (like the CORINE-system, the Habitat Directive and Natura 2000) must be revised, according to biogeographical points of view. Threatened species with scattered occurrence in Central Europe are often widely distributed in Eastern Europe. We have numerous species, vanishing or being in decline in Central and western Europe, which are represented in our region at least partly by strong populations. Strong, viable populations of such species can be successfully protected mostly in these regions, inter alia, in the Carpathian basin (*Euphydryas maturna*, *Lycaena dispar rutila*, *Maculinea teleius* etc.). In addition, the typical ecosystems of the Pannonian region (loess, sandy and alkali grasslands, rupicolous swards, white oak scrub forests etc.) exhibit numerous characteristic invertebrate species which do not occur more westwards than the Hungarian middle range, or in some cases the foothills of the Vienna Basin, South Slovakia and Moravia. Numerous characteristic species of the Pannonian region are connected with special habitat structures, like traditionally managed ecosystems, structured grasslands or forest-skirt/grassland complexes of the Pannonian forest-steppe (like many grasshopper and butterfly species). Effective conservation of them is possible only by preserving of the connectivity of their populations and metapopulation structures at the landscape level. The solution of these problems has outstanding importance for the protection of the natural heritage of the Carpathian basin, but also for Europe.

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Change index: a measure of change in range size that is independent of changes in survey effort

Mark Telfer

Abstract

A major problem in studying the range changes of invertebrates using atlas data, is discriminating the effects of changing survey effort from the real biological changes. Using the data sets collated by the UK Biological Records Centre, a method has been developed which allows for the effects of variation in survey effort, by calculating an index of relative change in range size. The method is applicable to a wide range of atlas data sets.

Key words: change index, decline, distribution atlas, recorder effort.

Introduction and rationale

Range size is an important measurement for conservationists. The allocation of Red Data Book threat statuses for invertebrates has often been based on range size, as a measure of rarity. More recently, a greater emphasis has been placed on decline in addition to rarity (IUCN 1994, 2001). An accurate measurement of change in range size is thus important to allow conservationists to set priorities, and to target limited resources with the greatest effect in the battle against extinction.

Though conservationists need to measure declines, it is equally important to be able to accurately measure increases in range size. In particular, there is a need to quantify the range expansions of invasive alien species in order to monitor the potential risks they pose. Range expansions of native invertebrates are also of considerable interest, linked as they are to climate change. A method is thus needed which measures both increases and decreases in range size on the same scale. To understand the impacts of climate change, of pollution, and of changes in land use on the distributions of invertebrates, it is valuable to be able to quantify change in range size accurately.

For most of the biota of even the best recorded countries, monitoring data do not exist with which to assess changes in range size. This is particularly true for invertebrates. However, biological atlas data sets do exist for many groups. For example, there are atlases of the Orthoptera and carabid beetles of the Netherlands (Kleukers et al. 1997, Turin 2000) and of Britain and Ireland (Haes and Harding 1997, Luff 1998). In Britain, such atlases provide the main source of data on the distributions and conservation statuses of the majority of the biota (Harding and Sheail 1992). These data sets generally include the results of at least one national survey, plus collated historical records, and so the data may be divided into two or more date periods. They are based on information gathered by recorders who visit a grid cell and record all the species (in the particular group) which they encounter.

Surveys rarely achieve complete geographical coverage. In Britain, the grid cells which tend not to be surveyed are in very remote upland areas, or are coastal or island squares with a small area of land. For a valid comparison of data from two survey periods, it is essential firstly to compare only the subset of grid cells which have been surveyed in each period.

Atlas data sets are generally based on survey work carried out largely or entirely by volunteers. It has proved impractical to impose rigid survey methodologies on volunteer recorders, without severely reducing the numbers of volunteers prepared to contribute. For this reason, most atlas data sets contain no information on the amount of survey effort expended (time spent and area covered) for each record submitted. However, information on survey effort is important for an accurate interpretation of atlas data.

The biases caused by differences in survey effort can be illustrated by considering atlas data for the silver-washed fritillary *Argynnis paphia* (Linnaeus, 1758). This local woodland butterfly of southern Britain was recorded from 381 British grid cells (10 km squares) during the 13 year (1970-1982) period of survey work for the first atlas (Heath et al. 1984), and from 495 such grid cells during the five year (1995-1999) period of survey work for the second atlas (Asher et al. 2001). This represents a 30% increase in recorded range size. However, this is a species which is believed to have declined in range over the period, albeit with a slight re-expansion of that range in some areas.

The apparently contradictory information for silver-washed fritillary, and several other British butterflies, may be better understood by considering the sizes of the two surveys being compared. The earlier survey collated 124 978 records over a 13 year period, whereas the later survey collated 1 548 963 records: an order of magnitude greater. This volume of data on a fauna of 62 species makes this the premier invertebrate data set in Britain. The numbers of records provides a good indication of the much greater survey effort expended on the later survey, although it should be noted that recorders in the earlier period had a greater tendency to summarise their records before submitting them. For the silver-washed fritillary, the greater survey effort during the 1990s lead to its being recorded from 30% more squares than during the 1970-1982 period, but not quite as many as would have been expected had its actual range size remained stable.

The rationale underpinning this new method is that the real biological change in actual range sizes is confounded with changes in survey effort. This makes the estimation of actual change in range size problematic. However, it is possible to calculate an index of relative change in range size, as outlined below.

The general method for calculating relative change in range size

In outline, the method is first to define the set of grid cells which have been surveyed in both survey periods; subsequent calculations are based solely on these cells. For each species, the number of recorded grid cells is counted for each period. These counts of grid cells are expressed as proportions of the total survey area, and then

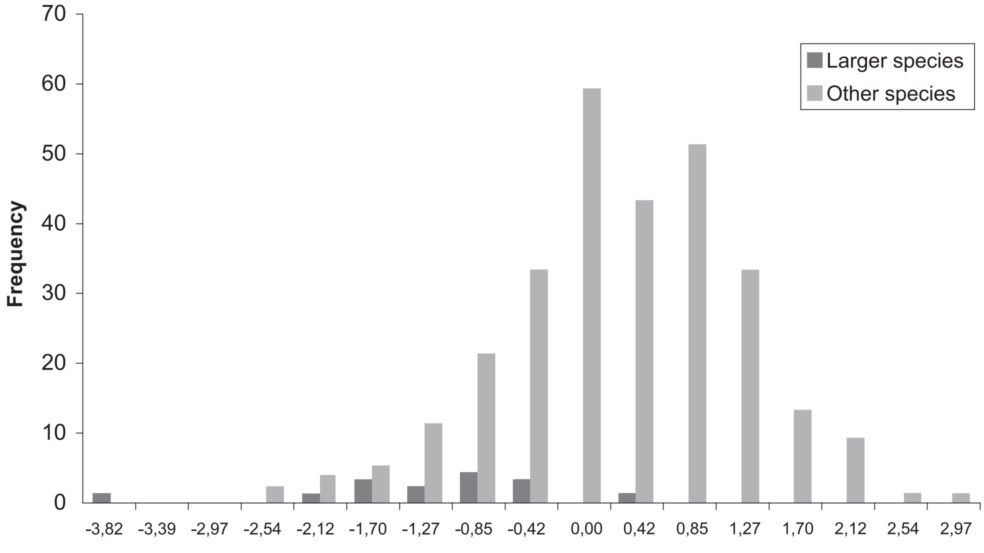

Figure 1
Frequency histogram for the British Change Indices of large carabids (in the genera *Cicindela*, *Carabus* and *Calosoma*), and of the remainder.

logit-transformed. A linear regression model is then fitted to the relationship between counts of grid cells in earlier and later survey periods. A weighted regression is used to allow for non-constant variance. The standardised residuals for each species provide its change index: an index of its change in range size relative to the trend in the whole group.

Full details of the method will be published elsewhere, including a detailed discussion of the assumptions underlying this method (Telfer et al. 2002).

Application of the method to a representative dataset

The Ground Beetle Recording Scheme (GBRS) data on British carabids is typical of an initial atlas data set, in which miscellaneous records made over a period of 70 years (1900-1969) before the formation of the recording scheme are available for comparison with a more systematic 10 km square survey (1970-the present). The data set analysed here is based on the data underlying the published atlas (Luff 1998), with subsequent updates. Change indices were calculated for each species.

A thorough analysis of the patterns of change in British carabids is in preparation. Here I present a simple comparison to illustrate the use of change indices for understanding the causes of change.

Desender & Turin (1989) analysed change in range size of the carabids of Denmark and the Low Countries, and found significant declines in most species of *Carabus*, and all of the *Cicindela* and *Calosoma* species. The British Change Indices of species in these genera are significantly lower than the remaining carabids (mean +/- standard error Change Index of *Cicindela*, *Carabus* and *Calosoma* = -1.39 +/- 0.91, mean of remainder = 0.08 +/- 0.95, $F_{1.301} = 36.63$, $p < 0.0005$; fig. 1).

An apparent decline of *Carabus* species, at least in south-eastern England, has been noted anecdotally by Allen (1983) and others (pers. comm.). It should be noted that species in these genera are all relatively large species, and Telfer et al. (2002) reports a significant negative relationship between adult body size and Change Index. It is not currently known why large body size should be correlated with declining range size.

When is this method suitable?

For a detailed comparison of this new method with previously published methods for the estimation of change in range size using atlas data, see Telfer et al. (2002), which also discusses the advantages and limitations of the new method. Here I outline the types of atlas data sets to which this method is applicable, with an emphasis on the invertebrates of Europe.

- The method has been successfully applied to national scale atlas data from Britain (Telfer et al. 2002, Preston et al. 2002), but is applicable to atlas data at a range of scales, national, regional and local.
- The method is best suited to survey data based on grid cells of equal area. However, it may also be used for data from grid systems where there is some variation in area of grid cells. It could also be applied to survey data based on political or organisational units (such as British parishes), especially where these tend to be of similar area.
- The method is ideally suited to analyse change between two similar surveys. However, where recording has taken place over a protracted period, it is usually possible to divide the records into two coherent periods to provide a valid comparison. Even where there have been closely comparable levels of survey effort, the present method will prove helpful, but it is especially valuable for comparisons between surveys of different intensities. For an analysis of more complex temporal trends in range sizes over three or more survey periods, a method such as that of Maes & van Swaay (1997) is appropriate.
- The change index works best for larger taxonomic groups. For data sets covering less than about 50 species, extreme range changes of individual species or suites of species may have a large influence on the regression model, and thus on the residuals and change indices of all other species.

This new method will provide a useful and widely applicable tool to enhance the value of biological atlas data on the invertebrates of Europe to nature conservation, and to our developing understanding of the causes of range expansions and contractions.

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The national biodiversity network in the UK

Paul Harding

Abstract

The National Biodiversity Network (NBN) has been developed in the United Kingdom over a period of about five years, forming the NBN Trust in March 2000. The NBN Trust brings together those with shared interests in the collection, management and use of data and information about species, biotopes and sites in the UK. These include volunteers and specialist societies, non-governmental wildlife organisations and the statutory nature conservation agencies and other governmental organisations. By working to common standards, agreeing priorities and sharing data, greater use can be made of the work of the specialists and skilled volunteers that collect biodiversity data in the field. NBN is still developing, but it is beginning to create new opportunities in surveying and monitoring species, managing data and particularly in disseminating data. Central to the development of NBN is a system for providing access to remotely held data sets using internet technology – the NBN Gateway. From a European perspective the most important aspects of the NBN are freedom of access to biodiversity data via the internet Gateway and agreed standards for data and their management and dissemination.

Key words: National Biodiversity Network, biodiversity, internet, data, information, standards.

Why we need the national biodiversity network (NBN) in the UK

Data and information about species, biotopes and sites are essential for informed decisions to be made affecting the natural environment and for wise use to be made of resources. To measure changes, in the range or abundance of species or biotopes, at least time-series observations and preferably a system for structured, repeated surveys (surveillance) are required. Although the UK has a long tradition of collecting data about the occurrence of species and, to a lesser extent, biotopes, the data have been widely dispersed and usually inaccessible except to the 'owner' of the data. Modern information technology enables greater sharing of data and information and offers a mechanism to provide access to dispersed and hitherto inaccessible data. But for sharing to be possible, those who collect or manage data and those that wish to use data must work together. Development of the National Biodiversity Network was initiated in 1996 to enable this process of change and improvement in access to biodiversity data and information to take place.

The origins of NBN

As early as 1984, many practitioners of biological recording recognised that the results of their field surveys and the associated data and information were not being used effectively. Also, there was considerable duplication of effort, particularly in the collation and management of data sets. Professionals working in nature conservation and development planning made little use of the vast community of volunteers with specialist knowledge of species, communities and sites. In many cases, volunteers distrusted the uses to which others might put their data. Nevertheless, the Biological Records Centre had been set up in 1964 to collate, manage and disseminate data on the occurrence of species collected mainly by national specialist societies. These data are used mainly in nature conservation and biogeographic and environmental research. Many local biological records centres had been set up in the 1970s to serve some of the local needs for similar data. Unfortunately there was little communication between these two main sources and routes for data.

A working party on biological surveillance, set up by the Linnean Society of London, reported on these problems in 1988 (Berry 1988). Prompted by this brief report, the Co-ordinating Commission for Biological Recording (CCBR) was set up in 1990 following a high-level meeting of more than 30 organisations with an interest in biological surveillance in the UK. These early developments, and the context within which they took place, are described by Wyatt (1992). CCBR carried out a detailed review of all aspects of biological recording in the UK, which was completed in 1994 (Burnett, Copp & Harding 1995). A draft of the CCBR report was used in the preparation of the UK's Biodiversity Action Plan (UKBAP), published in January 1994 (Cm 2428), which highlighted the need to underpin decisions effecting biodiversity with data and information. By this rather tortuous route, biological recording had become central to the UK government's ability to deliver its targets under the Rio Convention on Biological Diversity, to which it was a signatory in June 1992.

The development of NBN

One of the commitments of the UKBAP was to 'Improve the accessibility and co-ordination of existing biological data sets; provide common standards for future recording' (Cm 2428). This, combined with the detailed findings and recommendations of the CCBR report, helped promote an unprecedented partnership between governmental and voluntary organisations to form the National Biodiversity Network.

NBN started small and much of its activity in the first couple of years was to develop a business plan and seek funding for the plan and its component projects. The NBN project leaders and their managers soon realised that to develop a full national network, involving several hundred organisations, was potentially very expensive and also alarming, because nobody had ever done anything like it before. Unsuccessful bids for multi-million pound grants from the Millennium Commission and the Heritage Lottery Fund made us consider other routes by which the development of NBN could be funded. As a result, much of the developmental work of NBN in the last five years has been achieved by re-directing small areas of the work of organisations reliant on government funding. This enabled organisations to develop projects of direct benefit to their own business, but also of relevance to developing a national network. In this way, the Joint Nature Conservation Committee, English Nature, Scottish Natural Heritage, Natural Environment Research Council and Natural History Museum, in particular, have funded the development of key projects. A major non-governmental partner in NBN, The Wildlife Trusts, secured a three year grant from a charitable source to work with local records centres. During 2001, significant new funding for several NBN projects has come from the Department of the Environment, Food and Rural Affairs and the Heritage Lottery Fund. The timeliness of all these developments is recognised in a recent UK Parliamentary sub-committee report on biodiversity, which stated that a successful National Biodiversity Network is a lynch-pin of the whole Biodiversity Action Plan process.

An overview of the NBN projects

The basic project structure of NBN is concerned with three main areas: establishing and maintaining standards, linking data sources, and disseminating and using data. For the NBN to operate effectively it is essential to establish, agree and maintain the necessary standards, establish access to and linkages between data stores and the internet, and to develop the tools that will create the internet network. Each project is led by an NBN Trust member organisation to manage and direct their individual projects towards the overall objectives of NBN. All the projects are closely inter-linked to ensure that the full range of relationships needed for establishing the NBN are clearly identified and maintained.

Standards

One way in which the NBN will achieve its aims is through the promotion of common standards as a context to recording. These standards include the maintenance of a national dictionary of species names, promotion of agreed recording methodologies, a data model for the help of those designing recording software and methods for transferring data. At the operational level the NBN also promotes standards for the care and management of records and the means whereby copyright and confidentiality of data can be properly protected.

One example of how these standards have been applied to developing a new resource is *Recorder 2000*. This is a powerful piece of biological recording software and a considerable advance over previous versions of Recorder. The software is built on a variety of standards. They include the NBN's 'data model',which shows how biological data can be managed within relational databases, a transfer format and NBN dictionaries for species, biotopes and administrative areas. Using Recorder 2000, biotope and site surveys can also be made and combined with species-based recording. Recorder 2000 is a collect / collate system. This means that it is designed for individuals to collect their observations and pass them on to collation points. Recorder 2000 will be able to handle millions of observations, but it is not designed as a large corporate system that can provide access for hundreds of people.

The *NBN Dictionary* project will address the problems of nomenclature to enable the sharing of information about species and biotopes. Using the Dictionary it will be possible to translate between the names used in different sources of information, for example to relate the different scientific names used for the same species. The Species Dictionary is due to go live on the internet in November 2001.

Linking

NBN includes projects to link into the network many different types of organisations that are concerned with collecting, collating and managing data on species, biotopes and sites. These include three groups of organisational types.

- *Local records centres* – local, often county-based, foci to supply local needs for data, based mainly on local sources. There are about 50 local records centres in the UK, but they are unevenly distributed with many important gaps in coverage.
- *National societies and recording schemes* - specialist biological groups concerned with the survey and study of taxonomic groups, such as Odonata, Carabidae or Bryophyta. There are at least 70 such groups in the UK, but several major taxonomic groups are not covered by a society or scheme.
- *National data custodians* – a few organisations have an established position as custodians of their own and other people's data; for example the Biological Records Centre, Royal Society for the Protection of Birds, Marine Biological Association (especially the MarLIN project).

Disseminating and using data

The *NBN Index* will provide a facility for users of the NBN web site to find and browse information on UK biodiversity. The Index is still in development and is restricted to a very limited sample of biodiversity information that is being used as a demonstration to help gauge user requirements and to stimulate comments to guide further development.

The *NBN Gateway* is the system by which access, via the internet, can be obtained to metadata about data sets and, through a system of control filters, to data and associated information. The pilot NBN Gateway was launched in autumn 2000 and the first phase of a complete upgrade of the Gateway has gone live at the end of September 2001 (www.searchnbn.net). The level of access that any particular user can get to a given data set depends on a) the level of access granted by the supplier of the data, and b) the status of the user. Wherever possible, NBN intends that an interested member of the public will be able to access basic information about the national distribution of a species or biotope. In addition they will be able to see some ecological information about the species or biotope and basic metadata about relevant data sets, so that if they want to find out more they will know whom to contact. Specialists will be able to access more detailed data through whatever control mechanism they have agreed themselves. For example, at the present time members of the Spider Recording Scheme can get access to draft maps and text for a new atlas of British spiders by registering with the scheme organiser. In return they are requested to comment on the maps and text, as part of a validation process.

The aim of the *Education and Public Access* project is to investigate the requirements for access to biodiversity information from the education sector (both formal and informal) and from the general public. This work has not yet begun, but important stages will be to review current initiatives and to undertake trials to test ideas and develop guidance for use in the future. The aim will be to close the gap between data and the successful widespread use of those data by a wide variety of audiences.

Managing NBN

NBN is an ambitious concept and a complex matrix of some 20 inter-related projects. It already involves more than 100 organisations at various levels, with funding for projects coming from more than 20 different sources, in addition to the 'in kind' contributions of time, especially by volunteers. The task of managing this strange organism falls to a small group of honorary Trustees led by a very active Chairman. The central NBN staff are a Programme Manager, a Company Secretary and one part-time administrative support post. The Trustees are advised by two Committees dealing, respectively, with finance and management, and policy and programme. Communication and consultation between and among the individual projects is central to the success of NBN, ensuring that the inter-relationship of projects is recognised and responsibility for decisions is shared.

It could only happen in the UK?

I hope not because if we can make it work, with the scale and complexity of organisations involved in the UK, it could be simpler for other nations to take a similar approach to the problems of the supply, management and use of biodiversity data. Analogous systems have been set up or are being considered in several European countries. The real advantages of a more relaxed approach to the ownership of data, so that data can be used by more organisations for a wider range of applications, far outweigh the theoretical risks of misuse of data or perceptions of loss of 'ownership'.

A European perspective

We are still at the stage in the UK where NBN is proving to itself, to its component organisations and in particular to potential users and UK governmental organisations, that NBN can be useful to them. NBN is already beginning to think about an international perspective, but is unlikely to be able to take a lead at the present time. The standards adopted by NBN provide a potential model for international collaboration, but the NBN Gateway is the single most important concept and development in an international context. When the second phase of the Gateway is fully developed, it will be possible for anyone, in the UK or abroad, to gain access to data and information about UK biodiversity using the internet. In the longer term, the Gateway will enable the user to access data managed remotely on computers at many locations throughout the UK. It would be only a small technological step, but a major intellectual and administrative step, to use the functionality developed for the NBN Gateway to provide access to data held remotely in many countries.

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In the past, even very simple international projects to collate and disseminate data on species distributions have been notoriously difficult to fund and resource, but the importance of publications such as the European atlases of flowering plants, breeding birds, mammals and amphibians and reptiles is self evident. In approaching a project based on international collaboration, it will be essential to understand who needs data, about what, and what they might do with data, and to demonstrate that international collaboration is possible and rewarding for all concerned. At the present time NBN is unable to do more than publicise what is being achieved in the UK, but NBN would welcome it if these successes in the UK could be used as a model for developments in other countries or internationally.

Acknowledgements

This paper summarises more than five years work by many individuals in a large number of organisations. I am grateful to all my colleagues working on NBN projects for their commitment to the future of NBN. I am also grateful to Sir John Burnett, Chairman of the NBN Trust and Dr. Jim Munford, Programme Director for the NBN Trust for their comments on a draft of this paper.

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Web site addresses:
National Biodiversity Network: www.nbn.org.uk
Internet access to data via the pilot NBN Gateway: www.searchnbn.net
Biological Records Centre: www.brc.ac.uk

Contemporary distributions of *Panurginus* species and subspecies in Europe (Apoidea: Andrenidae: Panurginae)

Sébastien Patiny

Abstract

The largest number of Old World *Panurginus* Nylander, 1848 species is distributed in the West-Palaearctic. The genus is absent in Africa and rather rare in the East-Palaearctic. Warncke (1972, 1987), who is the main author treating Palaearctic Panurginae in the last decades, subdivided *Panurginus* into a small number of species, including two principal taxa admitting for each a very large number of subspecies: *Panurginus brullei* (Lepeletier, 1841) and *Panurginus montanus* Giraud, 1861. Following recent works, the two latter are in fact complexes of closely related species. In the West-Palaearctic context, distributions of certain species implied in these complexes appear as very singular, distinct of mostly all other Panurginae ranges and highly interesting from a fundamental point of view. Based on a cartographic approach, the causes which influence (or have conditioned, in the past) the observed ranges of these species are discussed.

Key words: Panurginae, biogeography, West-Palaearctic, speciation, glaciation.

Introduction

In the Old World Panurginae fauna, *Panurginus* Nylander, 1848 is one of the only two genera (with *Melitturga* Latreille, 1809) which are distributed in the entire Palaearctic region. The genera *Camptopoeum* Spinola, 1843 and *Panurgus* Panzer, 1806 are also represented in the East-Palaearctic (in northern Thailand), but too few data are available for these genera to make them the subject of particular considerations.

From the biogeographical point of view, *Panurginus* is even more singular in being the only Holarctic Panurginae genus. In spite of this particularly wide range, most of the known Old World *Panurginus* species are concentrated in the West-Palaearctic region.

As the largest part of the West-Palaearctic Panurginae systematics, the knowledge of *Panurginus* is mainly reported in Warncke's works (1972, 1987) and reviewed by some authors (Patiny 1999, 2001, Rasmont et al. 1995, Schwarz et al. 1996). According to all authors, two major species groups exist (and some other independant species), which were considered by Warncke as species including a large number of subspecies.

The taxa *Panurginus montanus* Giraud, 1861 sensu lato and *Panurginus brullei* (Lepeletier, 1841) sensu lato are studied in the present paper. The numerous particularities of their distributions are characterized and discussed here. The limits of these distributions were proposed and related to the contemporary and past developments which could have caused these ranges.

Catalogue of the old world species of *Panurginus*

Panurginus Nylander, 1848
  Type species: *Panurginus niger* Nylander, 1848
  = *Panurginus* Nylander, 1848
  = *Scrapteroides* Gribodo, 1894
  = *Panurgus* (*Panurginus*) (Nylander, 1848) in Warncke (1972).
  = *Panurginus* (*Panurginus*) Nylander, 1848 in Ruz (1986)

Panurginus albopilosus Lucas, 1849
  = *P. annulipes* Lucas, 1849
  = *P. politus* Benoist, 1937
  = *Panurgus* (*Panurginus*) *albopilosus* Lucas, 1849 in Warncke (1972)
Panurginus alpinus Warncke, 1972
  = *Panurgus* (*Panurginus*) *montanus alpinus* Warncke, 1972
Panurginus alticolus Morawitz, 1876

= *Panurgus* (*Panurginus*) *montanus alticolus* Morawitz, 1876 in Warncke, 1972
Panurginus annulatus (Sichel, 1859)
= *P. difformis* Gribodo, 1894
= *P. halictoides* Gribodo, 1861
= *Panurgus* (*Panurginus*) *brullei annulatus* (Sichel, 1859) in Warncke, 1972
Panurginus brullei (Lepeletier, 1841)
Panurginus clarus Warncke, 1987
= *Panurgus* (*Panurginus*) *brullei clarus* Warncke, 1987
Panurginus corpanus Warncke, 1972
Panurginus herzi Morawitz, 1892
= *Panurgus* (*Panurginus*) *montanus herzi* Morawitz, 1892 in Warncke, 1972
Panurginus labiatus (Eversmann, 1852)
= *Panurgus labiatus* Eversmann, 1852
= *Panurgus clypeatus* Eversmann, 1852
= *P. arenarius* Schenck, 1861.
Panurginus lactipennis Friese, 1897
Panurginus minutulus Warncke, 1987
Panurginus montanus Giraud, 1861
Panurginus ponticus Warncke, 1972
= *Panurgus* (*Panurginus*) *montanus ponticus* Warncke, 1972
Panurginus picipes Morawitz, 1890
Panurginus romani Aurivillius, 1914
Panurginus schwarzi Warncke, 1972
= *Panurgus* (*Panurginus*) *brullei schwarzi* Warncke, 1972
Panurginus sericatus Warncke, 1972
= *Panurgus* (*Panurginus*) *montanus sericatus* Warncke, 1972
Panurginus tunensis Warncke, 1972
= *Panurgus* (*Panurginus*) *brullei tunensis* Warncke, 1972
Panurginus turcomanicus Popov, 1936
= *Panurgus* (*Panurginus*) *brullei bytinski* Warncke, 1972
Panurginus tyrolensis (Richards, 1932)
= *Panurgus* (*Panurginus*) *montanus tyrolensis* (Richards, 1932) in Warncke, 1972

The distribution of *Panurginus* around the Mediterranean basin

The distribution of the genus *Panurginus* around the Mediterranean basin is shown in fig. 1.

Fig. 2 shows the distribution of three species associated by Warncke in the *Panurginus brullei* complex: *Panurginus albopilosus*, *P. annulatus* and *P. tunensis*. These ranges characterize the three kinds of *Panurginus* distribution in the western part of the Mediterranean basin. *Panurginus albopilosus* is typically Ibero-Maghrebian, *P. annulatus* is strictly Spanish and *P. tunensis* is only Maghrebian.

Fig. 3 shows the distribution of *P. labiatus* and *P. lactipennis* in the Balkan and Turkey.

Fig. 4 shows the distribution of four species pooled by Warncke in the *Panurginus montanus* complex: *P. alpinus*, *P. montanus*, *P. sericatus* and *P. tyrolensis*. These species exhibit a strong typicity of their distributions in the different Alpine and Balkanic mountain chains. *Panurginus alpinus* is a French species, the most occidental of the complex. *Panurginus montanus* and *P. sericatus* have a wider and more eastern distribution in the Alpine chain. *Panurginus tyrolensis* is a Balkanic taxon.

Discussion

Panurginus species are not uniformly distributed in the West-Palearctic and around the Mediteranean basin. The generic distribution presents three large disjunctions (fig. 1): a first one between the Alps and Spain (including the Pyrenees), an other at the Transdanubian plain between the Alpine and Balkanic populations and the third between western Lybia and southern Israel. All these disjunctions must not be considered *a priori* as homologous and have to be explained by clear argumentations.

The absence of *Panurginus* between Spain and the Alps (fig. 1) is easily understandable and may be described as the consequence of the characteristics of the different taxa. Firstly, the Iberian species (fig. 2) generally are strongly xerophylous and thermophylous (Patiny 2001, Patiny & Gaspar 2000). In France the climatic conditions rarely are favourable for these species, even in the Mediterranean area. Secondly, their distribution is restricted by the Pyrenean obstacle which only allows the migration of such species from time to time, for example in particular climatic configurations. In the east, the French *Panurginus* species (fig. 4) is strictly a mountain taxon which is unknown below 1500m altitude and apparently missing in the Pyrenees. These observations suggest that the central part of France is quite unfavourable to *Panurginus* expansion.

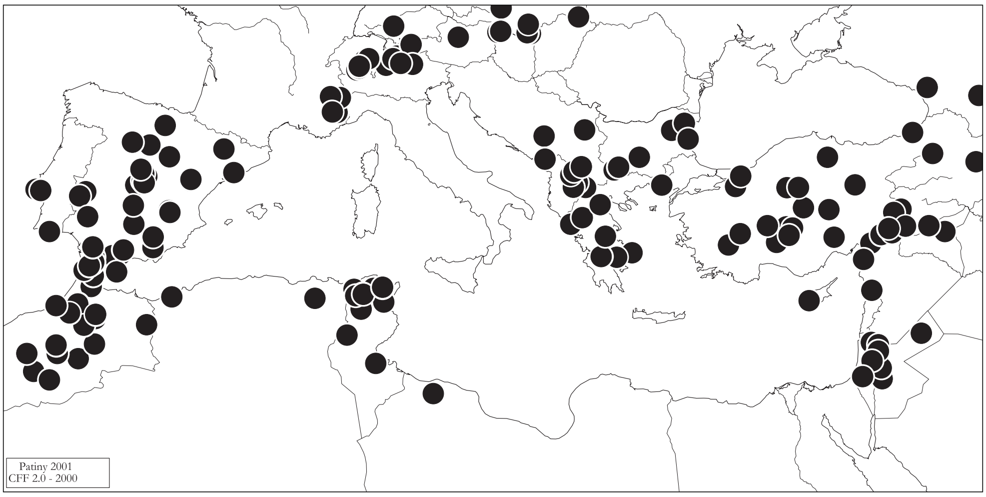

Figure 1
Distribution of the genus *Panurginus* around the Mediterranean basin.

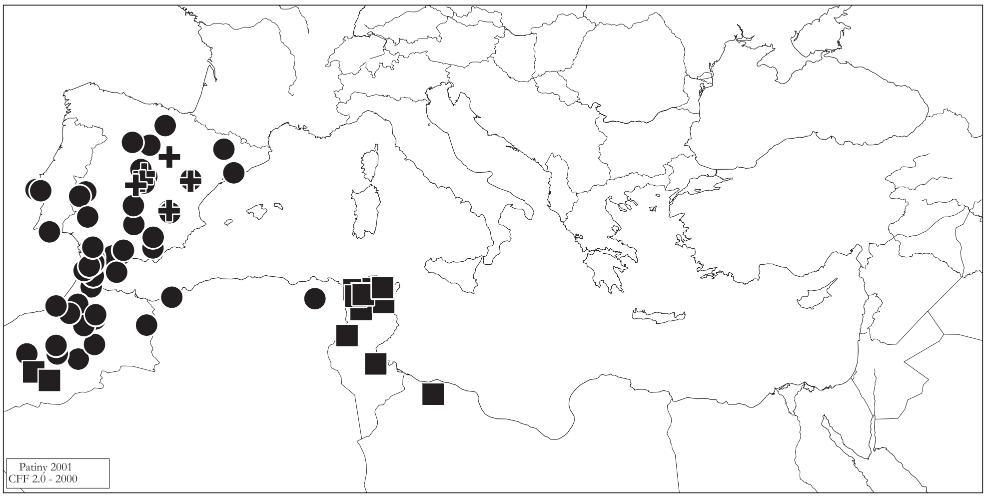

Figure 2
Distribution of three species of the *Panurginus brullei* complex: *Panurginus albopilosus*, *P. annulatus* and *P. tunensis*.

The second disjunction in the generic distribution is centered at the level of the Transdanubian plain (fig. 1, 3, 4). Once again, the mountain character of the *P. montanus* species group (fig. 4) may reliably explain the absence of these species in the plain. Endemic species related to *P. montanus* occur in the entire area surrounding this plain but none of those is found in the plain itself. The altitude can be considered to be the limiting factor of the concerned distributions. In cases of other species, we could also consider that the observed interruption can be the consequence of a lack of data. For example, *Panurginus labiatus* (fig. 3) is not a typical mountain species but it is also distributed on each side of the disjunction. It seems likely that this disjunction can at least for

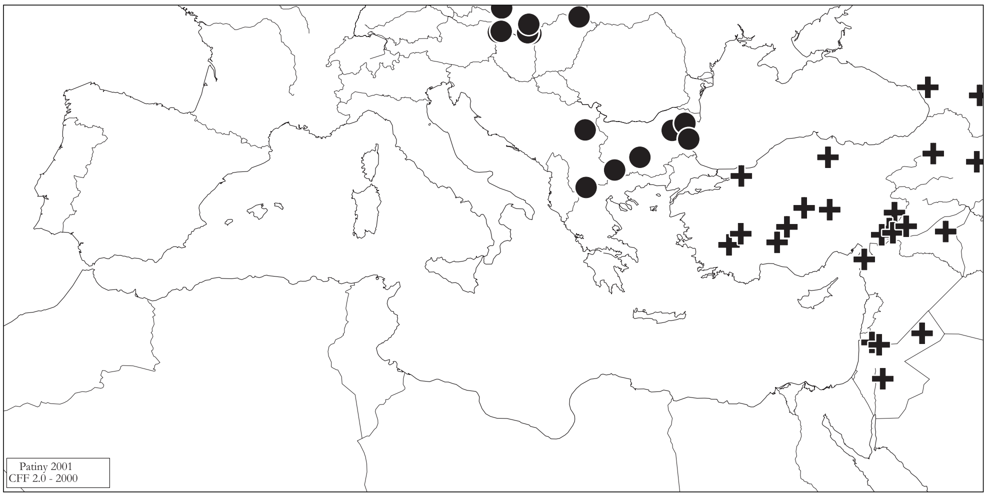

Figure 3
Distribution of *Panurginus labiatus* and *Panurginus lactipennis* in the Balkan and Turkey.

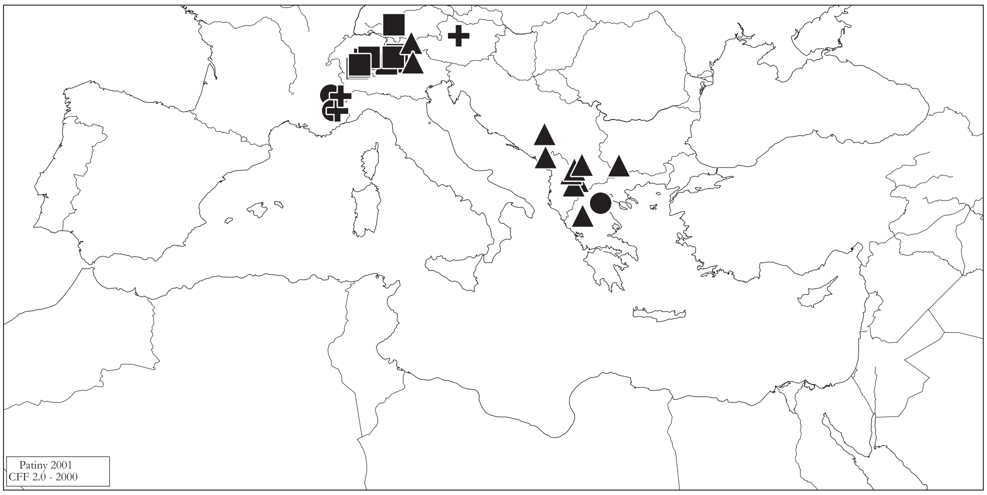

Figure 4
Distribution of four species of the *Panurginus montanus* complex: *Panurginus alpinus*, *P. montanus*, *P. sericatus* and *P. tyrolensis*.

some taxa be explained by a lack of data.

Panurginus species are not known between western Lybia and southern Israel (fig. 1, 2). Disjunctions of ranges in this part of North-Africa have been observed in numerous other groups. The relatively greater extension of the Sahara (and more generally this of desert ecosystems) can be considered to act against a larger distribution of the species in this part of North-Africa. In some other groups (for example in *Panurgus* Panzer, 1806) some intermediar isolated areas (this area is characterized by a high level of endemism, notably in Cyrenaika) and a wider distribution in eastern Egypt are observed. Perhaps this could also be revealed for *Panurginus* by an improvement of knowledge, keeping in mind that the main part of the disjunction would probably remain empty of any data.

Beside these major disjunctions, *Panurginus* species show several local concentrations acting in the West-Palaearctic frame as diversity pockets. *Panurginus albopilosus*, *P. annulatus* and *P. tunensis* (fig. 2) characterize one of the most important of these centers, the Ibero-Maghrebian. A more detailed study of the *Panurginus* ranges in the Ibero-Maghrebian area allows to distinguish different obvious origins and distribution patterns of the taxa. *Panurginus albopilosus* is almost equally distributed in southern Spain and northern (Atlantic) Morocco. *Panurginus annulatus* is restricted to Central Spain, while *P. tunensis* is typically Maghrebian, distributed along the southern slopes of the Atlas in Tunisia and Morocco (the rarity in Algeria should be considered as the direct consequence of a lack of data). The Ibero-Maghrebian frame which appears, by means of more general approaches (Patiny 2001, Patiny & Gaspar 2000), as a major dispersion and diversification centre for many Panurginae, is in fact composed by several small entities, partly characterized here based on *Panurginus* distributions. These areas are localised in Spain, northern Maghreb or the southern Atlas. It has to be mentioned that, closely related to the continental area by their fauna, the Canary islands can be described as a fourth area of isolation for Ibero-Maghrebian Panurginae. A reliable illustration is the range of *Panurginus brullei*.

Turkish species were deliberately chosen not to be entirely studied here. Previous studies (Oosterbroek & Arntzen 1992, Patiny 2001, Patiny & Gaspar 2000, Varga 1996) clearly show the high interest of Turkey and neighbouring areas for West-Palaearctic biodiversity problematics. This area obviously needs specific studies, because of its high biodiversity. Nevertheless, the Turkish species *P. lactipennis* is studied here in association with *P. labiatus*. These taxa ranges illustrate a particular aspect of the role of Turkey in the diversification of Panurginae. From the morphological point of view, *P. labiatus* was clearly observed to be the probable sister-group of *P. lactipennis* joined to its related species. Meanwhile, *P. lactipennis* is strictly distributed in Turkey and the oriental neighbouring area, while *P. labiatus* is strictly Balkanic. This importance of the Balkanic area in the diversity and diversification of *Panurginus* is quite exceptional, most other Panurginae being rather poorly diversified in this region. It is also well underlined by the case of *Panurginus montanus* and related species. Studying these taxa, specific divergences were observed all around the transdanubian plain in the different mountain chains. *Panurginus alpinus* has a western distribution, restricted to the western part of the Alpine chain. *Panurginus montanus* and *P. sericatus* are more Central-European but also strictly restricted to the Alps. In the southern Balkan, *Panurginus tyrolensis* is mainly distributed in the Pindos chain. All distributions seem to indicate that the *Panurginus montanus* group has diversified around the transdanubian plain. The Balkan can thus be designated for some Panurginae, *Panurginus* for example, as a centre of diversification and dispersion, as it is for numerous other groups (Fritz 1996, Hewitt 1999, De Lattin 1967, Reinig 1937, 1969).

The research on the causes of the contemporary biogeographic configurations generally – and in Apoidea in particular - lead to the Quaternary glaciations and their faunal implications. These phenomena constitute a particularly interesting explanation of the diversification of Apoidea. The two processes have indeed been fully contemporary. The Apoidea s.str. diverged from the Sphecoidea s.str. in late Secondary and their diversification took place during Tertiary and Quaternary (Engel 2001, Michener 2000, Radchencko & Pesenko 1994). The contemporary species can generally be considered as the result of a late Quaternary specification process (consequence of the Würm glaciation).

During glaciations following a now relatively well known process, a large ice sheet covered the southern Palaearctic. This northern ice sheet was followed by a large zone of tundra-like ecosystems which is totally unsuitable for survival of numerous species, in particular for the Apoidea. The two main consequences of these eco-climatic transformations are the extinction of most stenotypic taxa and the restriction of the more eurytopic species to small disconnected refugia distributed in meridional parts of continents (around the Mediterranean basin in case of the West-Palaearctic area). Other consequences of glaciations are notably the possibility of slight southward expansion due to the reduction of the sea level. The transformation of the distributions under the pressure of glaciations appears to be clearly favourable to diversification.

The observed restriction of the species related to *Panurginus albopilosus* to the Ibero-Maghrebian area is also particularly well explained and illustrated by this climatic transformation scheme. All available representations of ranges of ecosystems during the last glacial optimum show that the large general Ibero-Maghrebian refugium is in fact fragmented into several small entities (Hewitt 1999, Varga 1996). Distinct areas were distributed from Central Spain to the southern coast. Morocco was at least subdivided into two parts: a North-West Atlantic plain and the southern slopes of the Atlas, limited by desert in the south. A third entity seems to have been constituted by the Oued Souss plain (Southern Agadir). In the same complex of refugia the particular place occupied by the Canary Islands characterized by several endemic species and subspecies had to be observed. The Spanish endemism of *P. annulatus* can then be explained as the consequence of isolation in one of the Spanish refugia. The case of *P. albopilosus* case is more difficult to explain. This species is distributed in the whole Ibero-Maghrebian area and does not show any notable polarity. Meanwhile, this species was observed to be nearly exclusively distributed in the northern Atlas and particularly abundant in northern Morocco. This species could be considered as truely Moroccan, so it could only be an Atlantic taxon. Opposite to *Panurginus albopilosus*, *P. tunensis* is only present in Tunisia and southern parts of the Moroccan High Atlas, following a long peri-Saharian and trans-Maghrebian diagonal. A probable origin of this species is situated in the southern Atlas. *Panurginus brullei* is an endemic Canarian species, very probably the consequence of a population isolation in these islands.

Likewise, the segregation between *P. labiatus* and *lactipennis* can be easily explained in the same way. During glaciations the Balkan Peninsula constituted a refugium area separated from Turkey. This could have lead to the differentiation of *P. labiatus* while the relative homogeneity of the Balkanic refugium was not favourable to further speciation. Contrary to the Balkanic area, southern and eastern parts of Asia Minor are crumbled into numerous small refugia. This could be used to explain the diversification within the *Panurginus lactipennis* group.

West-Palaearctic species related to *Panurginus montanus* are mainly Balkanic and Central-European and distributed in the main mountain chains. In regard of this typical distribution, implying colder habitats than usual for Panurginae, it is plausible to presume that the origins of this species are probably different of the usual mediterranean refugia. During glaciation, between the periglacial tundra and the mediterranean relict habitats, there were intermediar ecosystems. The *pseudoperiglacial cold steppe* and *forest-steppe belts* as mentioned by Varga (1996) could have provided refugia for species featuring the ecological preferences of *Panurginus*. This hypothesis gains strength if the observed disjunction (fig. 4) between *P. tyrolensis* and the other species would correspond with the existence of a *pseudoperiglacial cold steppe* and *forest-steppe* isola in the Balkanic area.

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The beetles of the county of Salzburg - a contribution to the survey of European invertebrates (Coleoptera)

Elisabeth Geiser

Abstract

Recently the author has published the book 'Die Käfer des Landes Salzburg – Faunistische Bestandserfassung und tiergeographische Interpretation' ('The beetles of the county of Salzburg – faunistical survey and zoogeographical interpretation'). It contains more than 30 000 records, covering a period of more than 100 years. This large amount of information, combined with the co-operation with ZOBODAT (Linz, Austria), made it possible to conduct some statistical and biogeographical analyses. The county of Salzburg covers 7153 km^2, less than 1% of the area of central Europe. It was almost completely covered with ice during the last ice age period until 18 000 years ago. Despite this, 3750 beetle species have been found in the area. The main cause for this relatively high number of species is the high degree of heterogenity of the landscape in the county of Salzburg. Besides, the analysis of the distributional ranges of the beetles of Salzburg reveals that most of them occupy a very large range, which indicates a high dispersal capacity.

This faunistic study of beetles was published in the German language, because it will predominantly be used by colleagues from German speaking countries. Nevertheless, the book can also be used by entomologists without or with very little knowledge of the German language. The general chapters are richly illustrated and the distribution in Salzburg of 154 beetle-species is figured in grid maps. The recording sites are registered in an index, containing precise data on the locality including the coordinates according to a small scale grid. This comprehensive work of more than 700 pages can be considered as a contribution to the survey of the European invertebrate fauna.

Key words: Coleoptera, faunistics, biodiversity, Austria, Salzburg, Alps, biogeography.

Introduction

Faunistic research on Coleoptera has a long tradition in Central Europe. For most of the counties comprehensive studies exist, most of them written decades ago. These were updated from time to time by articles in local journals. Such intentions have also existed for the county of Salzburg, but a comprehensive study on the Coleoptera fauna was never published until 2001. Because of the accumulation of the information, this study grew to a book with more than 700 pages, which also contains some results of a zoogeographical analysis on the beetles of this small part of central Europe (Geiser 2001).

The county of Salzburg covers an area of 7153 km^2. It is part of the Federal Republic of Austria (fig. 1). From the view of a biogeographer it has the disadvantage that both the capital and the county are named Salzburg. In this article 'Salzburg' always means 'county of Salzburg'.

Data sources and methods

For this first comprehensive study on the Coleoptera of Salzburg it was necessary to collect all faunistic data from a period of more than 100 years. An important data source are insect collections. There are three important Coleoptera collections with a large amount of specimens from Salzburg, but more than 60 other collections were screened.

A lot of additional faunal information is scattered in papers and books. More than 200 publications could be found with more or less important faunal data from Salzburg.

The third important data source is the unpublished information from coleopterologists, which was gathered for their own research and for studies on behalf of nature conservation authorities. To obtain these records, it is necessary to know these coleopterologists, and they have to know the author. Otherwise you would not get the informa-

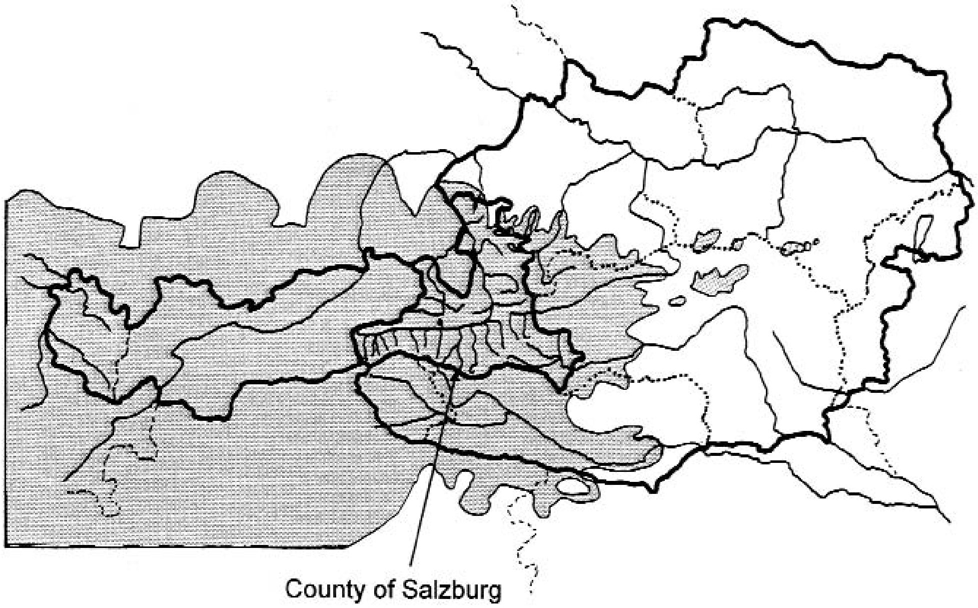


Figure 1
The eastern Alps during the Würm-glacial period, 20 000 years b.p.

tion and the permission to publish it. The author also has to decide whether this information is reliable.

The major part of the data collected from these sources was also sent to ZOBODAT (former: ZOODAT) in Linz.

Of course it is impossible to check every specimen in the screened collections. Besides, even if you are careful, you would not know whether the published or the unpublished records have all been identified correctly. If you collect data from a period of more than 100 years, even well identified specimens may belong to other species now, because of taxonomic revisions. Therefore, before the manuscript was finished, more than 50 renowned coleopterologists of central Europe were asked to have a look at that part of the manuscript which deals with their own taxonomic group. The coleopterologists quickly found the main mistakes, so these could be removed before the statistical analysis was started.

Table 1
Percentage of area and number of Coleoptera species of the county of Salzburg in comparison with Austria and some other countries and areas of Central Europe.

	number of Coleoptera species	**Salzburg: percentage of of the area**	**Salzburg: percentage of the number of species**
Central Europe	~9000	< 1%	40%
Germany	6479	2%	55%
Bavaria	5456	10%	65%
Austria	7379	8.5%	48.2%
South Tyrol	4475	96%	80%
Slovenia	6000	35%	60%

Numbers of records, species and records per species

For the county of Salzburg 3750 Coleoptera species have been recorded. This is the result of the collection of more than 30 000 records, most of which are published for the first time. These records are very heterogeneously distributed over the area of Salzburg (fig. 3).
The number of records per species is also very varied (fig. 2). For 624 species only one record is known, while 453 are represented by only two records. For 17 species more than 90 records could be found.

Statistical analysis

There are several definitions of Central Europe, but the area of the county of Salzburg is always

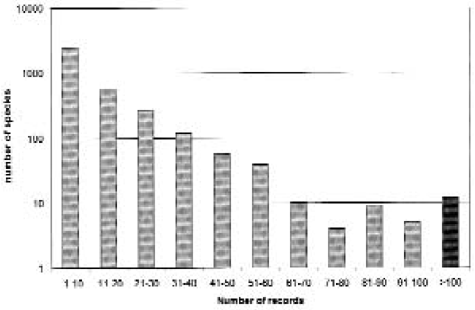
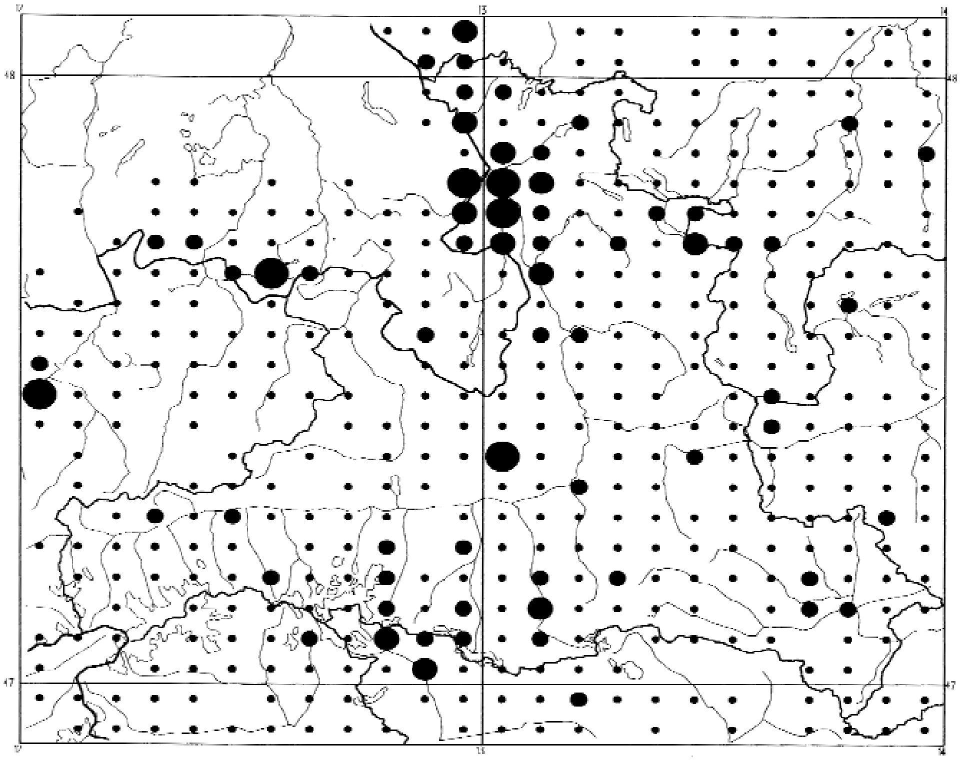


Figure 2
Frequency of records of the Coleoptera species from the county of Salzburg on a logarithmic scale.



Number of records:
● >1200 ● 601 - 1200 ● 201 - 600 • 1 - 200

Figure 3
Frequency of records of the Coleoptera fauna from the county of Salzburg in square grids of 3 x 5 arc minutes (about 6 x 5.5 km). Map produced by ZOBODAT (Linz, Austria), 26.i.2001.

smaller than 1% of the area of Central Europe. In comparison with other European areas at nearly the same degree of latitude, 3750 beetle species is a relatively high number for such a small county (table 1).

Zoogeographical analysis

There are always several factors which have an influence on the recent distribution of species. In Central Europe, especially in the Alps and their surroundings, the most important factor was the ice age, especially the Würm period, when the glaciers covered large parts of central Europe until 18 000 years ago (fig. 1). The area of Salzburg was almost completely covered with thick glaciers, except for a few species that survived on mountain tops (nunatakr species). It seems paradoxical that this recently devastated area is inhabited by a relatively high number of species, in comparison with counties of the same degree of latitude without such glacial devastation. What is the reason for such a high number of Coleoptera species in Salzburg?

1. High diversity in orography and geology and climate

Salzburg is an orographically very heterogeneous area of central Europe (fig. 4). There are low-

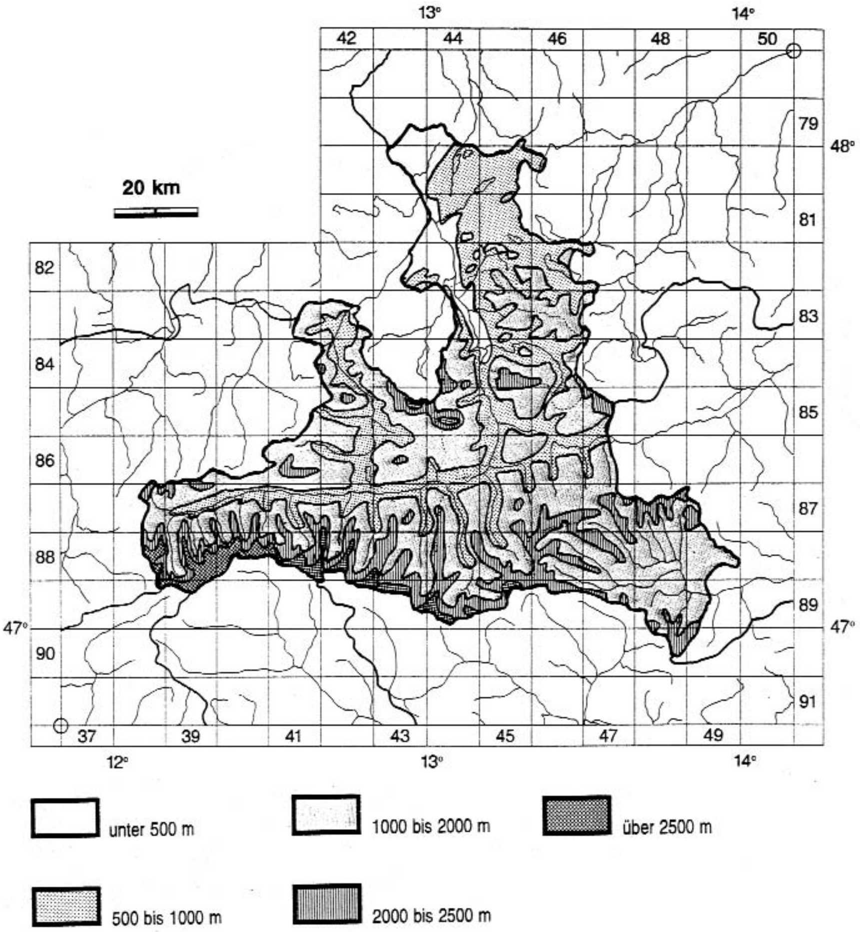


Figure 4
Orographic diversity of the county of Salzburg.

lands (only 400 m altitude) with alluvial forest regions and also some high mountain massifs with very diverse geology: the northern calcareous Alps with special soil conditions and vegetation, which differ in many features from the central Alps with silicate minerals and special landscape types. There are several mountain areas of more than 3000 m altitude, the habitat of a very specialized fauna.

These mountain massifs cause a sharp gradient in the climate. The city of Salzburg is well known for its frequent rain (about 1300 mm a year), but in the northern calcareous Alps the precipitation is even more (2400 mm a year). On the contrary, in some parts of the central Alps the annual precipitation is less than 1000 mm. The driest region of Salzburg is the ‘Lungau‘, which is situated south of the main ridge of the Alps. Some species which have their range in southern central Europe and even in southern Europe have been recorded there. As this dry region with a relatively high insolation is situated above 1000 m altitude, the typical xerothermic fauna, which occurs in the lowland of other counties of Austria, is absent.

2. Partition of the distribution types of the beetles of Salzburg

The major part of the Coleoptera species of Salzburg have a very large range (87% have a range which covers more than Central Europe), 33% of the species are recorded from several parts of the Palaearctic region (fig. 5). For these species we can assume a high dispersal capacity, so they resettled their habitats in Salzburg presumably within a few hundred years during the postglacial period. But the species with less dispersal capacity were also successful in the resettlement of their alpine habitats within a few thousand years (see also Geiser 1998).

Some remarkable species with a small range in central Europe have been recorded from Salzburg: 81 species endemics of the Eastern Alps and 37 arctoalpine species. Their contribution to the number of species in Salzburg is very small, but these Coleoptera species are of interest for biogeography, systematics and nature conservation.

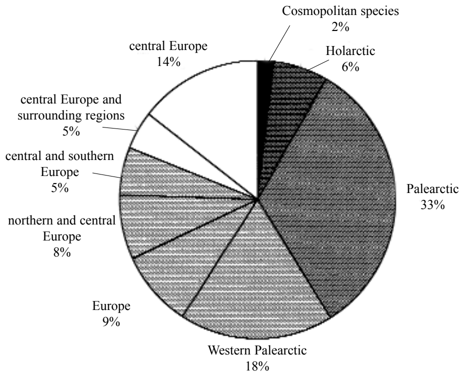


Figure 5
Partition of the distribution types of the beetles of Salzburg.

Further information about the comprehensive faunistic study on the Coleoptera of the county of Salzburg

Here it is only possible to give some hints of the results of this study of the Coleoptera of Salzburg. This book is a detailed survey of every record of beetles from Salzburg and also from sites in the immediate surrounding parts, which the author got to know until December 2000. In almost 500 pages you will find for more than 3750 species the exact site and the exact data source of the records, as well as the date, the collector and the identifier, as far as this information was available. One chapter deals with records which were published erroneously on the Coleoptera fauna of Salzburg. All mentioned geographical sites are listed alphabetically in the geographical index with further information on the exact site, the geographic grid and, if necessary, with further remarks on geographic homonyms.

This book is published in German, because most of the coleopterologists who will be interested in this information are German speaking persons. But this book is also useful for entomologists without or with only little knowledge of the German language. You will find the beetle species by their scientific names. The taxonomy is used consequently according to the well known series by Freude-Harde-Lohse ‘Die Käfer Mitteleuropas‘, volume 1 to 11 and the supplementary volumes 12 to 15. The sites of the records can be found easily on a map of Salzburg by the detailed geographic index. The chapters describing the orographical, geological and climatic conditions of the county are illustrated with many thematical maps. The other chapters contain a large variety of diagrams, maps and tables. For 154 frequently recorded species you will find grid maps of their distribution.

The European Invertebrate Survey has the ambitious goal to make European distribution maps for all invertebrates and the approach is only possible step by step. This Coleoptera fauna of Salzburg is such a step, for a very small part of Europe, but for a large and important group of invertebrates.

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Investigations of Gamasina mites in natural and man-affected soils in Latvia (Acari: Mesostigmata)

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Abstract

A short overview is presented on Gamasina material collected in 22 natural and man-disturbed habitats in Latvia. Species diversity, average density and species dominance were investigated. Altogether 167 Gamasina species from 14 families were found. The highest number of species was found for field margins and the lowest for pine forests and arable lands affected by calciferous dust. The highest densities of mites were observed for arable lands, and the lowest for coastal meadows. There were no habitats, neither natural nor man-affected, with both a high number of species and high densities. Some specific habitats such as spruce forests polluted by pig slurry and arable lands polluted by calciferous dust had a low number of species and high densities. Generally, man-affected habitats had higher average abundances, whereas natural habitats had higher species diversity. 25 Gamasina species were registered as eudominants or dominants. The most common species was the ubiquitous *Veigaia nemorensis*. The dominant species differed among polluted habitat types, but were similar for non-polluted sites within a habitat type.

Key words: soil Gamasina mites, natural and human-affected habitats, species diversity, average abundance, species dominance.

Introduction

Soil-dwelling mites and among them Gamasina mites (Acari, Mesostigmata; fig. 1, 2) are widely distributed in soils, rich in species and have great ecological significance in the respective ecosystems (Coleman & Crossley 1996, Koehler 1997, Lebrun 1979, Walter & Proctor 2000). Mites are known to be good indicators of various changes in the soil (Edwards & Bohlen 1995, Hogervorst et al. 1993, Kaczmarek 2000, Karg 1968, Krivolutsky 1994).

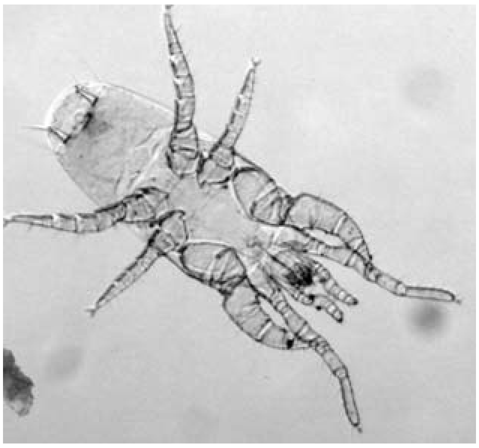

Figure 1
Dendrolaelaps nostricornutus (Rodacaridae).
Photo Ineta Salmane.

Since the middle of the last century studies have been conducted on predatory Gamasina in soils of Latvia (Eglitis 1954, 1972, Lapina 1976a, 1976b, 1988, Melecis et al. 1994, Paulina & Salmane 1999, Salmane 1996, 2000a, 2000b, 2000c, 2001, 2002, Salmane et al. 1999, Salmane & Heldt 2001) and on their response to different types of environmental pollution (Kachalova et al.1989, Karps et al. 1990, Lapina & Melecis 1985). Many species were found and published by Lapina (1988). During recent years, the author of the present paper has investigated mite communities of various habitats, and has found species new for the fauna of Latvia, especially in coastal meadows and seashore habitats.

A short overview is presented on soil Gamasina mites investigated in Latvia.

Discussion of results

Altogether 167 Gamasina species from 14 fami-

Table 1
List of Gamasina species found in the observed habitats.

Parasitidae
Parasitus kraepelini Berlese, 1903
P. fimetorum Berlese, 1903
P. numismaticus Vitzthum, 1930
P. lunaris Berlese, 1906
P. remberti (Oudemans, 1912)
P. celer (C. K. Koch, 1835)
P. loricatus (Wankel, 1861)
P. oudemansi Berlese, 1903
P. kempersi Oudemans, 1902
P. lunulatus (Muller, 1859)
P. halophilus (Sellnick, 1957)
P. brevicornis Berlese, 1903
Gamasodes spiniger (Trägardh, 1910)
Poecilochirus necrophori Vitzthum, 1930
Holoparasitus excipuliger (Berlese, 1905)
Pergamasus crassipes (Linnaeus, 1758)
P. septentrionalis (Oudemans, 1902)
P. vagabundus Karg, 1968
P. teutonicus Willmann, 1956
P. lapponicus Tragardh, 1910
P. wasmanni (Oudemans, 1902
P. suecicus (Trägardh, 1936)
P. quisquilarum (Canestrini, 1882)
P. mirabilis Willmann, 1951
P. robustus (Oudemans, 1902)
P. holzmanae Micherdzinsky, 1969
P. parrunciger Bhattacharyya, 1963
P. misellus Berlese, 1904

Veigaiaidae
Veigaia nemorensis (C.L. Koch, 1839)
V. cervus (Krämer, 1876)
V. exigua (Berlese, 1917)
V. kochi (Trägardh, 1901)
Gamasolaelaps excisus (C.L.Koch, 1879)

Ameroseiidae
Ameroseius corbicula (Sowerby, 1806)
A. insignis Bernhard, 1963
Epicriopsis horridus (Kramer, 1876)

Aceosejiidae
Aceoseius muricatus (C. L. Koch, 1839)
Neojordensia levis (Oudemans et Voigts, 1904)
Lasioseius youcefi Athias-Henriot, 1959
Cheiroseius borealis (Berlese, 1904)
C. necorniger (Oudemans, 1903)
C. viduus C. L. Koch, 1839
C. unguiculatus Berlese, 1887
C. serratus (Halbert, 1915)
Leioseius minusculus (Berlese, 1905)
L. montanulus Hirschmann, 1963
L. bicolor (Berlese, 1918)
L. insignis Hirschmann, 1963
L. halophilus (Willmann, 1949)
L. minutus (Halbert, 1915)
L. semiscissus (Berlese, 1892)
L. longispinosus Hirschmann, 1963
Platyseius italicus (Berlese, 1905)
Iphidozercon venustulus (Berlese, 1917)
Melichares juradeus Schweizer, 1949
Proctolaelaps pygmaeus (Müller, 1860)

Phytoseiidae
Amblyseius obtusus (C.L.Koch, 1839)
A. aurescens Athias-Henriot, 1961
A. zwoelferi (Dosse, 1957)
A. reductus Wainstein, 1962
A. rademacheri Dosse, 1958
A. bicaudus Wainstein, 1962
A. marinus (Willmann, 1952)
A. messor Wainstein, 1960
A. graminis Chant, 1956
A. meridionalis (Berlese, 1914)
A. agrestis (Karg, 1960)
A. andersoni (Chant, 1957)
A. bakeri (Garman, 1948)
A. herbarius Wainstein, 1960

Antennosejidae
Antennoseius borrusicus Sellnick, 1945
A. delicatus Berlese, 1916
A. bacatosimilis Karg, 1965

Rhodacaridae
Minirhodacarellus minimus (Karg, 1961)
Rhodacarellus silesiacus Willmann, 1936
Rhodacarus mandibularis Berlese, 1921
R. reconditus Athias-Henriot, 1961
R. haarlovi Shcherbak, 1977
Dendrolaelaps foveolatus (Leitner, 1949)
D. arenarius Karg, 1971
D. stammeri Hirschmann, 1960
D. cornutus (Krämer, 1886)
D. tenuipilus Hirschmann, 1960

D. latior (Leitner, 1949)
D. nostricornutus Hirschmann et Wisnewski, 1982
D. fallax (Leitner, 1949)
Dendrolaelaspis angulosus Willmann, 1936
Asca aphidioides (Linnaeus, 1758)
A. bicornis (Canestrini et Fazago, 1877)
Gamasellus montanus (Willmann, 1936)
Euryparasitus emarginatus (C. L. Koch, 1839)
Cyrtolaelaps minor Willmann, 1952
C. mucronatus G. et R. Canestrini, 1881
Halolaelaps balticus Willmann, 1954
H. incisus Hyatt, 1956
H. marinus (Brady, 1875)
H. communis Goetz, in Hirschmann, 1966

Macrochelidae

Macrocheles glaber (Muller, 1860)
M. montanus Willmann, 1951
M. submotus Falconer, 1924
M. decoloratus (C. L. Koch, 1839)
M. rotundiscutis Bregetova et Koroleva, 1960
M. merdarius (Berlese, 1889)
M. carinatus (C. L. Koch, 1839)
M. tardus (C. L. Koch, 1841)
Geholaspis mandibularis (Berlese, 1904)
G. longispinosus (Krämer, 1876)
Holostaspella subornata Bregetova et Koroleva, 1960
H. ornata (Berlese, 1904)

Pachylaelaptidae

Pachyseius humeralis Berlese, 1910
Pachylaelaps furcifer Oudemans, 1903
P. pectinifer (G.et R.Canestrini, 1882)
P. magnus Halbert, 1915
P. littoralis Halbert, 1915
P. sculptus Berlese, 1921
P. regularis Berlese, 1921
P. longisetis Halbert, 1915
P. fuscinuliger Berlese, 1921
P. siculus Berlese, 1892
P. karawaiewi Berlese, 1921

Laelaptidae

Eulaelaps stabularis (C. L. Koch, 1836)
Hypoaspis aculeifer (Canestrini, 1883)
H. praesternalis Willmann, 1949
H. vacua (Michael, 1891)
H. karawaiewi (Berlese, 1903)
H. incertus Bernhard, 1955
H. kargi Costa, 1968
H. angusticutatus Willmann, 1951
H. heyi Karg, 1962, var. latvicus
H. miles Berlese, 1881
H. rigensis Lapina, 1976
H. claviger (Berlese, 1883)
H. oblonga Halbert, 1915
H. lusisi Lapina, 1976
H. sclerotarsa Costa, 1968
H. similisetae Karg, 1965
H. austriacus (Sellnick, 1935)
Laelaspis markewitschi Pirianyk, 1959
L. astronomicus C. L. Koch, 1839
L. humerata (Berlese, 1904)
Ololaelaps placentula (Berlese, 1887)
O. sellnicki Bregetova et Koroleva, nom. n., 1964
O. veneta (Berlese, 1903)
Holotaspis montana (Berlese, 1904)
Haemolaelaps casalis (Berlese, 1887)
H. glasgowi (Ewing, 1925)

Haemogamasidae

Haemogamasus ambulans (Thorell, 1872)

Hirstionysidae

Hirstionyssus isabellinus Oudemans, 1913

Eviphidae

Alliphis siculus Oudemans, 1905
Eviphis ostrinus (C. L. Koch, 1836)
Iphidosoma fimetarium (Müller, 1859)
I. physogastris Karg, 1971
Thinoseius spinosus (Willmann, 1939)

Zerconidae

Prozercon kochi Sellnick, 1943
P. tragardhi (Halbert, 1923)
P. sellnicki Halaskova, 1963
P. sarakensis Willmann, 1939
Mixozercon sellnicki Schweizer, 1948
Zercon spatulatus Willmann, 1939
Z. zelawaiensis Sellnick, 1944
Z. forsslundi Sellnick, 1958
Z. carpathicus Sellnick, 1958
Z. jodathae Sellnick, 1944
Z. montanus Willmann, 1953
Z. fageticola Halaskova, 1970

lies were recorded in 22 natural and man-affected habitats of Latvia (table 1, 2). Parasitidae (28 species), Rhodacaridae (24) and Laelaptidae (21) were the most diverse families, Haemogamasidae and Hirstionyssidae were represented by only one species each.

The highest species diversity was found on margins of fields (90 species), followed by mixed forests and coastal meadows (fig. 3). The high species diversity in field margins is caused by the non-intensive agricultural practices and by plant litter (Lapina 1988). Coastal meadows consist of diverse habitats with a variation of microhabitats from xerophytic to flooded by sea (Eiduks 1982). Several authors have found that coastal meadow habitats support high species richness of microarthropods, among them Gamasina mites, due to the heterogeneity of environmental conditions (Paulina & Salmane 1996, 1999, Salmane et al. 1999, Salmane 2000a). High numbers of species in the mixed forests are related to the diverse environmental conditions: rich organic soils and abundant vegetation (Lapina 1988).

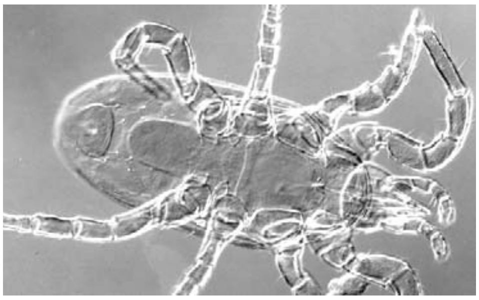

Figure 2
Hypoaspis sclerotarsa (Parasitidae). Photo Ineta Salmane.

The highest average abundance was observed in arable lands and inland meadows polluted by pig slurry (fig. 3), which was three times and two times higher, respectively, than in the other habitats. The Gamasina mites found and described by Lapina (1988) in arable lands are diverse. The agricultural practices and fertilizers used seemed to be quite favourable to support a high number of species, as well as high densities. Environmental conditions caused by pollution of inland

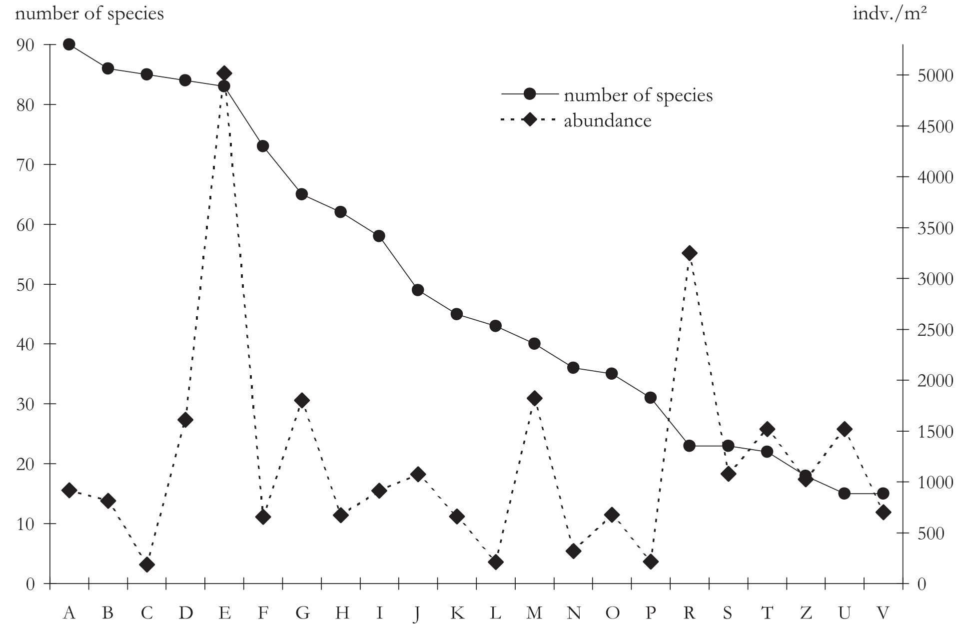

Figure 3
Species diversity and density of Gamasina mites in all observed habitats (abbreviations for habitats are given in table 2).

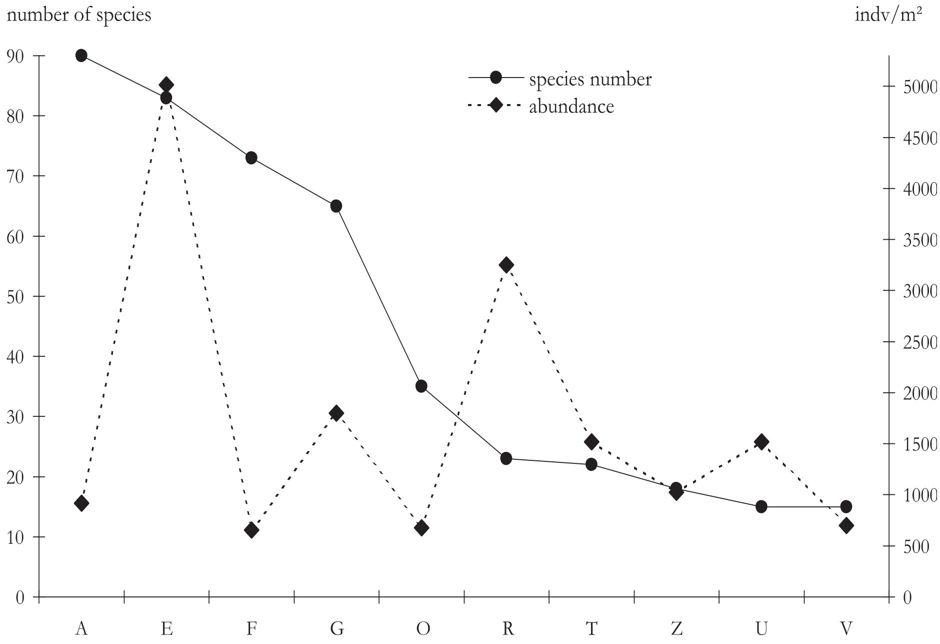

Figure 4
Species diversity and densities in the man-affected habitats (abbreviations for habitats are given in table 2).

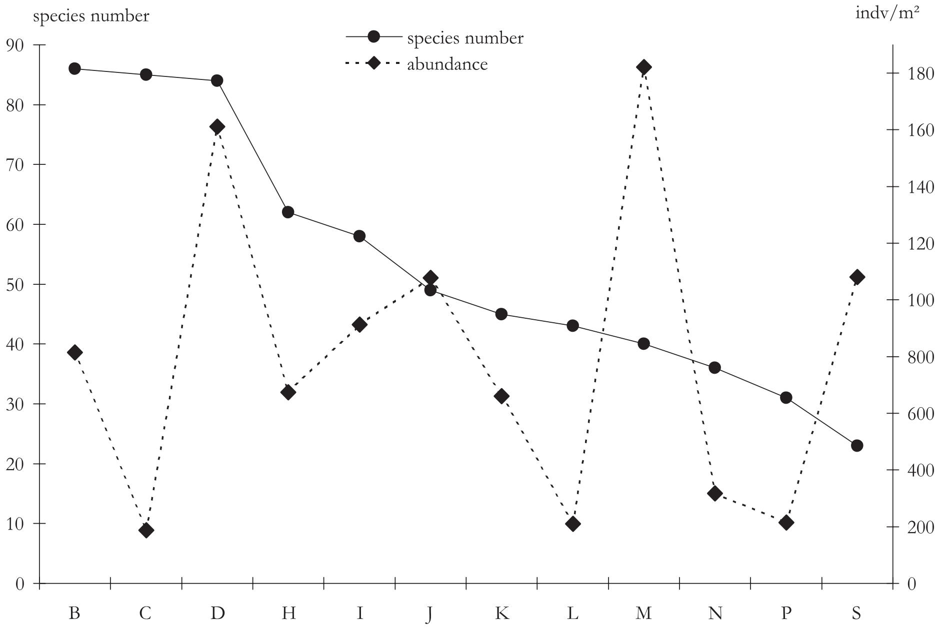

Figure 5
Species diversity and density in the natural habitats (abbreviations for habitats are given in table 2).

Table 2
Habitats investigated, number of Gamasina species (N) and average abundance (A) stated there.

Habitats	**Abbreviations to habitats used**	**N**	**A**
Edges of fields	A	90	918
Mixed forest	B	86	814
Coastal meadows	C	85	188
Piceetum oxalidosa	D	84	1612
Arable lands	E	83	5016
Inland meadows	F	73	654
Parks & Gardens	G	64	1763
Narrow-leaved forests	H	62	674
Pineetum vaccinosa	I	58	913
Broad-leaved forest	J	49	1077
Pineetum myrtilosa	K	45	660
White dunes	L	43	210
Bogs	M	40	1822
Grey dunes	N	36	318
Inland meadows polluted by calciferous dust	O	35	675
Primary dunes	P	31	214
Inland meadows polluted by pig slurry	R	23	3250
Driftline	S	23	1080
Piceetum oxalidosa polluted by pig slurry	T	22	1520
Reservoires with pig slurry	Z	18	1024
Arable lands polluted by calciferous dust	U	15	1520
Pine forest polluted by calciferous dust	V	15	700

meadows by pig slurry resulted in specific Gamasina species composition dominated by so-called ‘dung and compost’ species or ubiquists (Karps et al. 1990). Non-polluted inland meadows typically have high species diversity, but after release of large amounts of organic matter, favourable conditions remained only for some species-specialists, which became abundant. Spruce forests polluted by pig slurry were neither rich in species nor did they have high densities (Karps et al. 1990) (table 1).

Reservoirs with pig slurry are very specific habitats. In these habitats only 18 species were found and they were presented in high densities (fig. 3).

Washed ashore (driftline) material was comprised by different jetsam deposited by sea and was usually rich in organic matter. 23 Gamasina species were found there in high abundance.

Among the studied habitats none had high values for both density and diversity (fig. 3), only arable lands showed the highest density and also relatively high number of species. It is known from literature (Schwerdtfeger 1975) that high species diversity usually is associated with low densities.

The lowest number of species was recorded for arable lands and pine forests polluted by calciferous dust (fig. 3). Non-polluted arable lands had the highest densities and also the highest number of species, but when polluted by calciferous dust, densities decreased by more than three times and diversity more than five times. Inland meadows polluted by calciferous dust had twice as many species as the other two habitats polluted by this source, while densities were low.

The impact of pollutants on soil Gamasina communities is obvious for habitats polluted by pig slurry and by calciferous dust (fig. 3, 4). Gamasina mites diversity is enhanced by non-intensive human activity, which does not cause a drastic change in environmental conditions, such as at field margins or inland meadows. Nevertheless, arable lands also had high species diversities and densities (Lapina 1988). Natural habitats mostly have a high microhabitat diversity, which leads to diverse soil Gamasina communities (fig. 5). When the diversity of natural habitats is disturbed by human activities, environmental conditions change and become favourable only for a few Gamasina species or species communities. Pollution by calciferous dust is harmful for gamasins, while the degree of impact is highly dependent on the respective habitat type. In the case of pollution by pig slurry, a high number of mites was observed being distributed by means of phoresy on different insects, especially on dung beetles (Coleoptera) coming to slurry (Karps et al. 1990). The species lists of those Gamasina mites were almost similar for all habitats. In the habitats polluted by pig slurry the total number of species was not high (table 2).

Among the forest types, mixed forests had the highest Gamasina densities and the highest number of species. Of the seashore habitats, the sand dunes were the most rich in species, but the highest densities were found in the washed ashore material. Coastal meadows and inland meadows had the highest species diversity.

In total 12 natural and ten man-affected habitats were investigated and compared (fig. 4, 5). The average species diversity was higher in natural habitats, but the average densities were about three times higher in affected habitats. Among natural habitats, the highest number of species was observed in mixed forests, spruce forests and coastal meadows; among affected habitats – field margins and arable lands (fig. 4, 5). Among the natural habitats, the highest densities were found in bogs and spruce forests; and in man-affected habitats - arable lands and inland meadows - polluted by pig slurry.

The dominance structure of Gamasina mites was

Table 3

Gamasina species found in the respective habitats as eudominants or dominants.

	Pineetum myrtilosa	*Piceetum oxalidosa*	*Pineetum vaccinosa*	Mixed forest	Broad-leaved forest	Parks & Gardens	Inland meadows	Inland meadows polluted by calciferous dust	Inland meadows polluted by pig slurry	*Piceetum oxalidosa* polluted by pig slurry	Narrow-leaved forest	Edges of the fields	Reservoirs with pig slurry	Arable lands	Arable lands polluted by calciferous dust	Bogs	Coastal meadows	Driftline	Primary dunes	White dunes	Grey dunes	Pine forest polluted by calciferous dust
Parasitus lunaris														●	●							
P. fimetorum													●									
Pergamasus vagabundus		●	●	●	●						●	●										
P. lapponicus											●											
P. robustus						●																
P. teutonicus							●															
P. suecicus												●										
P. misellus								●														
P. wasmanni																						●
P. teutonicus									●													
P. brevicornis										●												
Veigaia nemorensis	●	●	●	●	●	●	●	●	●	●												
Cheiroseius necorniger																		●				
Leioseius bicolor																			●			
L. halophilus																			●			
L. insignis																				●		
Minirhodacarellus minimus																				●		
Asca aphidioides	●		●													●						
Halolaelaps balticus																				●	●	
Macrocheles glaber													●									
Hypoaspis aculeifer																	●					●
H. vacua																					●	
Alliphis siculus														●								
Thinoseius spinosus																		●				
Prozercon kochi	●															●	●					
Zercon carpathicus																					●	

also studied (table 3). 25 Species were registered as eudominants or dominants. The most common species was the ubiquitous *Veigaia nemorensis*, which was dominant in ten habitats. The most widely represented family was Parasitidae with 11 species, the most common being the ubiquitous *Pergamasus vagabundus*. The dominant species differed among the affected habitat types, but not among polluted and non-polluted habitats of a particular habitat. In the reservoirs with pig slurry, the 'dung species' *Macrocheles glaber* and *Parasitus fimetorum* clearly dominated.

Although samples were taken in different seasons and years, and the size and number of samples was different, the general trends of Gamasina occurrence and diversity in the diverse habitats were still apparent.

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