Acknowledgements

Field biologists recognise that the basic underpinning of any interpretative work is rarely acknowledged or recognised in relation to its importance. Nonetheless, it borders on impossible to name all who have contributed in some way to the creation of the SFOC foundation (Stichting Faunistisch Onderzoek Carabidae, Wageningen) database on which this book is based. For the older, faunistic data, which were also used to prepare distribution maps for all species, we refer to the Dutch carabid atlas (Turin 2000), where extensive acknowledgements are included. However, a large amount of new material has been included in the present book, some of which is accounted for in Appendix B, especially where these data have been used directly in figures and tables.

Many projects varying in size and duration that contributed to what we've been able to do here were carried out by amateur entomologists as well as by professional organisations. For their valuable contributions to building the basic pitfall trap database, we thank Kees Alders, Bas Allema, Berend Aukema, Martien Baars, Arno Braam, Matti Berg, Michiel Boeken, Kees Booij, Ben Brugge, Jan Burgers, Matthijs Courbois, Henk de Bruijn, Ron Felix, Kees de Kraker, Henk de Vries, Jeff Harvey, Robert Ketelaar, Erik Lam, Herman Lambrechts, Jorg Lambrechts (B), Ad Littel, Jinze Noordijk, Frank van Nunen, Herman Reimerink, Teun van Gijzen, Frans van Alebeek, Foppe van der Meer, Wouter van Steenis, Menno van Zuijen, Oscar Vorst, Alje Woldering and Menno Zijlstra. None of what has been accomplished here would have been possible without their efforts.

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Most fortunately, the Willem Beijerinck Biological Station (WBBS) foundation curated and managed the complete data from the pitfall research projects of the former Biological Station Wijster. Much of these data (1953-1996) were collected under the supervision of Piet den Boer or comprise the data from its own WBBS projects and have been compiled under the supervision of Rikjan Vermeulen. Both datasets are highly significant to the value of the current database, and we are very grateful for them. The older data were directly taken from Den Boer's tapes, and the more recent (after 1990) were made available to the current database by Tim Opsteeg. The full dataset was extensively checked by Roel van Klink. Roel also read an early version of the trend analysis (Chapter 6).

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Originals of illustrations in publications by Baars (1982), Bruschi (2013), Gebert (2015) and López and Oromi (2010) were made available by these authors, for which we offer our thanks. Additional habitat photos were provided by Michiel Boeken and Hannie van Noort. Ron Felix and Jan Muilwijk were very kind to carefully check the update to the second ground beetle atlas (Turin 2000; see Section 5.12) and they also provided unpublished data concerning observations of *Anillus caecus*. Data about a striking record of this species were also provided by Matti Berg. Teun van Gijzen checked many identifications to ensure the reliability of pitfall data used in the book.

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Preface

Ground beetles, the diverse coleopteran families Carabidae and Cicindelidae, include ca. 40,000 species worldwide, and 3,000 species in Europe alone. The established Dutch fauna is estimated to comprise ca. 370 species. Another ca. 20 species have been observed only incidentally and it is not always clear whether they have stable populations in the country. Regularly, new species are recorded, and recently, a few rare species became abundant in a relatively short period of time.

Besides providing a thorough description of the ground beetle fauna of the Netherlands, the main purpose of this book is to evaluate the method of pitfall trapping, illustrate a way in which heterogeneous pitfall trap data can be used to generate reliable results to describe and analyse the carabid beetle fauna of a specific faunistic area in detail, and suggest how the proposed tools can be used for conservation monitoring.

This book is mainly based on a large historical database, covering 66 years of pitfall trapping data, representing 1,500 short-term samples and ca. 4,340 year-samples, the last coming from 2,850 sites across the Netherlands.

All available pitfall year samples from Dutch locations, taken by amateur and professional carabidologists, are included in this database. We explicitly focus on carabidology in general and attempt to relate our findings with published biological and ecological studies. This book also provides an update to the second ground beetle atlas of the Netherlands (Turin 2000), but without providing detailed accounts or maps for all species.

The carabid beetle fauna of the Netherlands is described in detail and related to the Dutch landscape in terms of 17 habitat groups. About 260 of the 320 species captured in pitfalls have been classified into six main affinity groups, according to their patterns of habitat use. Both the classification of habitats and associated species are tested and used in various analyses in the book. Special attention has been given to long-term trends and to the useful aspects of nature management and conservation.

Contents

1. Introduction to the chapters

In 1977, the first atlas of the ground beetles of the Netherlands was released (Turin *et al.* 1977) as one of the first of such atlases for Carabidae in Europe. After the start of the Dutch office of the European Invertebrate Survey (EIS, Leiden) in the same year, it was decided to repeat this atlas project more thoroughly. This was made possible by a generous three-year grant from the Dutch 'Prins Bernhard Fonds'. An inventory of new faunistic data for this revised mapping scheme showed that, in addition to the usual information from insect collection labels and literature, a large amount of pitfall data existed for the Dutch territory. A large part of these data appeared to be unpublished. The results of this mapping project were published in a second carabid atlas (Turin 2000), which also provided an analysis to better define habitats of the species and their ecological preferences. In the years that followed, use of the database and especially the pitfall data was extended significantly (Section 3.2). This book is mainly based on the pitfall data, sampled by both amateur entomologists and professional ecologists, from the period 1953-2018. In addition to about 1,450 short-term samples, ca. 4,340 so called 'year-samples' (Section 3.1.2 and 4.2.5) covered the entire spring to fall reproductive season of ground beetles of full calendar years.

Chapter 2 provides a general introduction to carabidology in two main parts: Biology and Ecology. The biological part deals with aspects of carabid traits and behaviour, such as reproduction, activity patterns, feeding and dispersal abilities. The ecological part focusses on the relationships between species and their environments, as well as on population and dispersal ecology. This chapter is a review of carabidological research carried out after the classical compilation by Thiele (1977), without the slightest pretention of being complete. Our focus lies on studies carried out in Central-Europe and other work relevant to those themes, with special attention to research carried out in the Netherlands and adjacent countries, as well as on studies published after the last Dutch atlas in 2000. We refer to additional literature that assists with interpretation of these core studies.

Chapter 3 deals with the history and composition of the Dutch pitfall database (see the maps of samples localities in Figure 1.1 and 1.2). In the second part of the chapter, the pitfall method is discussed and its value for carabidological research evaluated.

Chapter 4 focuses on the data available for the Netherlands. We explore and discuss historical data from Dutch pitfall research programs. A solution is proposed for working effectively with data resulting from pitfall series with different numbers of traps and different trapping periods. The core of this method is what we refer to as 'habitat reference' and we explain it in Section 4.2. Using this method, habitats as well as species can be ecologically classified for the Dutch territory (Section 4.3 and 4.4). The first ecological classification for the Dutch species and habitats (**HAB1**), which was published by Turin *et al.* (1991), was based on 1,616 year-samples (period 1953-1983). For this project, photos as well as detailed environmental data, such as those about soil type, humidity, vegetation cover, as well as information about fertilisation and fragmentation, were recorded in the field for each of the 862 sampling localities and connected to the respective samples in the database. The **HAB1**-classification was applied to species and habitats in the second atlas (Turin 2000). New pitfall data gathered during 2000-2018, made it possible to evaluate the old classification and the result is published here as the **HAB2** classification. The **HAB2** classification is, with respect to the 33 habitat types (**X01-X33**), strictly the same as **H01-H33** in **HAB1** (Section 4.1). However, the division of these habitat types into 17 main habitat groups (**GR01-GR17**; Section 4.3) and the classification of species affinities

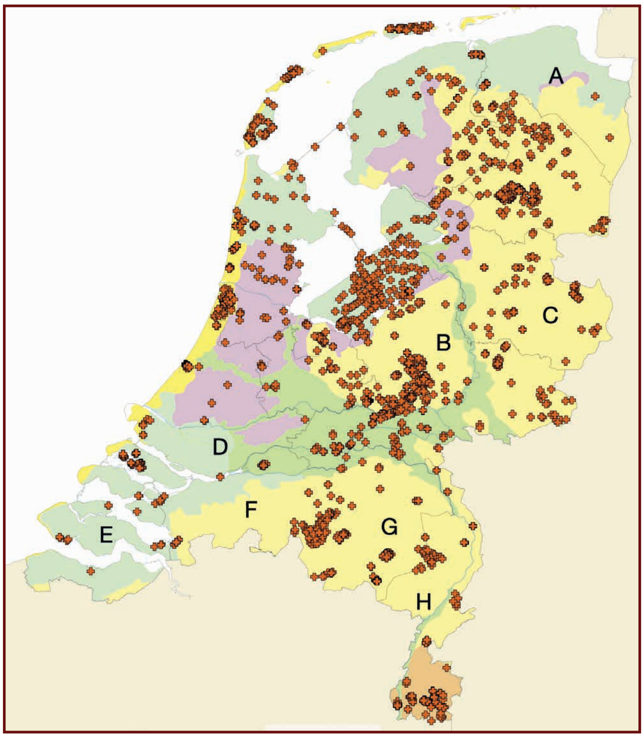

Figure 1.1. Localities of the 1×1 km-squares for which pitfall samples are present in the Dutch database (1953-2018). 'Pitfall deserts' mainly occur in the province of Groningen (A), the east of the Veluwe area (B), the centre of the province of Overijssel (C), in a large part of inland Zuid-Holland (D), most of the province of Zeeland (E), the western and eastern parts of the province of Noord-Brabant (F, G) and the north of the province of Limburg (H). The total number of records is ca. 116,940.

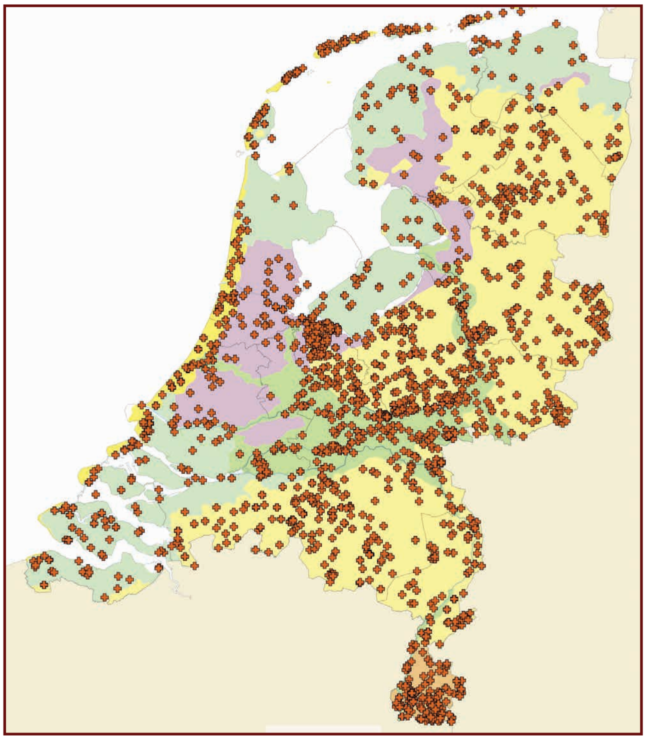

Figure 1.2. The 1×1 km-squares for which carabid records from hand sampling are present in the Dutch database, since about 1880. The earliest records in the Dutch collections, often labelled with a locality, but without a complete date, are probably from around 1850. The total number of records is ca. 179,420. (Basic map © NDFF).

into six affinity groups (Section 4.6) are new. In the chapter, the reliability of the Habitat Reference method is extensively tested.

Chapter 5. After a general introduction, the carabid fauna of the Netherlands is discussed according to a few themes, such as patterns in traits, distribution patterns and soil types and community ecology (Section 5.2-5.8). A separate section deals with biogeographical aspects (Section 5.9). The main part considers detailed descriptions of the 17 (**HAB2**) habitat groups (Section 5.10-5.11), in which **GR07** and **GR09** have been combined. The composition of the carabid fauna is discussed by habitat group, with special attention to characteristic species and the respective accompanying species. Chapter 5 concludes with a faunistic update to the last carabid atlas of the Netherlands (Turin 2000; Section 5.12).

Chapter 6 is a trend analysis, based on the 4,263 year-samples that met the criteria for inclusion. The samples span the period 1953-2018, but the analyses compare different periods in order to explore the effect of the oldest period on the trend curve, because it covered only a small range of dune habitats in one relatively narrow area. This overall analysis, based on a ca. 60-year dataset is unique for carabids and possibly for all insect groups. Up-to-date sophisticated methods are used to create trend analyses accounting for the heterogeneity of the dataset. The results are discussed, and we refer to earlier trend analyses that were carried out on Dutch data at the end of the last century, as well as to the recent most literature on trends in carabids and the general topic of insect decline.

Chapter 7 focuses on several aspects of conservation, important in the Dutch context, referring to the results of the trend analysis and the literature about threats to the carabid fauna. Suggestions are offered to enhance the protection of habitats and their species. Attention is paid to the value of the Dutch landscape for carabid diversity and nature management.

Chapter 8 summarises the general conclusions from the book.

The book concludes with a list of references, an appendix, a terms list and an index.

- **Appendix A** provides the 8-letter species codes used in many tables, by providing the full scientific names, as well as an overview of traits of the species (see also Section 5.4).
- In **Appendix B** justification is given about the origin of the samples that have been used for the graphs, tables, and landscape photos (e.g. Figure 1.3) that support the text and illustrate the results of various analyses.
- The **Terms list** defines the most important terms used throughout the book.
- The **Index** refers to the most important places in the book where respective items are covered. See also Appendix B and the Terms list.

Important notes:

- **Name codes –** It must be emphasised that the 8-character name codes for particular carabid species, used in various tables to save space for additional information, have remained consistent since the start of the Dutch database in the 1970's. Thus, for some modern genera, for example for *Ophonus* and *Poecilus*, the old 4-character genus codes ('HARP' and 'PTER') have been maintained. All codes are explained with their full valid scientific names in the species list with traits in **Appendix A**.
- **Calculations –** Because the basis for this book is an exceptionally large database (Chapter 3), it was not always possible to use exactly the same full set of samples for all calculations. In certain analyses, particular information was missing or was ambiguous for some year-samples. In such cases, these samples were excluded from the relevant analysis. Therefore, minor differences in species and/or sample totals may occur in the totals of some tables.
- **Habitat charts –** In the frequently used habitat charts (Section 4.2.2), we consider the global (visual) pattern of the configuration of the 33 Renkonen similarity values (Section 4.2.2) to be of greater importance than the exact height of the values. Therefore, for the sake of comparability, these graphs have been scaled to the highest value in the Y axis, as shown in the examples in Figure 1.3.

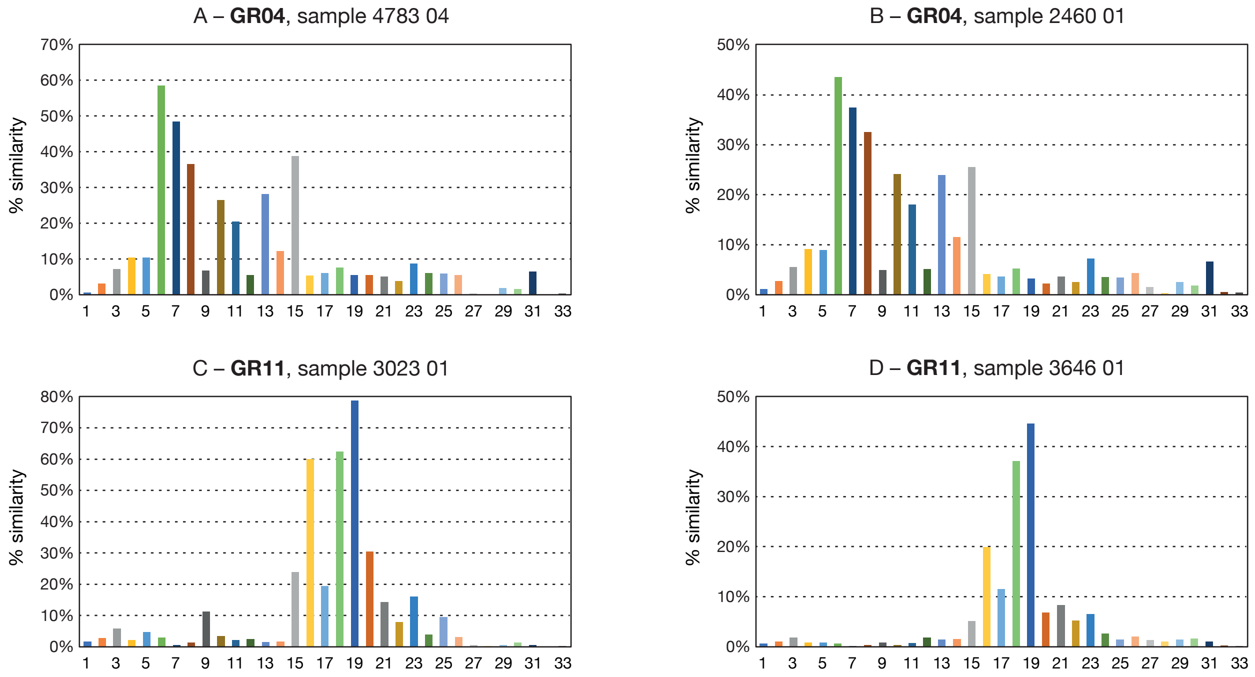

Figure 1.3. Examples of habitat charts that for comparability have been scaled to different maximum Y-values. A-B: Two samples belonging to habitat group **GR04** = drift sands and Corynephorus vegetations (Section 5.10.8). C-D: Examples from habitat group **GR11** = shadow-rich deciduous forests (Section 5.10.14).

2. Carabidology

2.1 Introduction

The term 'Carabidology' is relatively new as a description of a taxon-focused scientific endeavour that has found its feet over the past six or seven decades. Most entomologists know about the field because the study of ground-beetles has been a lively and interesting endeavour illuminating many general ecological principles, especially in the Netherlands. Although the number of species in this beetle family (Coleoptera, Carabidae), commonly referred to as ground-beetles or 'carabids', is estimated to be about 40,000 worldwide, the actual number is likely much higher as many species have not yet been discovered (Erwin 1982, 1991; Øddegaard 2000). It is certain that ground beetles are among the largest of the beetle families. Many species, especially from caves or tropical rainforests, remain unknown to science.

Carabids are cosmopolitan, inhabiting most terrestrial biotopes, including deserts, salt meadows, beaches, freshwater shores, swamps, rain forests up to the high canopy and all kinds of subterranean habitats and caves. With respect to habitat use, species can be stenotopic (highly specialised) or eurytopic (able to inhabit a wide range of divergent habitats) and everything in-between. And yet, the huge species diversity of this family has been elaborated based on a relatively simple body plan and most carabids are instantly recognisable as such. They are common, and the fact that many biologists encounter and recognise carabid beetles during their fieldwork, explains why this group is rather well known and relatively well-represented in museum collections. The Carabidae have been relatively well studied taxonomically and faunistically (Ball *et al.* 1992; Löbl and Löbl 2018), and they have long been favoured for ecological studies in western Europe (Lindroth 1945; Thiele 1977; Holland 2002). Nowadays, there is growing consensus that ground beetles are useful as indicators of the state of the surface-dwelling fauna, and by extension, of terrestrial habitats. Thus, carabids have become a relatively popular insect group for research in fundamental and applied ecology.

Most carabid species are predators, specialised or not, but phytophagous genera, such as *Ophonus* and *Zabrus*, also exist. Many species have excellent dispersal powers and are good flyers and/or walkers, yet many have also lost their ability to fly, or some species have a functional flight mechanism only periodically (Desender 1989; Van Huizen 1980). Furthermore, wing dimorphism and polymorphism are common in this family (Den Boer *et al.* 1980; Desender 1989; Lindroth 1949; Thiele 1977). But one of the features that really has promoted study of this group is that they are relatively easily captured by pitfall traps, except for those living at the water's edge or in very wet places. Altogether, this made, almost for a century now, ground beetles an increasingly popular object of study among ecologists and taxonomists. There is camaraderie amongst biologists studying this group of beetles, and for more than half a century now, they have found each other and gathered in enthusiastic groups, under the banner of 'carabidology'.

Taxonomy is at the heart of biological sciences. We owe a lot to those who make it possible to know the species identity of organisms that we are studying. There are many illustrious names from the past, such as Erik Arndt, George Ball, Martin Baehr, Pierre Basilewsky, Philip J. Darlington, Terry Erwin, Fritz Hieke, Ludwig Ganglbauer, René Jeannel, Oleg L. Kryzhanovskij, Carl H. Lindroth, Edmund Reitter, Stefano L. Straneo, Augusto Vigna-Taglianti among countless others who have dedicated their lives and careers to study of ground beetle systematics. They have brought order to this enormously diverse family. The first biologists interested in carabid beetles who went beyond taxonomy, were initially interested mainly in biogeography. This group includes Philip Darlington, Karl Holdhaus, René Jeannel and Carl Lindroth, but also Fritz Burmeister, Sven G. Larsson, Rolf Krogerus, Ernst Palmén and Adolf Horion who started their studies in the first half of the last century. The Swede, Carl Lindroth, in particular, who saw taxonomy, biogeography and ecology as inseparable disciplines, is often seen as the father of modern carabidology.

The foundational work that inspired so many biologists and amateur entomologists is the zoogeographical study 'Die Fennoskandischen Carabidae' (Lindroth 1945, 1949), later translated into English by the Smithsonian Institute, under the supervision of Joachim Adis and Terry Erwin as 'Ground Beetles (Carabidae) of Fennoscandia' (Adis and Erwin ed. 1992). After the Second World War, the number of publications about all aspects of ground beetles grew so rapidly that the German ecologist Hans-Ullrich Thiele decided to compile and review the wealth of information generated (Thiele 1977). He did this so well that the work is still cited in most modern ecological studies on carabid beetles and is an indispensable reference book for anyone involved in the study of carabids. Turin (1981) made an inventory of the literature on ground beetles in Europe that was published as a checklist, and later on followed by compilations of carabidological literature in general on cd rom (De Felici 2000; Penev 1991; Turin 1988). However, these and other attempts to summarise the carabidological literature were soon made obsolete by the digital reality of the Internet in the 1990s. The number of studies of carabid beetles is increasing exponentially, which makes it almost impossible nowadays to review the literature without access to specialised computer software. This chapter is intended as background information for the various topics and overviews covered in the following chapters. We hope to provide a brief overview of the most relevant literature on the biology and ecology of ground beetles, with particular reference to studies in Northern Europe. We must emphasise that our coverage of the extensive ground beetle literature is inevitably far from complete. We therefore refer once again to the masterly compilation of Thiele (1977) and to the more recent summary of the results of 40 years of European carabidological meetings, in the proceedings of the 14^{th} ECM (Kotze *et al.* 2001), held in the Netherlands (Westerbork 2009; Figure 2.1 and 2.2).

2.1.1 The Dutch database

In Chapter 3.2.5, a number of the larger Dutch projects are listed more or less chronologically (Table 3.4). These projects have provided the core of a very strong dataset about Dutch ground beetles, based on samples collected over an entire cycle of annual activity (referred to in this book as 'year-samples'). The first Dutch publication using pitfall traps was probably Joop van der Drift's investigation of the fauna of different types of litter in forests (Van der Drift 1951). Shortly thereafter, Piet den Boer, a pioneer of Dutch carabidology then based at the University of Leiden, started a seven-year study (1953-1959) that included 267 year-samples collected from the dunes of Meijendel, near The Hague (Den Boer 1956a,b; De Bruyn 1993). In 1957, Den Boer moved to the Biological Station of Wijster, where he led a long-term ecological project in population ecology that made him one of the most renowned ecologically oriented carabidologists in the world.

Figure 2.1. Impressions from the 14^{th} European Carabidologists Meeting (Westerbork 2009). A: The briefing by the ranger of the National Park 'Dwingelderveld'. B: The excursion to the Dwingelderveld by participants of the meeting. For the proceedings of this meeting, see Kotze *et al.* (2011). It was the 40^{th} anniversary of the European Carabidologists Meetings that started in 1969 at the former Biological Station of Wijster (WUR, Wageningen, the Netherlands), initiated by Piet den Boer (Den Boer *et al.* edit. 1971b). Photos by Hans Turin.

Figure 2.2. Four Dutch carabidologists who attended the first European Carabidologists Meeting in 1969, held at the former Biological Station of Wijster (WUR, Wageningen, the Netherlands; Den Boer 1971b). From left to right: Jan Meijer, Piet den Boer, Jaap Haeck and Rob Hengeveld. Jan Meijer conducted, in private, a 40-year study (1969-2008) in the Lauwersmeer, a closed-off area of the sea. Piet den Boer started a 7-year study (1953-1959) in the dune area of Meijendel, near The Hague. After that, he started a huge landscape, population-biology project (1959-1995) in the Biological Station in Wijster, which lead to theories that affected nature management, even today. In 1969, he initiated the European Carabidologist Meetings (ECM), which is still happening on a biennial basis. Jaap Haeck and Rob Hengeveld investigated colonisation and succession in the IJsselmeer polder 'Zuid Flevoland' (reclaimed in 1967) and carried out several experiments on the distribution and dispersal behaviour of ground beetles during 1967-1980. Photo by Hans Turin at the 14th ECM held in 2009, in Westerbork, the Netherlands.

The 'spreading of risk' and 'founding theory' projects that lasted until about 1995, attracted many PhD students, leading to a number of theses on carabids (e.g. Aukema 1995; Baars 1982; De Vries 1996; Mols 1993; Nelemans 1989; Vermeulen 1993), directly or indirectly inspired by Piet's work. Eight of his sampling series were, sometimes with short interruptions, continued by Rikjan Vermeulen (Table 3.4). Rikjan also started many new projects through his WBBS-foundation. The databases of Den Boer and Vermeulen together currently account for more than 800 year-samples of carabids, mainly from heathland biotopes.

A project on the colonisation of the newly reclaimed IJsselmeer polders, land officially brought together on January 1st of 1986 as the 12th Dutch province, named 'Flevoland', was started in the Institute of Ecology (Haeck 1971; Haeck *et al.* 1980; Hengeveld 1979). This work has contributed an additional 144 year-samples and 333 short-term samples to knowledge of the Dutch fauna. Within this project, the first Dutch ground-beetle mapping scheme was started in 1971 (Turin 1974a,b; Turin *et al.* 1977). In the Zoological Institute of the University of Utrecht, another population ecological project featuring carabids was also running in those years (e.g. Brunsting 1983; Brunsting and Heessen 1983, 1984). An additional 200 year-samples came from the Institute of Nature Management (RIN, Arnhem, Leersum) from various projects, mainly carried out in limestone grasslands in the province of Limburg (Mabelis and Turin 1982; Turin 1983) and hedgerows in the province of Overijssel (Mabelis and Van Velden 1992).

Apart from the large institutional projects, many smaller projects were conducted by both professional and amateur carabidologists, many by the Dutch Carabidological Foundation (ca. 890 samples, short-term as well as year-samples). Jan Meijer conceived and conducted one of the most remarkable projects (Figure 2.2). In 1969 he started a 40-year study of colonisation of the Lauwersmeerpolder by carabids and spiders (Meijer 1989). This project, resulting in some of the longest continuously running pitfall series so far, was carried out completely in private time (156 samples over 40 years from 1969 to 2008) leading to Meijer's (1980) doctoral dissertation. A final report of the project results was published recently (Meijer and Barendregt 2018). Also, special mention should be made of the huge number of projects carried out by the Bargerveen Foundation, established in 1991 by Hans Esselink and now an organisation with more than 10 employees. During the period 1997-2013, about 540 pitfall samples were taken, mainly from heathlands, drift sands, dune areas and limestone grasslands (e.g. Van Noordwijk *et al.* 2012; Vogels *et al.* 2011). Numerous smaller carabidological projects have been conducted by enthusiastic entomologists, often without any financial support. Good examples are the research that has been going on for several decades on the Wadden island of Texel, by members of the Carabid workgroup, Texel of the IVN (Instituut voor Natuurbeschermingseducatie), and the 'Kaaistoep' project, which has been carried out since 1995 by members of the KNNV (Koninklijke Nederlandse Natuurhistorische Vereniging) in collaboration with various authorities. The Kaaistoep is a nature reserve near Tilburg, where, among other insect groups, also the ground beetle fauna was monitored and analysed (Van Wielink *et al.* 2020). The data from this latter project make no part of the database and have not been used in the present book.

Drawing on these samples in this book, we have achieved a high degree of completeness with respect to the coverage of data from pitfalls in the Netherlands, with ca. 95% of the pitfall data included in the database analysed here (1953-

2018, Chapter 3). Although a few samples may have been inadvertently overlooked, the wealth of these consistently collected samples makes the Dutch carabidological database perhaps the most extensive in the world and provides a compelling rationale for this book which is focused on its analysis.

2.1.2 Carabidological gatherings

When the Dutch population biologist Piet den Boer initiated a round table discussion in 1969 with a number of renowned carabidologists, such as Carl Lindroth, Ernst Palmén and Hans-Ullrich Thiele at the Biological Station of Wijster, he did not realise that a long-term tradition was born. This meeting was followed by meetings in 1973 and 1978, both at the Rees-Grieterbush field station of the University of Cologne. From the fourth meeting at 'Haus Rothenberge' in Westphalia, the meetings were retroactively numbered under the name 'European Carabidologists' Meeting' (ECM). This phenomenon grew into a recurring, finally biannual tradition. From around 1990, the event began to attract carabidologists from outside Europe. In 2009, the 40th birthday of these meetings was celebrated during the 14th ECM, in Westerbork, the Netherlands, close to the former Biological Station of Wijster, where it all started (Vermeulen *et al.* 2008). It was attended by participants from 26 countries (Figure 2.1), which included a few carabidologists that had been present in 1969, especially Piet den Boer as the guest of honour, Jaap Haeck, Rob Hengeveld and Jan Meijer (Figure 2.2). The 2009 meeting was followed by the 15th edition in Daugavpils, Latvia (2011), the 16th in Prague, Czech Republic (2013), the 17th in Primosten, Croatia (2015), the 18th in Rennes, France (2017) and the 50th anniversary at the 19th ECM in Fiera, Italy (2019), which was also attended by a strong delegation from North America.

Since the start of the ECMs, more than 50 years ago, much has changed. Molecular techniques are widely used in both taxonomy and ecology and computers and software development have led to widespread use of new advanced statistical methods and building large databases. A constant factor however is that, for more than 65 years, the use of pitfall traps remains immensely popular in carabidology, even though the method has received considerable criticism (Anderssen 1995; Brown and Matthews 2016; Koivula *et al.* 2003; Mommertz *et al.* 1996; Radawiec and Alexandrowicz 2013; Skvarla *et al.* 2014 and others). Because this book is mainly based on a historical database of pitfall trapping, we will also consider and elaborate on the value of data acquired through this method despite the criticisms. We hope to be able to answer, at least partially, the question *to what extent the use of pitfall data can be justified* on the basis of a comprehensive review of the literature and on the basis of a number of studies in this book. We test the reliability of the methods used in Section 4.2.5.

It is likely that carabidology will change dramatically in the coming 50 years through use of new techniques such as DNA barcoding and image recognition with the help of smart cameras, smart software and hopefully, smart carabidologists. This is exactly as it should be in any science; however, the central goal of understanding the ecology and evolution of the Carabidae will remain fundamental to the field. An interesting question is whether new technologies will surpass, or replace the use of pitfall trapping by carabidologists, and by scientists studying other epigaeic invertebrates. What can certainly be expected, is whether the collection of large numbers of animals to determine population size and densities can be ethically justified in an era when bio-industry with farm factories, mass executions of cows, pigs and chickens in the event of outbreaks of animal diseases, and the killing of laboratory animals are more and more under public scrutiny and political discussion. It is not unlikely that pitfall trapping will also come under more pressure in the future (see e.g. New 1999; Pestell and Petit 2007). Live trapping is a solution in some cases but is more challenging because very frequent checks of the falls are needed to prevent predation from leaving only the large and most aggressive species. Exploring the Dutch database as thoroughly as possible will hopefully contribute, in addition to the many valuable publications that have appeared, to justifying the large-scale sampling in the past to a certain extend and to prevent superfluous sampling in the future.

In the proceedings of the 14th ECM in Westerbork, Johan Kotze, in collaboration with 20 participants at the congress, summarised the progress of 40 years of carabidology (Kotze *et al.*, 2011b). This review had to be limited in the context of the proceedings, but nevertheless yielded an interesting and much-cited article with a reference list of more than 600 publications. A few short passages derived from this article have been used in Chapter 3.3 about the method of pitfall trapping.

The following sections of this chapter attempt to highlight some areas of ground beetle biology and ecology, focusing on research conducted in the Netherlands and in Central-Europe.

2.2 Biology

The biological traits of a species have evolved to ensure access to food and other resources, to facilitate dispersal and to support reproduction and other aspects of establishing and maintaining populations. Many factors are important. For instance, dispersal may be required for individuals to reach new habitats if for some reason the area where they reside becomes unsuitable or facilitate expansion of populations into additional suitable areas. The need for dispersal may

3. Database work and pitfall traps

3.1 Introduction

3.1.1 Ground beetles and data from pitfall traps

Ground beetles (Coleoptera, Carabidae) or 'carabids', are subject to a broad variety of faunistic, biological and ecological studies (Kotze *et al.* 2011; Lövei and Sunderland 1996; Thiele 1977). This is particularly because they can be sampled relatively easily in a systematic way using pitfall traps. Worldwide, but especially in Europe, this method is used among carabidologists and other biologists that study surface dwelling invertebrates. In the Netherlands, pitfalls have been used since the 1950s, and systematic data – in the form of 'year-samples' (Section 3.1.2) – are available from 1953 onwards. Both ground beetles as a study subject and the pitfall trapping method became popular, in the first place because of the study on the Fennoscandiaan Carabidae, published by Car Lindroth (1945, 1949) but, not in the last place, also because of the work of Piet den Boer who started large scale population ecological studies in dunes near The Hague (Meijendel) and in the province of Drenthe (Den Boer 1954, 1956a,b, 1977; Kotze *et al.* 2011).

More than 90% of the available Dutch pitfall data was collated into a database, initially for a mapping scheme (Turin 2000). Gradually it expanded to become one of the largest pitfall trap datasets in Europe, now comprising more than 4,300 year-samples and more than 1,500 short-term samples. The core of the ground beetle database (Section 3.2) consists of records that each contains information on the number of individuals collected for a particular species in time and space. The nature and history of the data are rather heterogeneous. To a large extent, this applies especially to the faunistic data obtained from collections and the literature. Most of the data from hand sampling are based on incidental catches or, more rarely, systematically inventories. For this kind of data, each record represents one single observation. The faunistic data that were collected up to the end of the last century, for all Dutch species, were published in the second atlas of the ground beetles of the Netherlands (Turin 2000). In this book we largely do not focus on this data, except for purposes of creating maps on distributional patterns, to be as complete as possible (compare the new maps as used in Section 5.12.3: update to the 2000-atlas).

3.1.2 Series, year-samples and short-term samples

Data from systematic sampling, using pitfall traps (Kotze *et al.* 2011), consist mainly of sets of related records. Each set represents a 'sample', consisting of the species trapped and their abundances in a given period of time. Generally speaking, the sampling method is roughly similar, but can vary in certain details. The use of series of pitfall traps for ecological studies is usually done by placing traps, often in a straight line at 5-10 m distances, in a more or less well-defined landscape unit (see Section 3.5 for trapping designs). Ward *et al.* (2001) showed that traps placed at a spacing of 1 m significantly had a lower species richness that traps placed at 5 or 10 m. Cans, jars or constructions with funnels inside are often used, dug into the soil so that surface dwelling animals can easily fall into the trap (Section 3.3). To prevent predation in the trap, and to conserve flight muscles and/or organs, a preservation liquid is added, mostly a formalin solution of 3-5%, but also ethylene-glycol or vinegar (Section 3.3.5). Sometimes one or more traps in a trapping series is left dry, e.g. the large dataset from the collecting schemes of Piet den Boer (1959-1996, continued until the present by Rikjan Vermeulen and the WBBS-foundation). Initially the dry traps were added to allow mark and re-capture testing but were later on maintained for consistency. Within a trapping series, variation in a number of factors can be considerable. For example, the size and number of traps, and distances between traps vary. Major differences also exist in the time of year when traps were operational. Roughly, data used for this book were divided into two groups: samples that meet the criterion of a so called 'year-sample', and samples that do not, which will be named 'short-term' samples. A 'year-sample' is defined as traps functioning for at least eight consecutive weeks during the spring reproductive period and eight weeks during the autumn reproductive period of carabids. More than 4,300 samples meet this criterion (Section 3.2.2).

From comparative studies we know that spring reproduction in the Netherlands has its optimum in the period from the beginning of April to the end of June, while autumn reproduction is mainly from late August to the end of October. By including at least these two periods in the sampling programme, ca. 80-90% of the reproductive activity of ground beetles is covered (Section 4.2.5). The effectiveness of pitfalls is primarily based on the activity of animals living on the soil surface. The number of captured specimens during a certain period is therefore often referred to as 'activity density' ('**AD**', compare application in the trend analysis: Section 6.4.1). It must be emphasised that the way activity density is measured for different species can vary substantially, so that results of captured numbers cannot directly be compared.

The use of data from pitfalls is not without problems. Many studies on the method have already been published, such as Koivula *et al.* (2003), Zmilhorski and Sienkiewicz (2012), Svarla *et al.* (2014), Andersen and Arneberg (2016) and Brown and Matthews (2016). See also Chapter 4 and 6 for further discussions and solutions. One of the possible methods we propose to nevertheless be able to use the results of samples with unequal capture periods for comparing the fauna composition, is that of the 'Habitat Reference', based on using relative abundances, expressed in habitat charts and species (DCA) ordinations (Section 4.2) as well as plots of DCA-ordination centroids (Section 4.1 and 4.2.4). The reliability of the 'Habitat Reference' method is discussed and tested in Section 4.5.2. For the trend analysis (Section 6.4) as based on the present database of pitfall year-samples, in which for the inequality between the years should be corrected as accurately as possible, generally accepted statistics are used (Section 6.4.1).

3.2 The Dutch database of pitfall samples

3.2.1 History

The project on colonisation of the new IJsselmeer polders (present province of Flevoland) by plants and animals started in the sixties of last century. This initiated a long-term project using ground beetles, and from the moment of the reclamation of Zuid-Flevoland in 1967-1968, carabids were sampled systematically using pitfall traps. This project was carried out by the department 'Dispersal Ecology' of the 'Instituut voor Oecologisch Onderzoek' (IOO, now NIOO-KNAW, Wageningen) during the period 1967-1978 (Haeck 1971; Mook 1971). The fact that Piet den Boer already in 1964 sampled locations (Den Boer 1971) in the second big polder of Oost-Flevoland (reclaimed in 1957) – and Carl Lindroth's work on post-glacial history of the Fennoscandian ground beetle fauna (Lindroth 1945a,b, 1949), was of great importance for the choice of Carabidae as subject group. It appeared that ground beetles could be sampled and preserved easily and were subsequently examined for the development of wings and flight muscles. Lindroth's work demonstrated, unequivocally, the usefulness of ground beetles in dispersal ecology. Moreover, long-term population ecology research of Piet den Boer at the Biological Station of Wijster (Agricultural University of Wageningen, now Wageningen University and Research), provided strong arguments for studying carabid beetles. In the context of the polders project, it was important to know which ground beetle species could or could not colonise newly reclaimed land, which was largely separated from the mainland by 1-2 km-wide, surrounding waters (see Figure 2.42-2.45 and the province of Flevoland in the map of Figure 3.1). It was expected that colonisation would mainly occur by species with a good flying ability, but also with a distribution area that would be close to the polders. The mapping scheme was started in 1971 and the goal was to map the distribution patterns of all Dutch species. Data were mainly obtained from collection labels and faunistic literature. This resulted in the publication of the first zoological, computer-generated zoological atlas of the Netherlands (Turin *et al.* 1977). 80-column (Hollerith) punch cards were used as data carriers (Turin 1974a,b). Publishing this atlas was an important step towards the establishment of the Dutch office of the 'European Invertebrate Survey' (EIS) in 1977 by the Rijksmuseum voor Natuurlijke Historie (RMNH, now: Naturalis – Biodiversity Centre) in Leiden. EIS was a European initiative of the British Biological Station Monkswood and the Belgian University of Gembloux. Its aim was to create European distribution maps by means of standardising national maps, using the uniform geographical grid system (according to the UTM projection).

Initially, EIS used punch card formats as used by the ground beetle project for all animal groups, but since the arrival of personal computers in the 1980s, this methodology quickly

Figure 3.1. Provincial map of the Netherlands.

5.10.5 Habitat GR01 – Peat moor, peat bog – habitats on peaty soil

Habitat photos: Figure 5.33 and 5.38; Maps: Figure 5.32 and 5.34
Habitat type **X01** (135 samples)
European Habitats Directive 7110, 7120, 7140 and 7230

GR01 – Introduction

This habitat group results from the prolonged accumulation of dead plant material in areas that are completely dependent on rainwater, leading to peat formation. About 2000 years ago, peaty areas covered most of the Netherlands. These vast swamps have since been reclaimed and, due to oxidation, a large part of the area has been lost or covered by clay deposits (Jongmans *et al.* 2015). Nowadays, peat soil areas are scattered over the mid-western and north-eastern part of the country, and there are a few scattered areas in the east that are remains of largely reclaimed peat bogs (Figure 5.32). High moors, which originated during various phases in the Netherlands after the last ice age (Janssen and Schaminée 2003), can be found in the eastern part of the country, in several parts, originally connected with extensive peat areas in Germany. Although the peat soil area in the Netherlands is relatively large, little of it is left in a near-pristine condition. Most low peat bogs in the west and the northern provinces, Friesland, Groningen, Drenthe, and the north-western part of the province of Overijssel, were fully reclaimed in the eighteenth and nineteenth centuries and turned into agricultural pastures. Cities arose on this soft soil already longer ago, just like our capital Amsterdam.

Figure 5.32. Peat soil region in the Netherlands.

Figure 5.33. Peatmoor restoration area in the 'Dwingelderveld' national park (target habitat type **X01**). Species sampled nearby, in drier conditions, in 1991 and 2008 (Section 7.5.2, Case study 1): *Agonum ericeti*, *Amara lunicollis*, *Bradycellus ruficollis*, *Calathus erratus*, *Carabus arvensis*, *C. problematicus*, *Dyschirius globosus*, *Nebria salina*, *Notiophilus aquaticus*, *Poecilus lepidus*, *P. versicolor*, *Pterostichus diligens*, *P. minor*, *Trichocellus cognatus*. Photo by Theodoor Heijerman in 2018.

In the Netherlands, the following European habitats can be connected to the ground beetle habitat **GR01**: directive 7110, undisturbed, active peat moors, 7120, corroded peat bog, 7140 transitional bog with *Sphagnum* and 7230 alkaline peat bog (Janssen and Schaminée 2003). According to the ecological classification of Dutch ground beetles (Turin *et al.* 1991), **GR01** consists of only one ground-beetle habitat type: **X01** – Peat moor and peat bog, with 135 samples. Concerning the characteristic species of **GR01**, also some species falling in habitat **GR02** (and sometimes **GR03**) are ecologically closely related. **GR01** mainly contains the very wet habitats, while the dryer variants of nutrient-poor peat bogs, with Ericaceae and *Sphagnum* mosses are to be found in **GR02**. Some of the species emblematic of raised peat bogs for all of Europe, are found in these latter groups for the very reason that Sphagnum mosses often are more abundant in these groups, than they are in the wet, renatured habitats, which in their water bodies suffer from high nutrient input from the atmosphere. Figure 5.34A shows the pitfall sampling sites, located in the peat soil area of Figure 5.32. The pattern differs from that of the samples that have been classified in **GR01** (Figure 5.34B). This can be explained by the fact that the map in Figure 5.32 is based on soil science rather than vegetation criteria and certainly not on the composition of the ground beetle fauna. There are also many smaller sites with peaty vegetation and/or a corresponding carabid composition, outside the main peat area indicated on the map in Figure 5.32.

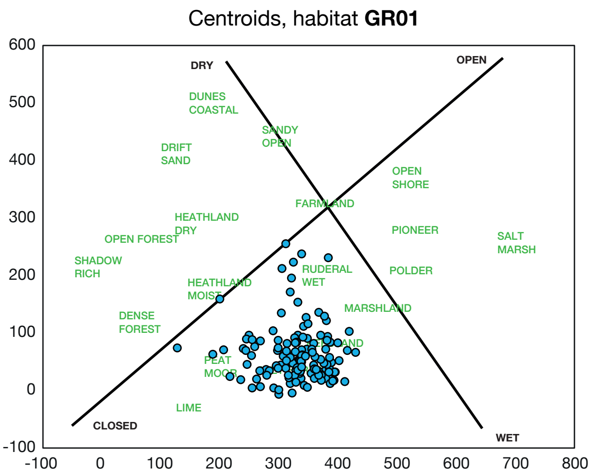

Figure 5.35. Plot of the centroids of all 135 year-samples in **GR01**, calculated from the species DCA's for each sample (for an explanation, see Section 4.2.4).

Plotting centroids of the DCA species' ordinations of all samples from peaty soil in the database (Figure 5.35) shows that most samples occur in a coherent dot cloud, which is close to the configurations in **GR02** (wet heathlands, Figure

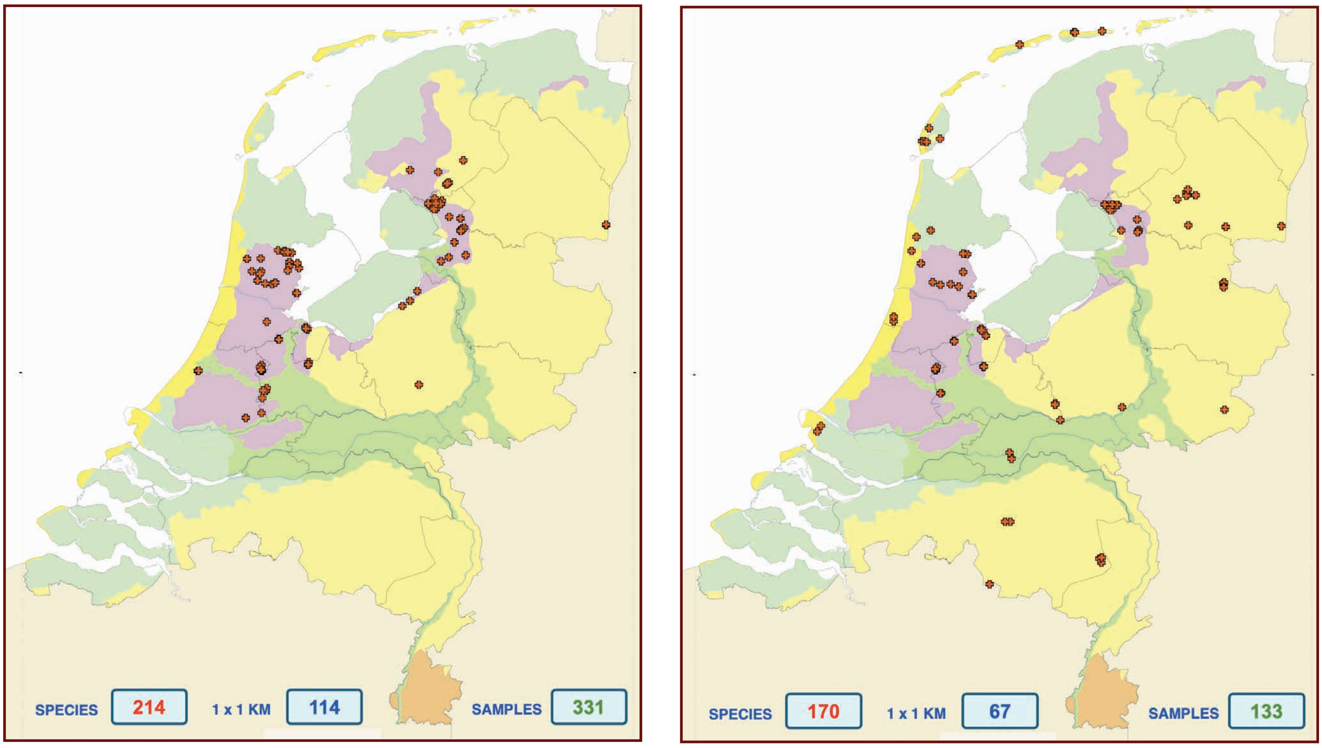

Figure 5.34. A: Pitfall sampling sites situated in the main peat soil region in 73 1×1 km-squares. B: Localities of the 135 samples that have been classified in habitat **GR01** (for explanation of both maps see text).

5.43), and shows a considerable overlap, with respect to moisture and vegetation density, with the plot of **GR12** (wet forests, Figure 5.141).

GR01 – Characteristic species

Characteristic species (Section 4.4.1) in this group are (primary species in bold):

Acupalpus flavicollis, Agonum fuliginosum, A. gracile, *A. thoreyi,* ***A. viduum*** (Figure 5.39), ***Badister dilatatus, B. peltatus, B. unipustulatus, Bembidion doris, Carabus granulatus*** (Figure 5.40), *Elaphrus cupreus, E. uliginosus,* ***Oodes helopioides,*** *Pterostichus anthracinus,* ***P. aterrimus, P. minor,*** *P. rhaeticus* and *Stenolophus mixtus.* For species to be expected in this list as belonging to the characteristic peat moor fauna, e.g. *Agonum ericeti, Bembidion humerale* and *Cymindis vaporariorum*, but these have been classified in closely related habitats because of their χ^2-values, see habitats **GR02** and **GR03** (Table 5.11 and 5.14).

Twelve species have a high χ^2 value in **GR01** (Table 5.8, CHAR = 01-(01)), names above in bold. The remaining species have their highest value in **GR02** (CHAR = 01-(02), moist heathland) or in **GR12** (CHAR = 01(12), wet forests).

Traits of these 12 characteristic species are presented in Table 5.9. All species are spring breeders (**RP** = SP and SS). The biogeographical origin of this group is mixed; 4 species have a central-northern (**DE** = 3) and 5 species a central mediterranean (**DE** = 9) distribution in Europe. For 3 species (25%), the Dutch territory is situated less than 150 km from the fringe of their European distribution (**AR** = 2), and only *Badister peltatus* occurs at the very edge of its distribution area (**AR** = 1). Most species have a scattered distribution pattern (**DN** = 0, R). Nearly all species of this group have flight observations (**DISP** = DIMF or MACR), except the brachypterous (**DISP** = brch) *Carabus granulatus*. Most species are rather stenotopic (**E** <6; compare Turin *et al.* (1991).

GR01 – Accompanying species

Table 5.10 lists 12 species having the highest frequencies in co-occurrence with the characteristic species in this group (Section 4.5). For instance, *Pterostichus diligens* and *Pterostichus nigrita* co-occur in a high percentage of samples in which 11-12 of the characteristic species are present. At least the first six accompanying species can be regarded a stable element in the carabid fauna of peat bogs and moors, five of which belong to the genus *Pterostichus*. All are eurytopic with a preference for moist conditions.

Table 5.8. Screen image of the affinity table for **GR01**.[1]

code	T	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	char
ACUPFLAV	322	37.3	14.5	1.5	1.1	3.2	1.0	3.3	0.1	2.9	3.4	4.1	0.3	0.9	2.9	6.3	1.7	0.9	01-(02)
AGONFULI	210	182.5	122.4	0.3	16.8	24.1	21.8	34.1	17.8	13.2	21.1	79.0	31.4	22.4	5.6	1.9	13.5	7.2	01-(02)
AGONGRLE	211	22.4	13.7	0.4	2.2	0.1	1.3	2.7	1.2	0.1	1.8	4.1	0.1	1.0	0.9	0.6	0.8	0.4	01-(02)
AGONVIDU	208	88.2	0.0	12.6	8.5	1.6	3.4	8.4	46.8	5.7	3.9	2.3	72.3	0.2	0.1	0.9	1.5	1.8	01-(12)
BADIDILA	333	229.5	0.2	5.0	2.2	1.7	1.4	1.0	3.0	1.5	3.7	1.3	19.1	0.0	0.0	0.7	0.9	0.5	01-(01)
BADIPELT	334	124.9	0.5	1.8	1.7	1.3	1.0	2.1	2.0	1.1	2.8	2.4	29.3	1.5	0.1	0.5	0.6	0.3	01-(01)
BADIUNIP	329	6.0	0.4	0.5	0.2	0.7	1.0	2.0	0.5	1.1	1.1	0.5	3.1	0.5	0.2	0.5	0.6	0.3	01-(12)
BEMBDORI	105	39.6	0.5	0.4	0.7	0.5	0.4	0.8	0.9	0.5	1.1	0.0	0.6	0.0	0.3	0.2	0.3	0.1	01-(01)
CARAGRAN	020	410.4	3.5	36.8	15.7	26.0	23.4	8.1	8.6	8.4	15.9	0.7	156.4	9.0	0.1	1.6	10.2	7.8	01-(12)
OODEHELO	342	810.2	0.0	20.6	11.0	7.8	8.2	8.4	3.0	8.8	17.7	14.2	52.6	0.7	1.5	0.0	3.2	2.7	01-(01)
PTERATER	157	35.7	2.1	1.7	8.2	0.6	0.5	0.9	1.0	0.5	0.0	0.0	0.6	1.5	0.3	0.2	0.3	0.2	01-(01)
PTERMINO	165	663.5	73.1	2.9	20.7	26.8	17.7	39.1	4.6	17.3	24.8	0.0	84.0	4.4	2.0	0.2	9.5	7.3	01-(01)

[1] Red cells indicate the highest χ^2 values. Code = species name code (full name, see Table 5.9 and Appendix A), T = species number in the ground beetle atlas (Turin 2000), orange and yellow cells indicate lower value, **01-17** = habitat groups (**GR01-GR17**, Section 4.3), char = characteristic species (Section 4.4). For further explanation, see Section 5.10.4.

Table 5.9. Traits for habitat **GR01**.[1]

T	Code	Species	CHAR	LI	TU	E	RP	H	DISP	DN	AR	DE
322	ACUPFLAV	*Acupalpus flavicollis*	01-(02)	H1	G2	4	SP	1	MACR	R	2	9
210	AGONFULI	*Agonum fuliginosum*	01-(02)	HW	EU	8	SP	1	DIMF	0	4	3
211	AGONGRLE	*Agonum gracile*	01-(02)	H1	D1	4	SP	1	MACR	R	3	3
208	AGONVIDU	*Agonum viduum*	01-(12)	H1	E1	5	SP	1	MACR	0	4	3
333	BADIDILA	*Badister dilatatus*	01-(01)	H1	FZ	2	SP	1	MACR	R	2	6
334	BADIPELT	*Badister peltatus*	01-(01)	H1	GZ	3	SP	1	MACR	R	1	9
329	BADIUNIP	*Badister unipustulatus*	01-(12)	HW	E1	5	SS	1	MACR	3	3	9
105	BEMBDORI	*Bembidion doris*	01-(01)	H1	AZ	1	SP	1	MACR	7	3	3
020	CARAGRAN	*Carabus granulatus*	01-(12)	H2	G2	7	SP	1	brch	0	3	5
342	OODEHELO	*Oodes helopioides*	01-(01)	H1	G2	5	SP		MACR	R	3	9
157	PTERATER	*Pterostichus aterrimus*	01-(01)	H1	A1	1	SP	1	MACR	R	2	9
165	PTERMINO	*Pterostichus minor*	01-(01)	H1	A1	7	SP	1	DIMF	0	3	9

[1] For explanation, see Section 5.10.4: '2. Characteristic species'.

Table 5.10. Accompanying species for **GR01**.[1]

Habitat GR01		Accomp. species											
		PTERDILI	PTERNIGR	PTERVERN	PTERNIGE	PTERSTRE	AGONTHOR	LORIPILI	PTERMELA	STENMIXT	DYSCGLOB	ELAPCUPR	PTERVERS
Char. Spec.	**N samples**	101	95	76	60	58	40	48	33	41	38	39	25
ACUPFLAV	11	100	64	91	46	73				55			
AGONFULI	60	92	65	50	47		47	48					
AGONGRLE	6	100			50								
AGONVIDU	21	81	91	71		57	48	67	43	43	48	48	
BADIDILA	10	80	70	40	50	40	60	50	40				
BADIPELT	9	89	78		67		78	67	56				56
BADIUNIP	3	67	100	100		100			67		67	67	
BEMBDORI	4	75	75	50	100		50	50		50			
CARAGRAN	89	74	71	56	39	41							
OODEHELO	74	80	69	58	43	49	45						
PTERATER	4	100	75	75		50	50	50	50	50	50	50	50
PTERMINO	108	88	73	57	51	45							
	Total	1,026	831	648	493	455	378	332	256	198	165	165	106
	N species	12	11	10	9	8	7	6	5	4	3	3	2
	Average %	85.5	69.3	54.0	41.1	37.9	31.5	27.7	21.3	16.5	13.8	13.8	8.8

[1] Percentages of co-occurrence for the characteristic (left column) and accompanying species (blue). **Char. Spec.** = name code, see Table 5.9 and Appendix A. **N samples** = number of samples in this habitat group in which the species was found. At the bottom of the table the summed percentages on which the ranking of the accompanying species is based. Red = species with a significant preference for habitat **GR01** but present in less than 25 samples in **GR01**. Green cells = co-occurrence 40-50%, Yellow cells = 50-100%.

In Figure 5.36 and 5.37, a representative selection of habitat charts for **GR01** is presented. Localities of the sampling sites are situated all over the country, but the Renkonen similarity pattern is surprisingly equal. Besides a dominant score in habitat type **X01**, a relation with heathland habitat types **X02-X05** is evident. In most cases, similarity with **X06-X20** is low, and there is a modest connection with types **X21-X30**, probably caused by the mutual presence of some moisture loving species. Figures 5.38 and 5.39 show the successfully restored peatmoor reserve 'Korenburgerveen' (province of Gelderland; 490 ha) and the characteristic species *Agonum viduum*.

GR01 – Summary

From the literature and inventories by hand, as well as from pitfall investigations, we know that, in addition to a group of more eurytope heathland species, the ground beetle fauna on peaty soils includes a small number of typical inhabitants, such as *Agonum ericeti*, *A. gracile*, *A. munsteri*, *Anisodactylus nemorivagus*, *Blethisa multipunctata, Bembidion humerale*, *Cymindis vaporariorum*, *Elaphrus uliginosus* and *Pterostichus rhaeticus*. Also, *Carabus clatratus, C. granulatus* (Figure 5.40) and *C. nitens* can be found on moist heathland and along fens, while *Pterostichus aterrimus* occurs both along eutrophic fens and pools in heathlands and in peat bogs. *Agonum ericeti* is still quite abundant in some larger reserves in Drenthe and Noord-Brabant, but several other species declined and two very rare species, both observed in Drenthe, *Agonum munsteri* (1 sample in 1959), and *Platynus krynickii* (6 samples in 1961 and 1969), are most probably extinct. Interestingly, the peat bog fauna is related to the fauna of heathlands (**GR01** and **GR03**). Habitats on peaty soil lack shore species that can be found, for example, in reed land and marshes on clayish soils (Holmes *et al.* 1993; Turin *et al.* 1991). Several of the abovementioned species did not show a significant preference for **GR01** in the present data, but rather for **GR02** or **GR03**, such as *Anisodactylus nemorivagus*, *Bembidion humerale* and *Carabus clatratus* (in **GR02**), as well as *Agonum ericeti*, *Carabus nitens*, and *Cymindis vaporariorum* (in **GR03**). This is probably because these species are not very well represented, due to local extinctions caused by severe fragmentation of this biotope. This holds especially for *Bembidion humerale* (see **GR02**) and *Agonum ericeti* (see **GR03** and De Vries 1996). Some of these species only survived in peaty spots in larger heathland fragments, of which the local fauna composition can be heavily influenced by influx of species from the surrounding heathland.

The effect of fragmentation in biotopes related to habitat **GR01** has been reinforced by the changing climate with a relative high frequency of extreme dry years, leading to the extinction of the most characteristic species in this group. Exceptions include *Carabus nitens*, but also *C. arvensis*, who both showed population recovery during the last decades, mainly due to excellent management that resulted in the rejuvenation of heathland vegetation. Especially the effects of sod cutting turned out to be very positive on populations of these species, who became dominant in several localities, sometimes for many years (Van Essen 1991).