

# **Technische Universität Dresden**

Fakultät Umweltwissenschaften

## **Effect of forest structure and small-scale environmental conditions on the community of epigeic arthropods (Carabidae, Araneae)**

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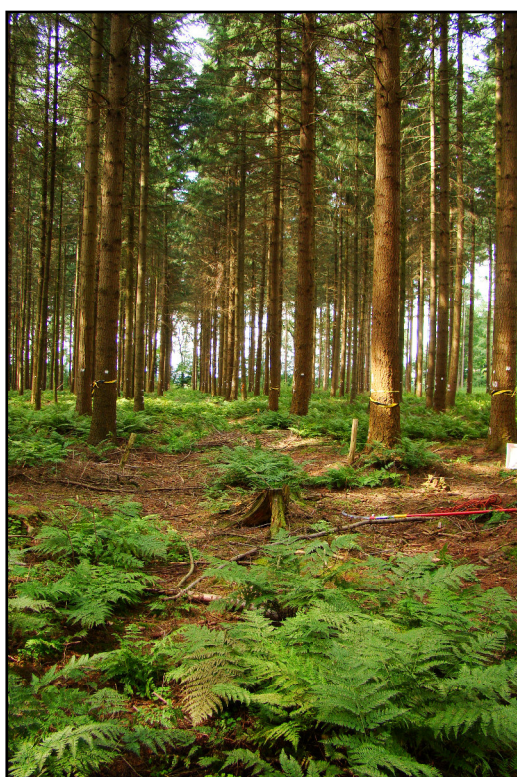
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Forests - from the patch to the landscape



## Zusammenfassung

In der vorliegenden Arbeit wurde in Wirtschaftswäldern der gemäßigten Breiten der Einfluss der Baumart und der Bestandesstruktur in Kombination mit kleinräumig ausgeprägten biotischen und abiotischen Umweltvariablen auf das Auftreten und die Verteilung bodenlebender Arthropodengruppen (Araneae, Carabidae) in mehreren Versuchsansätzen im Freiland untersucht. Ziel der Arbeit war es, Zusammenhänge zwischen raum-zeitlich veränderlichen Umweltbedingungen in Abhängigkeit von Bestandesalter und Bewirtschaftungseinfluss und der Zusammensetzung epigäischer Arthropodengemeinschaften zu erforschen, und solche Schlüsselfaktoren zu erkennen, die baumartenspezifisch und somit nur schwerlich von der Bestandesform zu trennen sind.

Die Studie fokussierte auf den Beitrag unterschiedlicher Altersstadien der Wälder zur Aufrechterhaltung der taxonomischen Vielfalt und funktionalen Integrität der Zoophagen, da diese als natürliche Gegenspieler in Waldökosystemen eine wichtige Funktion einnehmen.

Die untersuchten Wälder waren Reinbestände aus Fichte (*Picea abies*) und Douglasie (*Pseudotsuga menziesii*), sowie Mischbestände aus Fichte-Buche (*Picea abies*, *Fagus sylvatica*) und Eiche-Buche (*Quercus robur*, *Fagus sylvatica*, *Carpinus betulae*) und somit für die Region repräsentative Waldtypen. Es wurde angenommen, dass Laufkäfer und Spinnen von der überschirmenden Baumart unterschiedlich mit Blick auf aktive Verbreitungsmuster der Arten und Konkurrenzverschiebungen in Lebensgemeinschaften beeinflusst werden. Das Bestandesalter und eine übliche Bewirtschaftungsweise würden die Umweltbedingungen im Bestandesinneren in einer zu untersuchenden Weise modifizieren. Um die Frage zu klären, ob die Baumart oder forstliche Eingriffe die Artengemeinschaften stärker bestimmen wurden kontinuierlich und detailliert die Umweltbedingungen in einem Ausschnitt eines jeden Bestandes erfasst um über Gradienten die Ursachen für die Zusammensetzung der Lebensgemeinschaften zu beschreiben. Die Veränderung eines Waldökosystems

mit ansteigendem Alter und allen dafür typischen Wandlungen sowie die begleitenden Bewirtschaftungseingriffe modifizieren intrinsische Umweltbedingungen und sollten somit präzise analysiert werden.

Es konnte aufgezeigt werden, dass die Artenvielfalt der Spinnen und Laufkäfer generell mit dem Bestandesalter in den Wirtschaftswäldern ansteigt und Schlüssel-Umweltbedingungen über natürliche Änderungen im Bestand aber auch über den Bewirtschaftungseinfluss variieren. Erwartungsgemäß zeigen die Ergebnisse auf, dass die Artengemeinschaften sich in Wirtschaftswäldern nicht unmittelbar über die Baumart definieren sondern sich sehr kleinräumig über vorherrschende Umweltbedingungen verändern können. Viele der Arten sind nicht-zufällig am Waldboden verteilt und werden bei den Spinnen zum Einen über baumartentypische Faktoren geleitet wie die Streuart oder das noch unbelaubte Kronendach der Laubwälder im Frühjahr, zum Anderen über nicht-baumartengebundene Umweltbedingungen wie den Kronenschluss, die Bodenvegetation oder auch mikroklimatische Umweltbedingungen, welche ebenfalls eine saisonale Änderung erfahren können. Lichtangebot wie auch Temperaturbedingungen, Luftfeuchte und Streu- bzw. Substratfeuchte nehmen über geringe Distanzen eine Schlüsselrolle in der Bildung von Artengemeinschaften am Waldboden ein. Unterschiedliche Vegetationskomponenten in der Zusammensetzung der Gras-, Moos- oder Krautschicht beeinflussen die Spinnen auf kleinstem Raum während der gesamten Vegetationsperiode und am stärksten während des Sommer- und Herbstaspektes. Viele dieser Faktoren sind nur geringfügig typisch ausgeprägt für eine Baumart und somit zu einem hohen Anteil über die Bewirtschaftung beeinflussbar.

Die Wirkung der Umweltbedingungen auf Lebensgemeinschaften führt bei Spinnen soweit, dass der Abstand zum Einzel-Stamm sich unmittelbar auf die Artenzusammensetzung am Waldboden in einem zweiten Versuchsansatz auswirkt.

Laufkäfer (Carabidae) hingegen reagieren ähnlich auf die Umweltbedingungen, werden jedoch stärker geprägt vom pH-Wert von Streu oder Boden und weniger über die Streuart, womit diese Gruppe noch weniger über

baumartgebundene Faktoren direkt modifiziert wird als es bei Spinnen für das Frühjahr aufgezeigt werden konnte. Hinzu kommen baumartenübergreifende Faktoren wie der Kronenschluss, Bodenvegetation, Temperatur und Substratfeuchte.

Da sowohl günstige Umweltbedingungen als auch Nahrung (in Qualität, Verfügbarkeit und Zusammensetzung) eine Art fördern, wurden zudem Interaktionen zwischen Bestandesalter, intrinsischen kleinräumigen Umweltfaktoren und dem Reproduktionspotenzial am Beispiel weit verbreiteter generalistischer Laufkäfer (*Abax parallelepipedus*, *Pterostichus oblongopuntatus*, *Pt. burmeisteri*) für eine weitere Hypothese untersucht. So stieg das Reproduktionspotenzial der Arten wie auch die Zeitspanne der Reproduktion signifikant innerhalb eines Waldtypes mit dem Alter an, wenn nicht entsprechende forstliche Eingriffe der natürlichen Bestandesentwicklung gegenüber standen. Laufkäfer orientieren sich räumlich an für sie günstigen Umweltbedingungen und werden entsprechend in ihrer Entwicklung von diesen gefördert. Generell erhöhte sich das Reproduktionspotenzial der Arten mit günstigeren Temperaturbedingungen in den älteren Beständen und war signifikant von der Streu- und Substratfeuchte am Waldboden determiniert.

## Summary

The impact of the tree species and stand structure in combination with the small-scale mosaic of environmental parameters on composition, development and distribution of soil dwelling arthropods (spiders, carabids) were investigated in a study design of managed forests in temperate regions. The purposes of the examination were to assess the small-scale spatial distribution pattern of spider and ground beetle assemblages in different deciduous mixed and coniferous forest types, to reveal environmental key factors leading to a separation of species assemblages, and to identify those key factors that are intrinsic features of the tree species.

The study aimed at the management of forest ecosystems sustainably with knowledge about the reaction of species to habitat formation in age class forests and thus to avoid a considerable loss of diversity and potential ecological stability.

The investigated forests were clear stands of spruce (*Picea abies*) and Douglas fir (*Pseudotsuga mentziesii*), and mixed stands of spruce-beech (*Picea abies*, *Fagus sylvatica*) and oak-beech (*Quercus robur*, *Fagus sylvatica*, *Carpinus betulae*) representing common regional forest types. The stand type was assumed to influence the distribution pattern and interaction of carabid and spider species affecting the composition of inherent species assemblages. Besides, the age of forest habitats with all its successional alterations and management effects are likely to modify the intrinsic environmental conditions, and those influences are to be analysed precisely. To understand if the tree species or the forestry practice were more determinative, detailed environmental parameters were continuously recorded in a defined pattern to reveal strong gradients for causal analyses on the composition of arthropod assemblages and communities. The species diversity of carabids and spiders generally increased with the stand age in managed forests, while environmental key parameter change with stand age by nature but also through management impact.

The results document that in production forests the composition of arthropod assemblages varies not only between stand types but also and fundamentally



within a forest ecosystem due to a small-scale mosaic of environmental parameters along with the seasons. The investigation revealed a very sensitive segregation of spider assemblages and many species were non-randomly distributed at the forest floor. Confirming my expectations, the most important environmental parameters influencing the small-scale distribution of spiders comprised intrinsic factors of the covering tree species (like the litter type, deciduous or coniferous tree type) with a strong stand type effect in spring and factors not strictly attributed to the tree species itself during all seasons (like canopy closure, vegetation, and microclimatic parameters). Among the key habitat factors affecting the microhabitat distribution of spiders were abiotic parameters such as irradiation, temperature, air humidity, and water content of soil and litter. The study demonstrates that spiders respond to vegetation aspects during the vegetation period regardless of the tree species and most obvious in summer and fall. Several species showed strong adhesions to grass, moss and herb vegetation. Thus, the composition of the spider assemblage of a microhabitat was not strictly defined by the covering tree species (i.e. stand type) or the age class of forests. The conditions of several abiotic microhabitat parameters were affected by the degree of canopy closure, as a result of the tree species-specific crown architecture and silvicultural practice.

With the comparison of stem-close and stem-distant trap positions in a second experiment, an important small-scale spatial distribution pattern of a broad variety of spider species in forests has been shown.

Ground beetles though were distributed on a small spatial scale at the forest floor like spiders expressing a lower correlation to the stand type in spring (like characteristics of the litter and deciduous or coniferous tree type) while they are mostly impacted by factors not strictly attributed to the covering tree species itself (like canopy closure, vegetation, temperature, humidity, but also the litter depth and pH of litter and soil).

In a third experiment the thesis was tested that the reproductive rate of ground beetle species is affected by the age of forest habitats. As habitat age is the result of the specification of a broad variety of environmental factors, the question

raised if there are specific habitat parameters including nutritional influences that affect the reproductive potential of carabid species in forest habitats. Therefore, the reproductive rate of three common silvicolous ground beetle species (*Abax parallelepipedus*, *Pterostichus oblongopunctatus*, *Pt. burmeisteri*) was examined. Within the forest types the egg-load of the ground beetle species showed statistically significant relations to the age of the stand type accompanied by a longer duration of the reproduction period. The reproductive rate was generally increasing with temperature aspects in forest sites and was significantly influenced by moisture parameters. The results emphasize the role of abiotic parameters on the reproductive rate of ground beetles contributing to the explanation of habitat carrying capacity and potential population size in age class forests.

# 1 General Introduction

*Principles of ecosystem management and sustainable development.  
Sustainability has become the primary goal of both economic  
development and natural resource management  
(Frank J. McCormick 2002)*

## 1.1 Arthropods as a permanent component of forest ecosystems

Forests are more than a stand of trees in the landscape. They represent a complex, functional system of interacting and often interdependent biological, physical and chemical components (Kimmins 1997). In the past, complex interactions were increasingly recognized over time as food webs, abiotic processes and biotic feedbacks since then defined as the forest ecosystem. Trees grow in a world of multitrophic interactions (van der Putten et al. 2001). One component of this functional system is represented in several aspects by spiders and insects, as they contribute considerably to the biodiversity and ecosystem functioning in forest habitats (Watt et al. 1997).

There is knowledge on the community composition of several forests of different stand type or tree species composition referring to soil dwelling arthropods. Moreover, studies often highlight the orientation of single arthropod species on abiotic factors or the composition of species assemblages in case studies; these represent ecologically well described groups that can be used as indicators of habitat quality (Pearce and Venier 2006; Cardoso et al. 2004). Evidence on the scale of interactions between the species and their environment are rare. This applies particularly to examples based on fine spatial and temporal scales.

Temperate forests are known for a high level of heterogeneity and complexity resulting in diverse arthropod communities (Southwood et al. 1983; Dajoz 2000).

As the trees generate defined and characteristic environmental conditions in forest ecosystems, they modify the habitat below the canopy due to alterations of several factors, which are among those potential forces that drive population change and community structure (Hunter and Price 1992). It is generally accepted that structural components contribute to a high diversity in forest ecosystems (Otto 1994; McElhinny et al. 2005; Gilliam 2007). Though, basic knowledge on the complex relation between tree species, microhabitat heterogeneity and species communities are not abundant (e.g. Niemelä et al. 1996; Lassau et al. 2005).

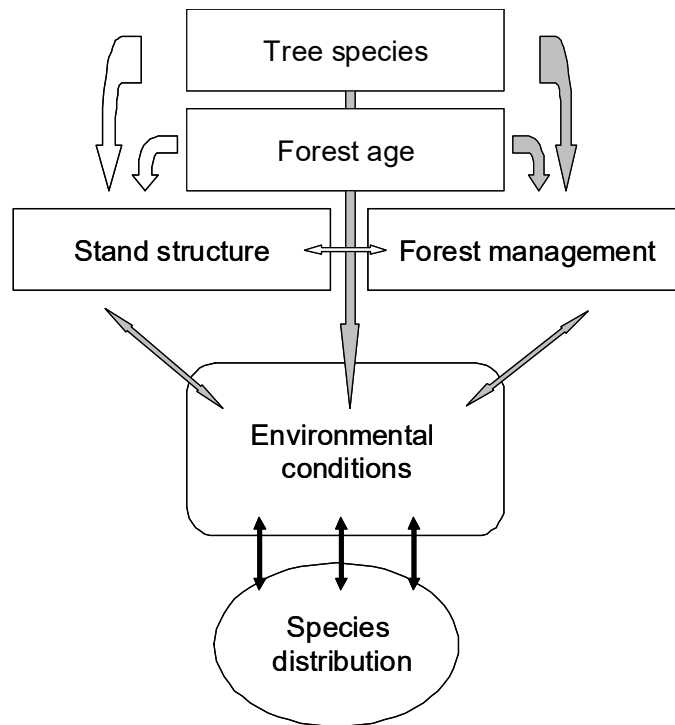
As already mentioned, the tree species plays a key role in the expression of certain biotic and abiotic environmental factors of a given area. Stand type and tree composition may thus be important in determining feedbacks between structural complexity and arthropod communities (Fig. 1.1.). On the other hand forest structures are superimposed by management resulting in pronounced effects on the natural growth cycle of temperate coniferous and deciduous forests.

Although several investigations propose diversity measures in forest ecosystems, it is difficult to untangle interactions among stand type, stand structure, and potential forces in community structuring. MacArthur and MacArthur (1961) evidenced that the physical structure of a plant community, i.e. how the foliage is distributed vertically, may be more important for a species group than the actual composition of plant species.

Basically, there is evidence on general host-plant specificity of several herbivores in temperate forests such as caterpillars (Dyer et al. 2007), – chewing or sucking – Coleoptera and Heteroptera (Watt et al. 1997). For herbivorous insects, one mechanism leading to species diversity could be increased ecological specialization in a given forest, resulting in a greater proportion of insect species occupying narrow niches within a community (Nakashizuka 2001; Novotny and Basset 2005).

Although predatory arthropods do not rely on the plant tissue, mechanisms encouraging the assemblage structuring might be consistent referring to environmental conditions and structural components or the presence of lower trophic levels (Otto et al. 2007). Abiotic factors may directly and unambiguously

influence habitat selection of many spiders (Wise 1995) and carabids (Luff 1996; Koivula 2011). Thus, tree species effects on predator abundance may be mediated by indirect interactions with inherent environmental factors.



**Fig. 1.1** Pattern of interactions between environmental conditions and stand structure affected by forest management (grey arrows) during the growth cycle (from the large to the small scale). Management applies to distinct pure and mixed forests according to the tree species and forest age.

Nevertheless, populations and communities of organisms are influenced by a host of abiotic and biotic factors, among them climate, availability of nutrients, quality and quantity of other resources, competitors, symbionts, parasites, as well as natural enemies (Hunter and Price 1992). But the attempt to define keystone structures to responses of different species groups remains crucial (Tews et al. 2004; Smith et al. 2008).

This knowledge may facilitate nature conservation strategies. Conservation recommendations generally depend on focussed investigations to determine the relative role of (single) environmental variation in community processes and to interpret, which are actually of importance and at what scale they act. Therefore, detailed knowledge about species and community reactions is essential for the understanding of biodiversity issues and their functional role.

Finally, one main challenge for ecologists is to untangle interactions among these driving forces, determining their impact and particular to unravel key factors that explain diversity patterns in nature.

## **1.2 Spiders and carabids in forest ecosystems**

Early ecological studies already recognized that generalist predators – like spiders and carabids – occupy a crucial position in food webs and they are well known since as beneficial components in terrestrial ecosystems (Van Hook 1971; Diaz and Cabido 2001). In the same vein there was evidence that both arthropod groups have strong potential as ecological indicators (Wiehle 1956; Thiele 1977) as they orientate on gradients of environmental factors (e.g. light, humidity, temperature) and they often rely on a distinct complex of environmental habitat factors (Langor and Spence 2006).

However, forests are changing with time as trees grow, resources accumulate, and single trees outcompete others (Kimmins 1997). Environmental heterogeneity – not stable over time – and structural variation (e.g. litter layer, coarse woody debris, herbs and shrubs) is affected, while tree growing dynamics often result in significant changes of the microclimate at the forest floor (Humphrey et al. 1999).

Those changes are progressing slowly allowing inherent communities to adapt to environmental conditions, though the composition of the fauna also changes over the growth cycle of a forest (Otto 1994; Pearce et al. 2004). The spatial and temporal dynamics of above- and belowground herbivores, detritivores,

decomposers and their predators (e.g. spiders and carabids) can differ over time (van der Putten et al. 2001).

Insect and spider diversity in forests increases generally in response to the progressive structural and trophical complexity along the growth cycle of a stand (Brown and Southwood 1987; Ziesche et al. 2004; Oxbrough et al. 2005). Consequently, forest age may alter the structure of competitive or trophic communities.

Despite the fact that habitat age is related to the specification of a broad variety of environmental factors, the question raises if there are specific habitat parameters that affect life history traits of spider and carabid populations of forest habitats. Environmental conditions may restrict or promote growth rates contributing to population or community changes (i.e. competitive or distributional forces). Although spider and carabid populations should be examined both spatially and temporally in the search for regulatory processes also in forests (Begon et al. 2006), few studies investigated these effects (Lindenmayer et al. 2006).

Single trees add up to shape a forest ecosystem – by the time the canopy exceeds a minimum coverage by definition ( $>0.5$  ha; 10 percent canopy closure – FAO) – and they play a key role in structuring the small-scale pattern of environmental conditions at the forest floor (Niemelä et al. 1996). The trees of a forest though are making the whole more complex than the sum of the parts and the effect on specific environmental forces may be tree species specific (Vehviläinen et al. 2008) or at least characteristic for single factors (e.g. pH and structure of the litter layer).

Other characteristics with regard to the stand structure might be overlaid by management practice (Fig. 1.1.). Intensive forest management may pose one of the most important direct threats to the structure and function of ecosystem diversity (Kuuluvainen et al. 1996). Forestry intensification can negatively impact biological diversity as a consequence of decreased heterogeneity in forest landscapes attributed to a lower plant diversification or age class variation (Carnus et al. 2006; Paillet et al. 2010; Vuidot et al. 2011).

However, on first sight many commercial forests appear to be homogeneously structured, but for insects and spiders a diverse microhabitat mosaic exists at the forest floor with respect to various habitat factors such as irradiation, humidity, litter layer, and other soil characteristics, or the established ground vegetation. Those factors are likely of relevance for species assemblages of spiders and carabids with effects on ecological processes and community forces (Pearce et al. 2004).

Environmental heterogeneity reflects in this context gradients driving population change and community composition. The interactions between environmental gradients and species distribution may be direct in forests (Hunter and Price 1992; Turner 2005), while those forces on the other hand might be overlaid or impaired by inter- or intraspecific interactions in communities leading to indirect non-linear effects (Begon et al. 2006). The strength of direct environmental influences might be weak, strong or species specific as has been addressed in several case studies (Thiele 1977; Luff 1996; Koivula 2011).

Fundamental structural components and forces at the forest ecosystem scale are affected in certain intervals by forest management (e.g. selective felling, thinning, forest harvesting trails) and represent non-natural ecosystem disturbance (Bengtsson et al. 2000). Therefore, the aim of managing forest ecosystems sustainably without knowing the reaction of species to habitat formation can lead to a considerable loss of diversity and consequently ecological stability.

Moreover, in the quest to conserve biological resources there has been growing recognition that it requires an integrated approach in management practices to develop sustainable biodiversity conservation strategies. As organisms are influenced by processes acting across a range of scales – microhabitat selection/species interaction, immigration/emigration referring to biodiversity aspects ( $\alpha$ – $\beta$ – $\gamma$ –diversity), landscape changes, or climate change – it is important that efforts in forest management aim to enhance habitat variability within and between stands as well as across landscapes (Hendrickx et al. 2007).



### **1.3 Are spiders and carabids in ecosystems dispensable? – Functional diversity in natural antagonists**

The importance of biodiversity maintenance and interaction between species diversity and ecosystem functions has been increasingly recognized in recent years (Lehman and Tilman 2000; Hector et al. 2001; Benayas et al. 2009). Studies suggested links between diversity and ecosystem processes and there have been many novel hypotheses developed (e.g. Naem and Li 1997; Thébault and Loreau 2005, 2006; Folke et al. 2004; Tilman et al. 1996, 2006).

Spiders and carabids contribute in this context, as generalist predators, to the regulation of herbivore populations and may thus occupy an important strategic functional position in forest food webs (Ferris et al. 2000). Moreover, the influence of arthropod diversity on the stability and resistance of forest ecosystems has been stressed in several studies of temperate regions (MacArthur 1955; Jactel et al. 2005; Carnus et al. 2006).

A fundamental property of an ecological community is its stability. As the term “stability” may be misleading in “eco”systems that change markedly over time, we might define it as a measure of the constancy of properties of an ecological system or its components (Grimm and Wissel 1997).

Generally, arthropod predators are integrated into complex trophic webs, being controlled by “bottom-up” – the availability of food – and “top-down” effects – referring to a complex of higher predators. Within forests, a number of species are connected by interspecific interactions such as trophic, mutualistic, and parasitic interactions, forming a complex network of biological communities (Thébault and Fontaine 2010; Symstad et al. 2003).

Studies of the energy flow through food webs indicate that spiders play a major role in the predatory fauna and they capture a substantial fraction of the insects in lower trophic levels (Wise 1995). The same applies to ground beetles, though they are not as strictly bound to insect prey such as spiders (Stork 1990). The role as

antagonists of both groups affects functional traits of insect communities, also with regard to species that may reach harmful densities in forests.

The interaction between predatory arthropods and function or sustainability of forest ecosystems may depend on the biological diversity (Loreau et al. 2002) and effects may critically depend on trophic complexity (Jiang and Pu 2009). Consequently, a major challenge in community ecology and evolutionary biogeography is to reveal the mechanisms underlying these differences. After all, the conservation of biodiversity is one of the fundamental guiding principles for ecologically sustainable forest management (Lindenmayer and Franklin 2002).

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## 1.4 Objectives

I aimed with this investigation at the impact of biotic and abiotic environmental conditions – modified by the stand structure and stand type – on the small-scaled composition of species assemblages of spiders and carabids in forest ecosystems. The study describes different aspects of heterogeneity in space and time attributed to the stand type effect, the age of a forest and the segregation of species on a very fine spatial scale. Impacts on the functionality of arthropods as natural enemies on the level of the forest ecosystem are discussed.

First, I focussed on the activity density of both arthropod groups (spiders and carabids) in forest ecosystems of representative tree species composition and comparable age classes in relation to twenty five continuously measured environmental parameters. Main aim of this investigation was to test for the contribution of fundamental environmental factors on the regulation of species communities at the forest floor. I hypothesized that the composition of spider and carabid assemblages depends on environmental parameters affecting species over short distances. Forest management was assumed to affect key factors of stand types, which significantly and in a characteristic way influence the epigeic species communities. Moreover, spiders and carabids were expected to react differently to habitat parameters requiring one main study design but two separate analyses (Chapter 2, Chapter 4).

In an additional field experiment, I tested the scale of distribution of spider species at the forest floor when environmental heterogeneity is taken into account. Therefore, I hypothesized that structural and environmental factors change significantly with the distance to the tree resulting in effects that drive species composition on a very small spatial scale. Since tree species – or even coniferous vs. deciduous trees – affect distinct environmental conditions differently below the canopy and near the stem I investigated if the effect of tree distance is influenced by the tree species (Chapter 3).



To entangle the effect of the stand age and environmental conditions on population change during the growth phase, the reproductive potential of three widespread carabid species was assessed for one reproductive season. The study proposed that the age of forest habitats with all its successional alterations is likely to influence the fitness of individual arthropods and population traits in forests. The objective declared that key factors in managed forests are strongly influenced by thinning and selective felling, beside variation of driving forces during the growth cycle, resulting in increased reproductive rates with rising stand age (Chapter 5).



## **2 Influence of environmental parameters on small-scale distribution of soil-dwelling spiders in forests: what makes the difference, tree species or microhabitat?**

### **2.1 Abstract**

We surveyed the soil dwelling spider communities of four stand types of forests (pure stands: spruce, Douglas fir; mixed stands: beech-spruce, oak-beech) along a successional gradient (four age classes: 15–112 yr) to show the effects of small-scale microhabitat heterogeneity on the composition of spider assemblages. The investigation was carried out in south Germany. Spiders were collected by pitfall traps ( $n = 96$ ) in 4-wk intervals. To reveal key environmental factors that affect spider communities, abiotic and biotic habitat parameters (e.g., temperature, air humidity, soil characteristics, and vegetation parameters) were systematically assessed around each pitfall trap. Spider species showed a small-scale distribution pattern on the forest floor, significantly affected by litter type, degree of canopy closure, temperature and humidity parameters, as well as cover of grass, moss, herb, and natural regeneration according to discriminant analysis and ordinations. The relevance of habitat parameters changed with the growing season. While many species were correlated to litter type and canopy closure in spring, the influence of ground vegetation and humidity parameters prevailed during summer. In fall, the strength of correlations decreased besides ground vegetation and soil humidity. The species assemblages assessed in the four forest types of different age classes indicate that the covering tree species has a profound influence on the small-scale distribution of spider species. Nevertheless, the high similarity in the composition of spider assemblages from different stand types but with similar formations of ground vegetation, microclimatic parameter and canopy closure displayed a considerable impact of environmental factors not necessarily bound to the stand type itself.

**Keywords:** araneae, biodiversity, microhabitat selection, production forest, sustainable forest management

## 2.2 Introduction

Spiders are the most abundant arthropod predators in many terrestrial ecosystems, supposedly playing an important role in ecosystem functioning throughout habitats (Van Hook 1971). As generalist predators, they contribute to the regulation of herbivore populations in forest communities (Lawrence and Wise 2000) and thus occupy a strategic functional position in terrestrial food webs (Ferris et al. 2000).

While spiders in forest ecosystems contribute to the maintenance of insect community equilibrium, the distribution of species and the composition of assemblages are significantly influenced by environmental conditions. This is documented in the use of epigeic spiders as bioindicators for environmental changes (Kremen et al. 1993; Cardoso et al. 2004; Scott et al. 2006). Many spiders often rely on a distinct complex of environmental habitat factors with respect to species-specific ecological demands. And there is experimental evidence that habitat alterations due to forest succession, natural disturbances, or forestry practice result in structural changes of the spider community (Pearce et al. 2004; Ziesche et al. 2004; Oxbrough et al. 2005; Finch and Szumelda 2007). In particular, the formation of ground vegetation and the resulting microclimate are most likely to affect the abundance and distribution of spider species and this is probably a major reason for the formation of specific species assemblages in a habitat (Bultman and Uetz 1982; Hurd and Fagan 1992; Gibson et al. 1992). In this context, the formation of tree crown canopies creates distinct and often small-scale microclimates at the soil surface (Mc Caughey et al. 1997) and thus exerts important controls on the composition of the ground vegetation and many biochemical processes, along with seasons (Grimmond et al. 2000). Although many forest ecosystems appear to be homogeneously structured, a diverse microhabitat mosaic exists at the forest floor with respect to various relevant environmental parameters such as irradiation, humidity, ground vegetation, litter layer, and other soil characteristics (e.g., Niemelä et al. 1996; Holst et al. 2004; Oheimb et al. 2005).

Based on this knowledge, it is natural to assume a species-specific distribution pattern of spiders on a small-scale spatial and temporal level. This also applies to production forests that are characterized by silvicultural measures in all stages of the forest cycle. A detailed knowledge of small-scale distribution of spider species in forests and the impact of environmental key factors is essential for the understanding of the composition of spider assemblages and their functional role. Finally, this knowledge is important in evaluating the effects of forest management and in proposing various biodiversity conservation strategies (Ferris and Humphrey 1999; Guisan et al. 2006).

The purposes of our examination were to (1) assess the small-scale spatial distribution pattern of spider assemblages in different and common deciduous and coniferous production forest types, (2) reveal the environmental key factors leading to a separation of species assemblages, and (3) identify those key factors that are intrinsic features of the tree species.

## **2.3 Methods and materials**

### **Study sites and sampling**

The investigation was carried out in the cultural landscape around Augsburg, a historically well-forested area of south Germany (Central Bavaria, 48° 19′/11° 06′). The study sites comprised pure stands of spruce (*Picea abies*) and Douglas fir (*Pseudotsuga menziesii*), mixed stands of beech-spruce (*Fagus sylvatica* - *Picea abies*) and oak-beech (*Quercus robur* - *Fagus sylvatica*). We chose 12 study sites (100 x 100 m) that represented four age classes of these stand types to define comparable forest successional stages: young stand (YS), mature stand (MS), mature stand with upcoming (MR), and established regeneration (eMR) (Table 1). The age classes referred to silvicultural thinning measures representative of forestry practice. Age classes of the respective forest type that were not integrated in the study design were not present in the study area (i.e., oak-beech, MS; Douglas fir, MS).

The study sites correspond in terms of soil conditions, altitude (510–545 m above sea level) and the subatlantic climatic conditions. Annual mean temperatures varied between 7.5 and 8.0 °C, average of annual precipitation ranged between 700 and 900 mm. The soils on these sites were fertile brown and parabrown earths.

**Table 1**

Characteristics of the forest study sites.

Study site	Stand type	Age [yr]	Trees per ha [n]	Medium Hight [m]	Pitfall group	
					A	B
Ps - YS	Douglas fir	15	938	13-14	D2	D1
Ps - MR	Douglas fir	80	314	37-39	D4	D3
Pi - YR	Spruce	30	1852	12-13	P2	P1
Pi - MS	Spruce	62	680	26-28	P4	P3
Pi - MR	Spruce	89	432	34-36	P6	P5
FaPi - YS	Beech-spruce	38	1604	12-16	F2	F1
FaPi - MS	Beech-spruce	73	618	29-31	F3	F4
FaPi - MR	Beech-spruce	89	404	31-33	F5	F6
FaPi - eMR	Beech-spruce	105	312	32-34	F7	F8
QuFa - YS	Oak-beech	28	1564	13-14	Q1	Q2
QuFa - MS	Oak-beech	75	1058	32-33	Q3	Q4
QuFa - eMR	Oak-beech	112	234	36-37	Q6	Q5

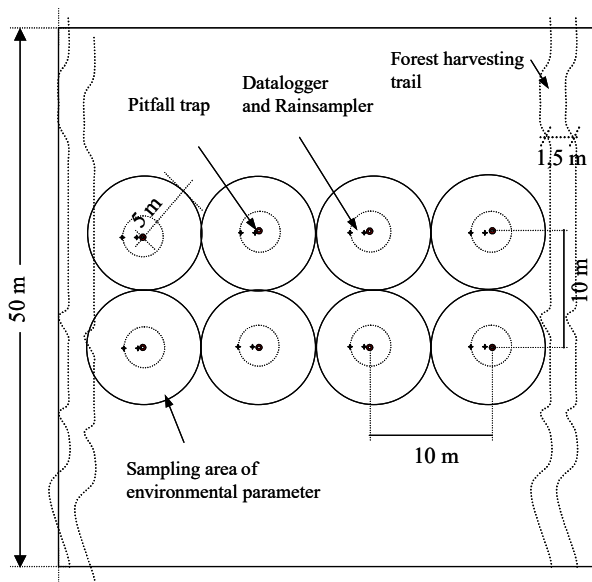
Young stand (YS), mature stand (MS), mature stand with upcoming regeneration (MR), mature stand with established regeneration (eMR) – Grouping of four pitfall locations (i.e., microhabitat) according to degree of canopy closure within the study sites: pitfall trap locations with a high (A) and low (B) degree of canopy closure during the period of complete foliation.

To exclude side effects from adjacent forests, a core investigation area of 50 x 50 m was established in the center of each study site for the sampling of spiders and the assessment of environmental parameters (Fig. 1). The core area of each study site was surrounded by a belt (width: at least 25 m) of the same stand type representing a buffer zone (Molnar et al. 2001) and beyond that by further forest ecosystems up to a distance of several kilometers. The distance between the study

sites, varied between 150 m and 25 km. The distance between the age classes within a stand type covered 1–2 km on average.

In contrast to the oak-beech stands with a homogeneous mixture of deciduous trees, the beech-spruce stands consisted of beech groups, separated from areas covered with pure spruce. Hence, in beech-spruce stands, the core area was established: one half was covered with spruce, the other with beech.

We collected spiders by pitfall trapping (glass jar,  $\varnothing = 7.5$  cm, fixing agent: solution of saturated benzoic acid and detergent), since they sample a high number of ground- and litter-dwelling species (Curtis 1980), while measuring the activity density of species at the floor (Green 1999; Topping and Sunderland 1992). The method is common and proven in ecological research (Granström 1973). Eight traps in two linear transects with four traps each were arranged within the core area of each study site (Fig. 1). The distance of the traps between and within the transect covered 10 m.



**Fig. 1** Design of data sampling in the core investigation area (50 x 50 m) within each study site (1 ha).

Each core area offered a gradient in the degree of canopy closure due to harvesting trails (width <1.5 m) located at two sides of the core area (Fig. 1). This degree of canopy closure was reflected along the transects of pitfall traps, providing the opportunity to define microhabitats (with four pitfall traps, each) with a high (pitfall group A) and low (pitfall group B) degree of canopy closure at each study site (Table 1). In the beech-spruce stands, one transect of four pitfall traps was established under beech (microhabitats: F1, F3, F5, and F7), the other transect under spruce (microhabitats: F2, F4, F6, F8; Table 1).

The traps were emptied every 4-wk between 18 March and 22 October of 2002. The determination of spider species followed the identification keys of Wiehle (1956, 1960), Roberts (1985, 1987, 1998), and Heimer and Nentwig (1991). The ecological characterization was based on Martin (1991), Maurer and Hänggi (1990). The nomenclature of spiders followed Platnick (2006).

### **Assessment of environmental variables**

Twenty-five environmental parameters were surveyed during the investigation period (Table 2). Soil surface temperature was measured continuously every 45 min at each pitfall trap (at a depth of 1 cm in the litter layer) by data logger (Tinytalk II/TK-0023, Spectra Computersysteme, Leinfelden-Echterdingen). Air temperature and relative humidity values were taken every 90 min twice in a trap line (80 cm above the ground) by Tinytags Ultra (TGU 1500, Spectra Computersysteme, Leinfelden-Echterdingen). For climatic parameters calculated from the recorded data see Table 2. The seasonal (spring, summer, fall) averages were calculated from the daily data.



**Table 2**  
Environmental parameters surveyed at each pitfall trap.

<b>Vegetation cover [%]</b>	pH of litter layer
Degree of canopy closure	Litter type
Natural regeneration	Litter depth
Herbs	Litter cover
Grass	<b>Microclimate</b>
Moss	Air humidity [%]
Total standing vegetation	Precipitation per trap [ml]
<b>Vegetation hight [cm]</b>	Soil surface temperature [C°]
Natural regeneration	t – min soil surface
Grass layer	t - max soil surface
Herb layer	t - variation
<b>Soil characteristic</b>	Mean temperature per year /
season	
Soil moisture [%]	Temperature – air
pH of the soil	Days above 8°C [ n ]
Moisture of litter layer	

The depth of the litter layer above the mineral soil was measured every 4-wk at four randomly chosen locations around each trap (diameter of 2 m) to estimate mean thickness. Precipitation was measured at each pitfall trap by rain samplers in a distance of 80 cm (funnel diameter: 7.6 cm), gathering the precipitation of 4-wk intervals. Soil and litter samples for the determination of moisture (Scheffer and Schachtschnabel 1989) and pH (H<sub>2</sub>O) were taken in spring (9 April), summer (30 July), and fall (24 September) within a radius of 1 m around each trap. The degree of canopy closure, the cover value of natural regeneration, herb, grass, moss, and litter were assessed according to Braun-Blanquet (Mühlenberg 1989), within a radius of 5 m around each trap following the 4-wk intervals of pitfall trap sampling. Litter type was also assessed every 4-wks as the proportion of the tree species-specific litter covering the soil (in mixed stands, according to the predominating litter type) within a radius of 5 m around each trap (classification of

litter types: Douglas fir, spruce, spruce-beech, beech-spruce, beech, beech-oak, oak-beech, oak).

We distinguished three time periods to assess the effects of seasonal habitat alterations on the spider community, mainly based on the development of the crown canopy and the ground vegetation. Spring was defined as the time period from the beginning of the study until the foliation of the deciduous trees was completed (18 March –5 June). Summer season was the time period when trees have a fully developed crown canopy and when mean temperatures were higher than those in spring (6 June–28 August). Fall season started with the beginning of the leaf fall accompanied by dropping temperatures (29 August–22 October).

### **Statistical analysis**

To compensate possible differences in catch results of pitfall traps due to different levels of activity density between the 24 microhabitats we used relative abundance data (dominance in %) for statistical analyses (Honek 1988), to emphasise differences in the assessed species composition.

TWINSPAN analyses (Hill 1979) were carried out to detect corresponding and deviating patterns in the composition of spider assemblages of microhabitats (i.e., grouping of four pitfall traps with a similar degree of canopy closure and tree species composition;  $n = 24$ , Table 1). This hierarchical ordination method classifies microhabitats based on structural parameters of species assemblages (e.g., species spectrum, dominance position) and combines corresponding spider assemblages of microhabitats to microhabitat groupings. Additionally, the analysis identifies character species for each classified division of microhabitats that may be present in low number in other microhabitats.

We used discriminant analyses (DA) to reveal significant environmental factors that contribute to the explanation of the spider assemblage classification in the TWINSPAN analyses. Applying a forward stepwise procedure, the DA determined those environmental key parameters that discriminate best between the TWINSPAN microhabitat groupings of the spring, summer, and fall aspects,

respectively. Subsequently, all seasonal environmental parameters of microhabitats were examined by DA to evaluate the effects of intrinsic characteristics of the tree species composition. Therefore, all age classes of the same stand type (Douglas fir, spruce, beech-spruce, oak-beech) were pooled in the statistical procedure.

To reveal correlations between the distribution pattern of spider species and environmental conditions the catch results of species of each single trap ( $n = 96$ ) were related with environmental parameters (Spearman rank, SPSS 12.0) assessed in the surrounding of each trap.

A species-centred principal component analysis (PCA) was run to determine the main environmental parameters affecting the distribution pattern of spider species and microhabitats during spring, summer, and fall. Finally, a redundancy analysis (RDA) (stepwise forward selection,  $p < 0.05$ , unrestricted Monte Carlo permutations;  $n = 9999$ , CANOCO 4.5) was performed for the graphical ordination of the environmental key parameters that contribute best to the characteristic pattern of spider assemblages (Legendre and Anderson 1999; ter Braak and Smilauer 2002; Jongman et al. 1995). Analyses separate species and sites according to an indirect gradient (PCA) and additionally give indication of the main environmental parameters involved in the partition of species assemblages (RDA).

To reduce the pitfall method specific overestimation of the most active species, the activity density data of the 24 microhabitats were log-normal transformed. A preliminary detrended correspondence analysis (DCA) indicated a strong linear response of the species variance to the environmental parameters (Hill and Gauch 1980) which is common with proportional data. Thus, we used PCA and subsequent RDA (Leps and Smilauer 2003). The results of the PCA and RDA environmental variables were tested on multicollinearity. All analyses comprised only species with  $>3$  individuals in total catch of each season.

Because litter type was only assessed as a qualitative parameter, not representing a linear gradient, this environmental parameter was excluded from the PCA and RDA.

## 2.4 Results

During the investigation 8,488 adult spiders were assessed representing 142 species. According to the pitfall catches, the activity density of spiders revealed similar levels in spring (3,419 individuals from 89 species, 51 species > 3 individuals) and summer (3,703 individuals from 105 species, 49 species > 3 individuals). In fall, the relative abundance decreased to 1,366 individuals from 58 species (32 species > 3 individuals). Nine species (Linyphiidae: *Diplocephalus latifrons*, *Micrargus herbigradus*, *Tenuiphantes tenebricola*, *Erigonella hiemalis*, *Diplostyla concolor*; Hahniidae: *Hahnia pusilla*, Amaurobiidae: *Coelotes terrestris*, *Coelotes inermis*; Agelenidae: *Histoipona torpida*) made up 49.5% of all individuals collected. Despite *C. inermis* (spring and fall), these species were assessed during all three seasons in high individual numbers. Altogether, 25 species occurred with more than three individuals during all seasons. Almost 84% of the species were commonly known forest (69%) and forest edge species (14.7%). Only 16.3% of the species were characteristic of open habitats. These species were barely the subject of statistical analyses (only two species), since they occurred in low individual numbers (50 individuals from 22 species).

### Classification of species assemblages

#### Spring season

The TWINSpan classification for the spring aspect separated nine microhabitat groupings (MG) and 14 species groupings (SG, Fig. 2). The species composition of the microhabitat groupings differed clearly from each other, although several spider species occurred in more than one microhabitat grouping or were even widespread like *M. herbigradus* and *D. latifrons* (SG 3).

The arrangement of microhabitat groupings in spring followed significantly the respective tree species (stand type) covering the ground. This was proven by the uniform composition of the microhabitat groupings with respect to the tree

species (MG 1–3, 5–7, 9) or the tree species type (i.e., deciduous or coniferous tree species; MG 8). The only exception represented microhabitat grouping 4 with beech (F1, F3 and F5) and spruce (F6) of beech–spruce stands.

In the first division, the analysis separated microhabitat grouping 9 (*Ps–MR*: D3 and D4) from all other study sites. This separation was mainly caused by the restriction of a group of hygrophilous species (SG 1) to the microhabitats of the mature Douglas fir stand, while many species, which were common to the other deciduous and coniferous forests, were almost missing here, like the stenombrophilous character species *C. inermis* (Fig. 2, dendrogram).

In the second division, all microhabitats of the oak-beech stands (MG 1 and 2) and microhabitat F7 (MG 3, situated under beech in *FaPi–eMR*) were arranged and separated from the microhabitats in younger stands covered with beech (MG 4: F1, F3 and F5) or coniferous trees (MG 5–8). A high prevalence of hygrophilous linyphiid species (e.g. SG 2, 5, and 6) was characteristic of these microhabitat groupings (MG 1–3) of that division.

Besides, the microhabitat groupings (MG 1–4) covered with deciduous trees (except F6, covered with spruce of beech-spruce) were marked by a high species richness ( $n = 20 - 25$ ) and increased activity density during the spring season.

In the third division of this microhabitat cluster, a deviating pattern in the species composition of the mature oak-beech stand with established regeneration was obvious (MG 1: Q5 and Q6) compared with younger oak-beech stands (MG 2 and 3, SG 4 and 10).

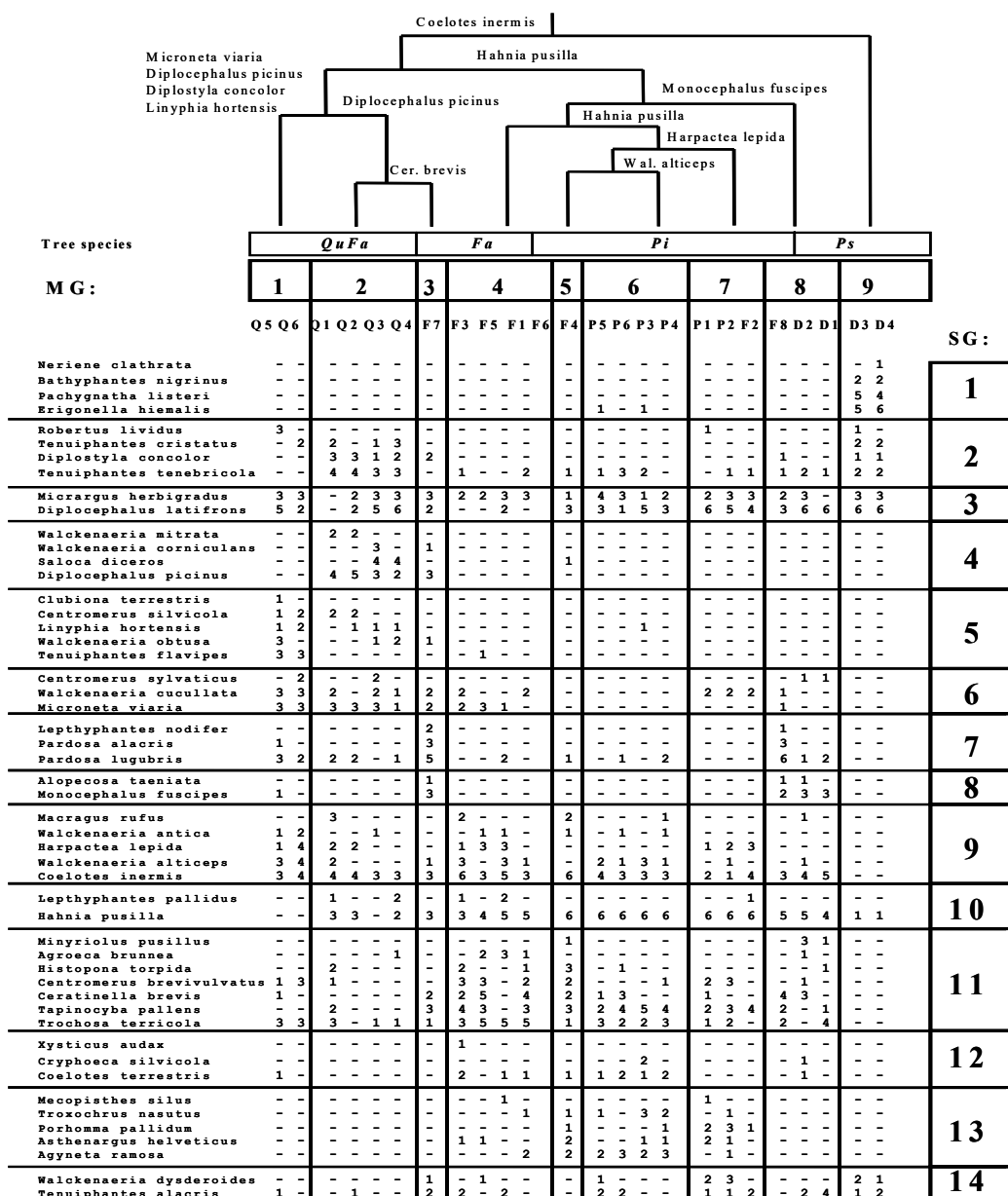


Fig. 2 TWINSpan classification of spider assemblages in the forest study sites in spring. Character species are written in italics. The relative frequency of each species is indicated by numbers from 1 to 6 (1 = 0–1.9%, 2 = 2–3.9%, 3 = 4–4.9%, 4 = 10–14.9%, 5 = 15–24.9%, 6 => 25%). Microhabitats: spruce = P1–P6, Douglas fir = D1–D4, beech-spruce = F1–F8 (beech: F1, F3, F5 and F7; spruce: F2, F4, F6 and F8), oak-beech = Q1–Q6. MG = microhabitat groupings, SG = species groupings.

The further division of microhabitat groupings (MG 4 - 8), marked by the presence of *H. pusilla*, displayed the young Douglas fir stand (MG 8: D1 and D2) and the spruce-dominated microhabitat (MG 8; F8) of the old beech-spruce stand with established regeneration as a well-defined subcluster. It was characterized by the presence of species grouping 8 (meso-hygrophilous forest species) with *Monocephalus fuscipes* as character species, while species grouping 13 was completely missing. In the next division, the beech (MG 4: F1, F3 and F5) and one spruce covered microhabitat of beech-spruce (MG 4: F6) were separated from microhabitats covered by spruce (MG 5, 6, 7). This was reflected in the distribution pattern of representatives of species groupings 6 (*Microneta viaria*) and 11 (*Agroeca brunnea*). The next division of microhabitats covered with spruce separated microhabitat grouping 7 (young spruce stands) from the older ones.

### **Summer season**

The overall activity density of spiders increased in June and July at several study sites with rising temperatures and the development of understory vegetation. The TWINSpan classification for the summer aspect separated nine microhabitat groupings as in spring, but 19 species groupings (Fig. 3). The enhanced number of species groupings suggests a higher diversification of microhabitat usage by the spider assemblages, since the total number of species corresponded in the spring and summer aspect. Like in spring, the species composition of microhabitat groupings differed clearly, despite three euryoecious species (SG 11), which were barely missing at any pitfall trap.

Also, regarding the first divisions of the analysis, there was a shift in the composition of microhabitat and species groupings compared with that in the spring season. Nevertheless, the final microhabitat groupings (MG 1–9) were still mainly arranged according to the tree species covering the ground (Fig. 3).

The first TWINSPAN division grouped the microhabitats of the mature oak-beech stand (Q3, Q4) together with all microhabitats covered with beech of the mixed beech-spruce stands (F1, F3, F5 and F7) as well as the microhabitats covered with spruce in the young (F2) and the mature beech-spruce stand with established regeneration (F8). These microhabitat groupings (MG 7–9) were characterized by the presence of ombrophilous-hygrophilous species (SG 17–19). Some species common to the deciduous stands in spring, such as *M. viaria* restricted their distribution to those strongly shaded sites in summer. Other species such as *H. torpida* and *C. terrestris* extended their distribution pattern.

The second subcluster of the first division (MG 1–6) comprised the Douglas fir stands, the pure spruce stands, microhabitats covered with spruce in the mature beech-spruce stand as well as microhabitats of the young (Q1, Q2) and old oak-beech stand with established regeneration (Q5 and Q6). In the second division, the oak-beech stands (MG 2) and the mature Douglas fir stand (MG 1) formed a group due to obvious deviations of the species composition (e.g. SG 1–3, 6–9, 15) compared with the young Douglas fir stand and spruce covered microhabitats of pure and mixed spruce stands (MG 3–6). In the third division, the spider assemblages of these coniferous microhabitat groupings were separated mainly along with the age class gradient of the stands (Fig. 3).

### **Fall season**

In fall, the overall activity density of spiders has decreased. Only 32 species were caught in individual numbers, adequate for statistical analyses. The TWINSPAN analysis of the spider assemblages revealed eight microhabitat groupings and 11 species groupings with a species distribution pattern differing from the spring and summer aspect. Effects of the stand type or tree species on the TWINSPAN divisions were less obvious than in summer.



Effect of small-scale environmental parameters on spiders

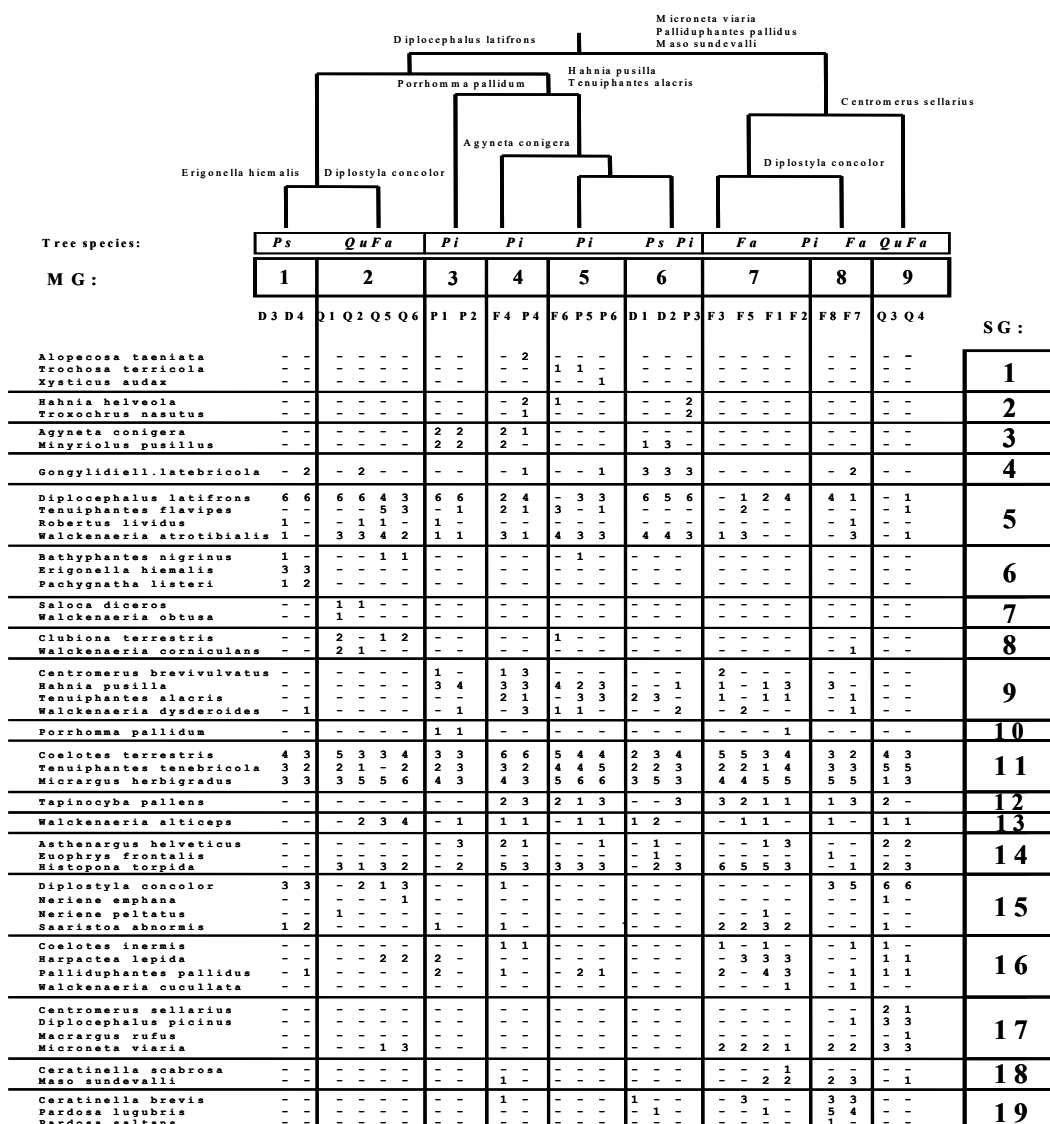


Fig. 3 TWINSpan classification of spider assemblages in the forest study sites during summer. Character species are written in italics. The relative frequency of each species is indicated by numbers from 1 to 6 (1 = 0–1.9%, 2 = 2–3.9%, 3 = 4–4.9%, 4 = 10–14.9%, 5 = 15–24.9%, 6 => 25%). Microhabitats: spruce = P1–P6, Douglas fir = D1–D4, beech-spruce = F1–F8 (beech: F1, F3, F5 and F7; spruce: F2, F4, F6 and F8), oak–beech = Q1–Q6. MG = microhabitat groupings, SG = species groupings.

### **Environmental factors explaining the TWINSpan classification of spider assemblages**

The results of a forward stepwise DA revealed significant environmental key parameters explaining the arrangement of the TWINSpan microhabitat groupings. The results confirmed a seasonal shift in significant environmental factors that affected the distribution pattern of species assemblages.

The spring aspect was defined by a strong gradient in the degree of canopy closure between evergreen coniferous stands and stands with deciduous trees, starting with the leaf formation in May. Also, a gradient of canopy closure was obvious within the coniferous stands due to their differences in age and as a consequence of silvicultural practice. This apparent feature was reflected by recorded environmental conditions affecting the spider species distribution significantly.

For the spring aspect, the significant discriminating variables explaining the classification of TWINSpan groupings ( $n = 9$ ) were the degree in canopy closure ( $F = 15.09$ ,  $p < 0.001$ ), the litter type ( $F = 12.942$ ,  $p < 0.001$ ), the mean temperature ( $F = 11.243$ ,  $p < 0.001$ ), cover value of moss ( $F = 9.792$ ,  $p < 0.001$ ), the soil moisture ( $F = 4.174$ ,  $p < 0.002$ ), and the cover value of natural regeneration ( $F = 4.05$ ,  $p < 0.04$ ).

The summer aspect was visually characterized by deciduous trees with fully developed foliage, shading the forest floor. The spring vegetation nearly vanished and the summer vegetation succession has taken place. These alterations were accompanied by changes in the significance of the variables.

In summer, litter type ( $F = 16.629$ ,  $p < 0.001$ ) was the first significant discriminating factor for the separation of microhabitat groupings ( $n=9$ ) identified from the TWINSpan classification. It was followed by degree in canopy closure ( $F = 8.081$ ,  $p < 0.001$ ), cover value of grass ( $F = 7.610$ ,  $p < 0.001$ ), and moss ( $F = 6.897$ ,  $p < 0.001$ ). Soil moisture ( $F = 6.691$ ,  $p < 0.05$ ) and cover value of natural

regeneration ( $F = 5.483$ ,  $p < 0.05$ ) were also significant factors of microhabitat groupings.

The fall aspect was characterized by the defoliation of deciduous trees but still by a fully developed herb and grass vegetation. The only significant variable in fall contributing to a separation of microhabitat groupings in the TWINSPAN analysis appeared to be soil moisture ( $F = 4.925$ ,  $p < 0.001$ ).

To judge whether these discriminating factors were intrinsic features of the tree species covering the ground, a forward stepwise DA was conducted, combining all microhabitats ( $n = 24$ ) of the same stand type. In spring, the different stand types were separated by the litter type ( $F = 57.412$ ,  $p < 0.001$ ) and the cover value of natural regeneration ( $F = 25.211$ ,  $p < 0.001$ ). The pH of the soil ( $F = 16.606$ ,  $p < 0.001$ ) and canopy closure ( $F = 7.69$ ,  $p < 0.001$ ) represented further significant discriminating variables. In summer, still the litter type ( $F = 45.571$ ,  $p < 0.001$ ), the cover value of natural regeneration ( $F = 15.802$ ,  $p < 0.001$ ), as well as air humidity ( $F = 15.3$ ,  $p < 0.001$ ) and mean temperature of the season ( $F = 6.01$ ,  $p < 0.001$ ) differed most between the stand types. In fall, litter type ( $F = 90.401$ ,  $p < 0.001$ ), cover value of natural regeneration ( $F = 30.073$ ,  $p < 0.001$ ), and soil moisture ( $F = 10.61$ ,  $p < 0.001$ ) were the most important variables separating the stand types.

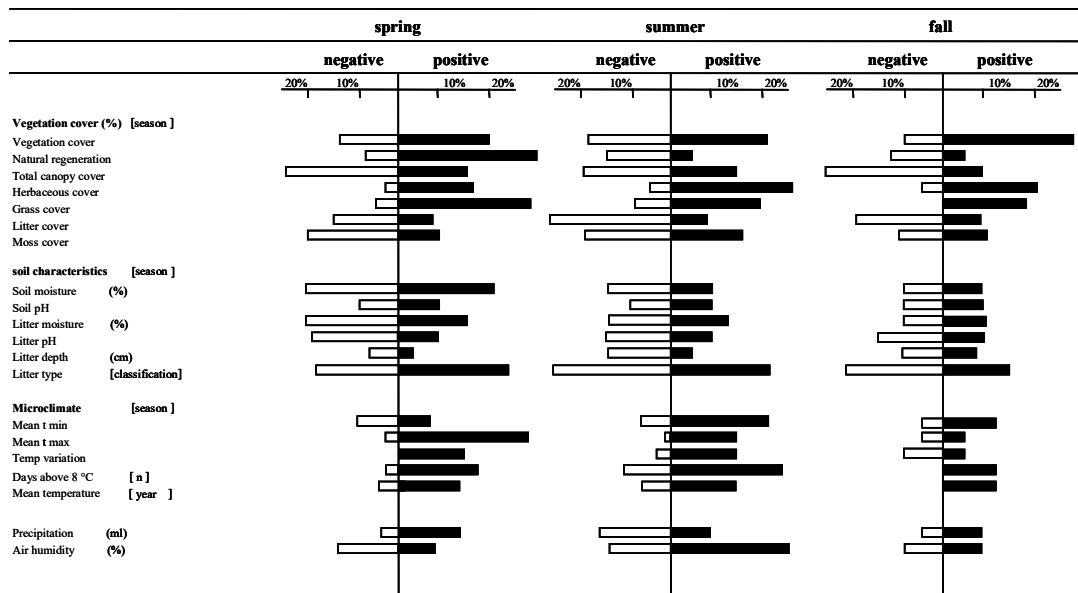
### **Environmental factors explaining the distribution pattern of single species (Spearman rank)**

A high number of species showed significant ( $p < 0.05$ ) positive and negative correlations to environmental parameters assessed in spring, summer, and fall (Table 6), respectively (Fig. 4). Apparently, for the spring season, the overall vegetation cover and particularly the cover value of natural regeneration, grass (positive) and moss (negative correlation), as well as soil moisture, mean maximum temperature, litter type, and degree of canopy closure (positive and negative correlation) contributed significantly to the distribution pattern of almost 75% of all spider species.

The results of the Spearman rank correlation (Fig. 4) displayed a shift in the relevance of environmental parameters, affecting the spider assemblages along with the growing season. Only 51% of all significant correlations documented in spring were maintained in summer. Thus, the impact of natural regeneration and mean maximum temperature decreased, while parameters such as air humidity, days above 8°C, litter type, cover value of litter, herb, and moss gained a stronger influence. These factors explained the summer distribution of 67% of all species.

The degree of canopy closure still had a striking positive or negative impact on many species. But the results did not reveal high correlations to soil characteristics like water content, pH, or depth of the litter layer. The same applied to the amount of precipitation.

In fall, correlations of the species to ground vegetation characteristics such as total vegetation cover or the cover value of herb and grass remained high. Besides, many species were negatively correlated to the degree of canopy closure. The litter type, that covered the trap area ( $\varnothing = 10$  m), showed highly significant negative and positive correlations and thus represented a major habitat factor influencing species distribution just like in spring and summer. Altogether, the species responses to environmental factors subsided and the strength of correlations decreased significantly.



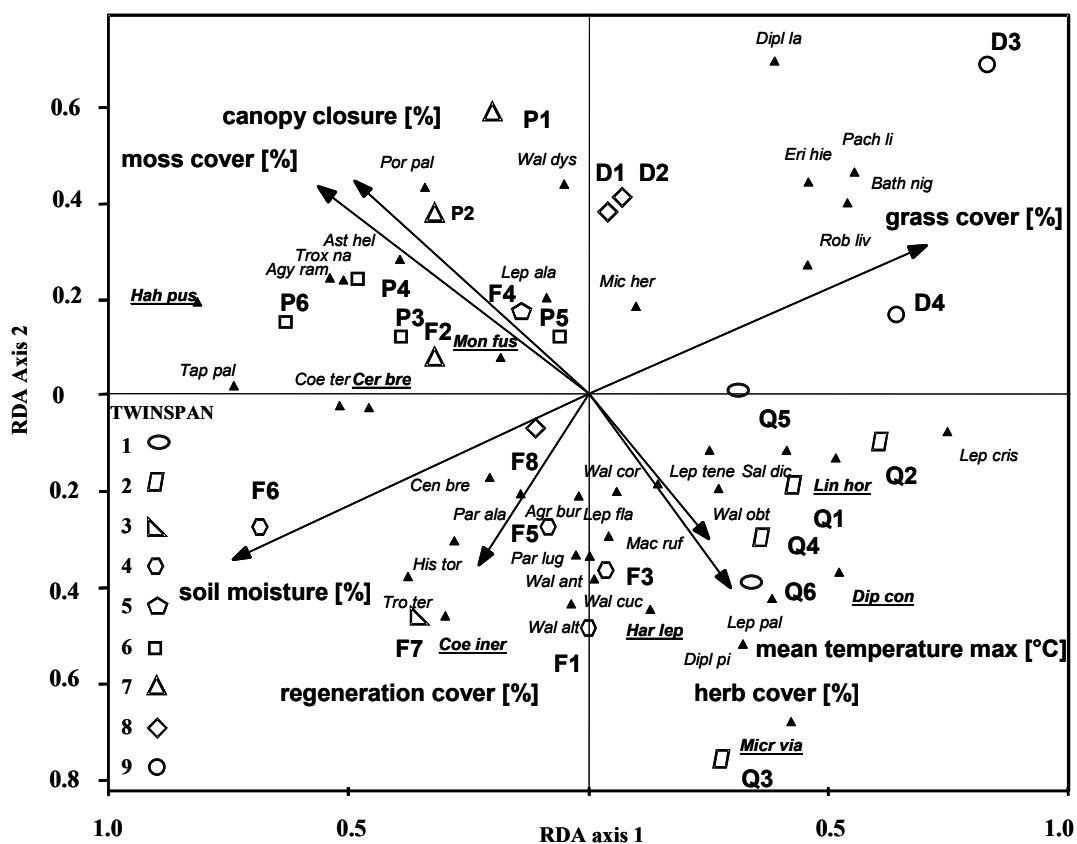
**Fig. 4** Environmental parameters explaining the seasonal (spring, summer and fall) distribution pattern of spider species in different types of forests: results of Spearman rank correlations expressed as the percentage of spider species showing significantly negative (white bars) or positive (black bars) correlations to the respective microhabitat factors.

### PCA / RDA ordinations

Multivariate analyses revealed a distinct distribution pattern of species and microhabitats (Fig. 5, 6). The RDA in combination with PCA for the data sets of spring and summer resulted in a good separation of microhabitats as well as species (Table 3). This corresponded with the results of the TWINSPLAN analysis. Thus, microhabitats were arranged mainly according to the cover tree species. The first four PCA axes for the spring season explained 59.7% of the variance of the species, displayed in the biplot, and 74.5% of the correlations between species and environmental factors chosen in the RDA.

In spring the first axis was mainly related to grass cover as well as to soil moisture, the second axis to canopy closure, and the cover value of moss, herbs and natural regeneration as well as maximum temperature (Fig. 5, Table 4). This separation was reflected in a strong grouping of the microhabitats according to the covering tree species. Thus, the first axis separated the oak-beech (Q1–Q6) and the Douglas fir (D3 and D4) from all beech and spruce microhabitats. Along the second axis, microhabitats under coniferous canopy were separated from the oak-beech and beech-covered sites. The only exceptions were F6 and F8, covered with spruce but characterized by a litter layer mainly consisting of beech. At the lower left side of the biplot, we recognize a group of all beech-covered microhabitats and the microhabitats F6 and F8 of beech-spruce stands with increased soil moisture and a high cover value of natural regeneration. On the lower right side, the oak-beech microhabitats with a high cover value of herbs and high mean maximum temperature were placed in a group. At the upper left side of the biplot, spruce-covered microhabitats with a high degree of canopy closure and cover value of moss were separated from the Douglas fir microhabitats with a high cover of grass and low soil moisture on the upper right side (D3, D4). The microhabitats D1 and D2 (Douglas fir, YS) were arranged between the left and right quadrant due to the high cover value of moss and grass with a patchy distribution.

Regarding species distribution pattern, four groups were obvious. At the upper left quadrant, species commonly known as coniferous forest species aggregated.. At the upper right quadrant, hygrophilous species grouped. The species group at the lower right and left quadrant of the biplot comprised character species of the TWINSPAN analysis, which are common in deciduous forests.

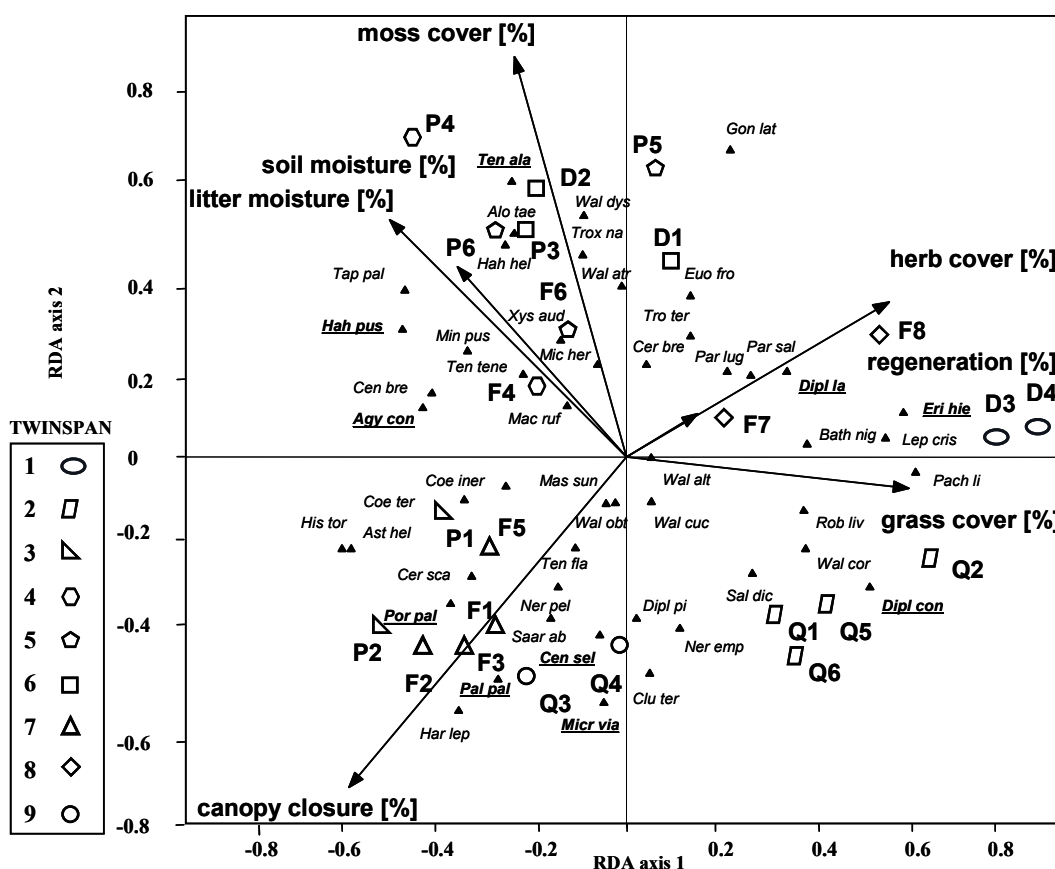


**Fig. 5** RDA ordination for the spring season (first and second axes). Species are represented by points to facilitate the readability of the graphic, environmental variables by arrows. Their relative length is directly proportional to the impact strength. The microhabitat types are named according to the covering tree species (P: spruce, D: Douglas fir, F: beech-spruce (beech: F1, F3, F5 and F7; spruce: F2, F4, F6 and F8) and Q: oak-beech). The site endgroups defined by TWINSpan are indicated as different symbols, the character species are underlined.

### Summer season

The multivariate analysis for the summer data set revealed a deviating pattern in the separation of microhabitats and species as has been documented by the TWINSpan analysis. Together, the first four PCA axes explained 60.7% of the variance of the species data and 76.4% of the variance of the correlations between

species and the environmental factors chosen in the RDA (Fig. 6). The first axis was mainly related to the cover of grass and herb, whereas much of the variance of the second axis was explained by the degree of canopy closure, the cover of moss, soil and litter moisture (Fig. 6 and Table 5). Under the fully developed foliage in summer, shadowed microhabitats separated from the more open sites.



**Fig. 6** RDA ordination for the summer season (first and second axes). Species are represented by points to facilitate the readability of the graphic, environmental variables by arrows. The microhabitat types are named according to the covering tree species (P: spruce, D: Douglas fir, F: beech-spruce (beech: F1, F3, F5 and F7; spruce: F2, F4, F6 and F8) and Q: oak-beech). The site endgroups defined by TWINSpan are indicated as different symbols (legend left), the character species are underlined.



Along with increasing moss cover and litter moisture the microhabitats of older spruce (P3–P6) and beech-spruce stands (F4 and F6) as well as the young Douglas fir (D1 and D2) grouped at the upper side of the biplot together with the species commonly known as coniferous species. The lower side of the biplot assembled microhabitats of beech (F1, F3, and F5), oak-beech (Q3 and Q4) and spruce (P1, P2 and F2) with a dense canopy closure on the left and separated them from oak-beech microhabitats (Q1, Q2, Q5 and Q6) with a high grass cover on the right side (Fig. 6).

Several species typically found in deciduous forests were arranged in the lower part of the biplot. At the upper right configured a microhabitat group with more open canopy closure and already established vegetation cover of shrub, herb, and grass. This group comprised microhabitats of the mature stands of Douglas fir (D3 and D4), and the mature stand with established regeneration of beech-spruce (F7 and F8) with the character species *D. concolor* and *E. hiemalis*, which were significantly enhanced by a high cover value of grass and herb.

## 2.5 Discussion

With 142 species, the investigation of temperate pure (spruce, Douglas fir) and mixed forests (beech-spruce, oak-beech) revealed a species-rich spider fauna, including rare species (e.g., *Monocephalus fuscipes*) and species recorded in the Red Data Book (Platen et al. 1998) of Bavaria and Germany (e.g., *Centromerus silvicola*, *Pardosa saltans*, *Pelecopsis elongata*). As has been described by several authors, a high number of species is attributed to a strong heterogeneity in habitat structure (e.g., Niemelä et al. 1996). The different stand types and age classes of the production forests generated a high variation of microhabitat conditions in the course of the seasons. Though the sampling scale of 4-wk intervals resulted in a certain averaging, the broad spectrum of microhabitats allowed us to detect specific responses of species to a variety of micro-environmental parameter gradients and it revealed a very sensitive segregation of spider assemblages. Many

species proved to be nonrandomly distributed and especially the Douglas fir and oak-beech stands provided some specific spider assemblages.

Affinities of spiders to habitat parameters have been described until now mostly at the level of stand types and forest vegetation communities (Martin 1987; Maurer and Hänggi 1990; Pearce et al. 2004; Oxbrough et al. 2006), but merely on that fine spatio-temporal scale. In our study was shown that environmental factors and thus species distribution changed within a stand on a fine temporal and spatial scale, as has been described for ground beetles (Antvogel and Bonn 2001; Niemelä et al. 1992), rove beetles (Pohl et al. 2007), and saprophagous soil invertebrates (Sharon et al. 2001; Aubert et al. 2003).

**Table 3**

Comparison of results obtained by PCA and RDA for the spring and summer data set: species environment coefficients for the first four axes.

Axis	1	2	3	4
Correlation coefficients				
Spring				
PCA	0.864	0.865	0.810	0.722
RDA	0.906	0.881	0.824	0.813
Correlation coefficients				
Summer				
PCA	0.805	0.776	0.760	0.719
RDA	0.870	0.837	0.822	0.873

The results of the DA confirmed a distinct characteristic influence of the stand type on the species distribution of spiders in forest ecosystems. Particularly in spring, the impact of the covering tree species was expressed by a high similarity of spider assemblages of microhabitats under spruce, Douglas fir, and beech or oak-beech, respectively. An intrinsic parameter of the tree species, affecting the composition of spider assemblages, was the evergreen or deciduous character of the stand type, determining the degree of foliation in spring. Among the strongest

environmental factors contributing to the explanation of spider species distribution was litter type, which is obviously correlated to tree species composition (stand type). But, since especially in mixed stands, deciduous litter was drifted by wind, the litter type of a microhabitat could differ from the covering tree species. Thus, similar litter types were characterized by similar species assemblages independent of the covering tree species (e.g., beech-spruce: MG F6 and F8).

The litter type is influencing the microhabitat conditions in a diverse way (Welke and Hope, 2005). It provides characteristic features, regarding humidity, pH, structural components, and the spectrum and availability of prey (Vargas 2000; Facelli and Pickett 1991). Many spider species live inside the litter layer using the interstitial space to build their horizontal webs or to escape unfavorable climatic conditions and predation (Topping 1993; Wagner et al. 2003). A strong influence of the deciduous litter cover on microhabitat selection of ground-dwelling spiders has already been postulated by several authors (Gunnarsson, 1990; Uetz 1991; Bultmann and Uetz 1984). As an example, deciduous leaf litter may be very important for lycosids as a place for drumming during mating. Uetz (1976) found in temperate deciduous forests that spider diversity and species richness were correlated with depth and interstitial volume of litter. Several species were also bound to the coniferous litter type. According to Jocque (1973), differences in litter type are accompanied by differences in the composition of the spider fauna.

But the intrinsic factors of the tree species spectrum covering the ground are not the exclusive environmental variables, which explained the small-scale distribution pattern of spider assemblages. Thus, the composition of the spider assemblage of a microhabitat was not strictly defined by the covering tree species (i.e., stand type) or the age class of forests. And even single species were barely restricted to a single tree species or stand type during the whole season.

**Table 4**

Impact strength of environmental variables selected by unrestricted permutation (single and cumulative contribution of variables in forward stepwise analysis) in the PCA and RDA for the spring data set (intra-set correlation).

	Explained variance %			Correlation coefficients			
	Single	Cumulative	p	Axis 1	Axis 2	Axis 3	Axis 4
Soil moisture	0.14	0.14	< 0.0002	- 0.67	0.08	- 0.12	0.19
Canopy closure	0.11	0.25	< 0.0021	- 0.34	- 0.47	0.14	- 0.24
Moss cover	0.12	0.35	< 0.0025	- 0.38	- 0.50	- 0.15	0.33
Gras cover	0.12	0.44	< 0.001	0.65	- 0.12	- 0.06	- 0.14
Natural regeneration	0.09	0.52	< 0.044	- 0.21	0.26	- 0.13	0.61
Herb cover	0.09	0.59	< 0.025	0.17	0.34	- 0.56	- 0.18
Mean temperature max	0.07	0.64	< 0.05	0.16	0.28	- 0.05	0.04

**Table 5**

Impact strength of environmental variables selected by unrestricted permutation (single and cumulative contribution of variables in forward stepwise analysis) in the PCA and RDA for the summer data set (intra-set correlation).

	Explained variance %			Correlation coefficients			
	Single	Cumulative	p	Axis 1	Axis 2	Axis 3	Axis 4
Canopy closure	0.12	0.12	< 0.001	0.55	- 0.11	0.29	0.55
Moss cover	0.13	0.25	< 0.001	- 0.24	- 0.51	- 0.40	- 0.44
Natural regeneration	0.12	0.37	< 0.001	0.27	0.38	- 0.38	- 0.51
Soil moisture	0.09	0.44	< 0.035	0.08	- 0.35	- 0.54	- 0.02
Litter moisture	0.11	0.50	< 0.06	0.30	- 0.49	- 0.34	- 0.45
Herb cover	0.07	0.55	< 0.05	- 0.39	0.14	- 0.17	- 0.06
Grass cover	0.08	0.59	< 0.06	- 0.36	0.36	0.21	0.13

Among the key habitat factors affecting the microhabitat distribution of spiders were abiotic parameters such as irradiation, temperature, air humidity, and water content of soil and litter, respectively. Those factors explained a great part of the species variation as determined by the discriminant, correlation and ordination (PCA, RDA) analyses. Strong gradients of these microspatial conditions became obvious during summer with the foliation of the deciduous trees and during fall with the fully developed ground vegetation. The impact of

those microhabitat parameters, which were not strictly attributed to the tree species itself increased during the growing season, while the covering tree species exerted its influence at all times. Several species showed additional or enhanced adhesions to grass, moss and herb vegetation later in the season.

Obviously, the conditions of several abiotic microhabitat parameters were affected by the degree of canopy closure, which is a result of the tree species specific crown architecture and silvicultural practice. Canopy closure has been regarded an important factor in forests, because it affects the microclimatic conditions of the lower forest strata in a diverse way (Lindh and Muir 2004). In our study it was proven to have a profound influence on the small-scale regime of climatic conditions at the forest floor. The degree of canopy closure was shown to be one important factor during all seasons, resulting in alterations of species composition of spider assemblages.

In our study, an increase in irradiation caused by a decrease of canopy closure was connected with a rise in temperature and air humidity. In spring soil temperature was a key habitat factor explaining the site classification in the TWINSpan analysis by DA. The effect of the temperature decreased with the overall rising temperature from spring to summer. Thus, the temperature characteristics of the summer season reflected no significant influence on the assemblage classification of microhabitat groupings anymore. Accordingly, we assume that the temperature conditions during summer season reached a satisfactory level for a number of forest species. Temperature and humidity have been shown to influence the abundance and distribution of spiders across habitats (Wise 1993; Riechert and Tracey 1975). The Spearman rank correlations revealed significant relations of spider species to air humidity during summer, while many species preferred dry microhabitats in spring, e.g. areas under deciduous trees.

The results also indicate that the composition and cover of ground vegetation, which are also affected by the degree of canopy closure (Hurd and Fagan 1992; Watt et al. 1997; Wilson and Puettmann 2007) and thus by forestry management (Schowalter et al. 2003; Khanina et al. 2007) were of major importance. This matches the findings of ter Braak (1987) and Ysnel and Canard (2000) who

derived close correlations between vegetation structure of the habitat and spider assemblages. The share of herbs and grasses covering the ground contributed in this study significantly to the explanation of the variance (DA, RDA, Spearman rank correlations) in species composition, regardless of the covering tree species of the microhabitat groupings. The ground vegetation aspect expressed strong effects on the distribution of several species at all times, but it increased from spring to autumn ( $P < 0.01$ ) reflecting a seasonal shifting key factor (Hatley and Macmahon 1980; Niemelä et al. 1994).

The same applied to moss vegetation, especially during spring and summer. Huhta (1971) described the vertical assembly of several linyphiid spiders in moss habitats, occupying different interstitial spaces and using vertically arranged net constructions. This niche occupation was often promoted by humid conditions within the moss layer and even in the litter layer below.

Moreover, in spring, many species seem to adapt to the portion of natural regeneration (i.e., shrub layer), which offers possible protection from predation (Gunnarsson 1996). This applies in our study in spring, probably also for the grass cover remaining from the previous year. Thus, several species were associated to those grass patches (Fig. 5 and 6), indicating a relationship between the spider species spectrum and the structure of plant communities, as suggested by Southwood et al. (1979) and Gunnarsson (1990).

Structural heterogeneity due to vegetation parameters may also influence spider communities indirectly by its positive effect on prey densities. For instance, herbivorous invertebrates reach higher densities in structurally more diverse habitats because they benefit from the greater variety of food resources themselves (Harmon et al. 2003; Siira-Pietikainen et al. 2003; Crist et al. 2006). The development of a diverse vegetation structure might, besides giving rise to beneficial environmental conditions, increase the niche differentiation (Greenstone 1984; Dennis et al. 1998).

## 2.6 Conclusions

The aim of managing forest ecosystems sustainably without knowing the reaction of species to habitat formation can lead to a considerable loss of diversity and ecological stability. Recent examples of the susceptibility of forests to insect calamities are large-scale monocultures of spruce on inadequate sites in Europe.

Our results document that in production forests the composition of spider assemblages varies not only between stand types but also within a forest ecosystem due to the small-scale mosaic of environmental parameters along with the seasons.

Confirming our expectations, the most important environmental parameters affecting the small-scale distribution of spider species and spider assemblages along with the seasons comprised intrinsic factors of the covering tree species (like the litter type, deciduous or coniferous tree type) and factors not strictly attributed to the tree species itself (like canopy closure, vegetation, and microclimatic parameters). Those results confirm the influence of forestry practice on the composition of the soil-dwelling spider community – beside the selection of the tree species. Thus, we conclude that forest management, resulting in a shift of environmental key factors such as light, moisture, temperature, and ground vegetation cause substantial changes in surface dwelling spider assemblages. In production forests, these changes are generated by alterations of the degree of canopy closure by thinning or variation of the tree species spectrum. As a consequence, identical stand types most likely differ in the composition and distribution pattern of spider assemblages, when environmental key factors care for varied microhabitat conditions. On the other hand, different stand types may correspond in their spider community if they comprise of the same microhabitat pattern.

Further investigations have to show if impacts on the functionality of spiders on the level of the forest ecosystem are likely to occur as a consequence of altered microspatial environmental gradients. Nevertheless, the investigation on small-

scale spider distribution enhances the understanding of species requirements to habitat factors since the ecology of several spider species in forests is still not well understood. Moreover, our results on spiders are likely to assume that the composition of further functional guilds and indicator taxa may show correlations to small-scale environmental conditions of a forest stand (e.g., Taylor and Doran 2001; Grand and Mello 2004; Buddle et al. 2006; Pihlaja et al. 2006) and react with community alterations on human-induced habitat changes (see Charnley et al. 2007; Pohl et al. 2007).

Considering conservation aspects, given heterogeneity in forests due to small spatial scale gradients of environmental parameters along with the seasons will promote species diversity. This applies particularly for taxa like spiders that are not strictly bound to tree species like many herbivorous insects. Thus, sustainable forestry practice plays an important role for maintaining biodiversity.



	Stand type																							
	Douglas fir ( <i>P. menziesii</i> )				Spruce ( <i>Picea abies</i> )						beech-spruce ( <i>Fagus sylv. – Picea abies</i> )								Oak-beech ( <i>Quercus r.-Fagus sylv.</i> )					
	YS <sup>a</sup>		MR <sup>a</sup>		YS <sup>a</sup>		MS <sup>a</sup>		MR <sup>a</sup>		YS <sup>a</sup>		MS <sup>a</sup>		MR <sup>a</sup>		eMR <sup>a</sup>		YS <sup>a</sup>		MR <sup>a</sup>		eMR <sup>a</sup>	
	D1 <sup>b</sup>	D2 <sup>b</sup>	D3 <sup>b</sup>	D4 <sup>b</sup>	P1 <sup>b</sup>	P2 <sup>b</sup>	P3 <sup>b</sup>	P4 <sup>b</sup>	P5 <sup>b</sup>	P6 <sup>b</sup>	F1 <sup>b</sup>	F2 <sup>b</sup>	F3 <sup>b</sup>	F4 <sup>b</sup>	F5 <sup>b</sup>	F6 <sup>b</sup>	F7 <sup>b</sup>	F8 <sup>b</sup>	Q1 <sup>b</sup>	Q2 <sup>b</sup>	Q3 <sup>b</sup>	Q4 <sup>b</sup>	Q5 <sup>b</sup>	Q6 <sup>b</sup>
<b>Spring</b>																								
Soil moisture	31.38	30.74	26.10	25.28	31.28	35.67	38.32	38.11	38.32	42.93	33.67	36.51	33.29	34.31	39.15	42.80	39.77	38.51	28.84	32.78	33.69	37.67	29.97	28.67
Canopy closure	46.25	42.50	40.00	40.00	78.50	69.00	50.00	52.50	38.50	50.00	45.00	67.50	42.50	45.00	40.00	49.00	31.25	41.25	41.25	30.00	38.75	35.00	44.00	38.75
Moss cover	75.00	97.50	21.25	8.75	3.75	18.75	60.00	71.25	57.50	81.25	0.00	6.25	7.50	43.75	2.50	43.75	16.25	20.00	0.00	0.00	2.50	2.50	2.50	0.00
Old grass cover	3.50	7.50	48.75	20.00	0.00	1.25	6.25	0.00	18.75	2.50	0.00	0.00	0.00	0.00	23.75	1.25	0.00	2.50	11.25	35.00	1.25	30.00	11.25	2.50
Regeneration	0.00	0.00	0.00	0.00	0.00	0.00	1.25	0.00	11.25	6.25	0.00	0.00	17.50	21.25	23.75	15.00	76.25	53.75	5.00	3.75	10.00	5.00	6.25	0.00
Herb cover	8.75	21.25	15.00	27.50	3.75	3.75	7.50	7.50	28.75	16.25	0.00	1.25	13.75	7.50	13.75	35.00	7.50	20.00	26.25	22.50	67.50	46.25	6.25	3.75
Temperature	6.92	6.46	7.41	7.78	6.49	6.63	7.04	6.86	7.18	7.00	7.19	6.33	7.00	7.08	7.53	10.10	8.04	8.33	8.25	8.54	8.30	8.03	7.46	7.66
<b>Summer</b>																								
Canopy closure	46.00	43.75	38.50	38.00	69.25	78.75	50.00	52.50	39.00	49.25	75.00	77.50	70.75	53.75	64.50	49.50	45.00	37.50	64.00	54.25	76.25	65.75	59.50	58.75
Moss cover	75.00	97.50	21.25	8.75	18.75	3.75	90.00	97.50	75.00	87.50	0.00	6.25	7.50	62.50	2.50	55.00	16.25	20.00	0.00	0.00	2.50	2.50	2.50	0.00
Regeneration	0.00	0.00	0.00	0.00	0.00	0.00	1.25	0.00	11.25	5.00	0.00	0.00	22.50	15.00	23.75	11.25	75.00	53.75	5.00	3.75	10.00	5.00	6.25	0.00
Soil moisture	41.70	38.56	33.69	37.67	51.93	48.45	40.03	52.61	47.16	40.42	47.13	41.52	34.65	33.85	51.43	43.55	45.02	52.06	31.65	33.00	34.16	32.64	32.04	32.58
Litter moisture	60.27	69.06	57.95	54.71	65.31	62.85	64.19	67.52	68.86	67.59	58.23	60.47	65.25	64.83	69.55	70.35	67.83	61.50	55.99	46.91	52.95	60.08	55.88	63.43
Herb cover	8.75	21.25	21.25	63.75	3.75	3.75	7.50	7.50	31.25	18.75	0.00	1.25	12.50	7.50	13.75	22.50	7.50	20.00	8.75	17.50	7.50	8.75	6.25	3.75
Grass cover	3.50	7.50	48.75	20.00	1.25	0.00	6.25	0.00	16.25	2.50	0.00	0.00	0.00	0.00	23.75	2.50	0.00	5.00	11.25	31.25	1.25	30.00	11.25	2.50
<b>Spring</b>																								
Soil moisture						1																		
Canopy closure					-0.028			1																
Moss cover					0.194		0.2				1													
Old grass cover					-0.131						-0.145			1										
Regeneration					.310**						-0.009			-0.02				1						
Herb cover					-0.066						0.061		.361**			.363**					1			
Temperature max					0.065								.291**			.422**					.444**			1
<b>Summer</b>																								
Canopy closure						1																		
Moss cover								1																
Regeneration													1											
Soil moisture																								
Litter moisture																								
Herb cover																								
Grass cover																								

Sign. corr. \*p &lt; 0.05; \*\*p &lt; 0.01.

<sup>a</sup> Age class.<sup>b</sup> Microhabitat.

Table 6  
Environmental parameters of microhabitats for spring and summer and relations of habitat parameters (i.e. spearman rank correlations of all 96 pitfall trap data)

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### **3 Microhabitat heterogeneity in temperate forests: Is distance to stems affecting ground-dwelling spider communities?**

#### **3.1 Abstract**

Spiders contribute essentially to the arthropod community of forests and are known to be distributed in non-random pattern according to environmental, structural, competitive, and predacious conditions. The aim of the study was to investigate the effects of the distance to trees on the distribution pattern of soil-dwelling spiders. We verified the hypothesis that stem-close and stem-distant microhabitats differ with respect to taxonomical and ecological characteristics of spider assemblages, hence, functional performance in forest communities.

Ground-dwelling spiders were collected with pitfall traps in positions close (20-30 cm) and distant (2 m) to the stem bases in mature forests of different stand types (spruce, Douglas fir, beech-spruce, oak-beech). To identify significant drivers of spider assemblage composition, environmental parameters were assessed in relation with the arrangement of pitfall traps.

The study documented significant variability in the composition of spider assemblages of stem-close and stem-distant pitfall traps within each of the study sites. The position of traps strongly affected species richness, species composition, activity density, and dominance structure. Thus, the sampling at both positions revealed a number of spider species with spatial restriction. Moreover, spider assemblage structure differed in the classification of species to size and ecological preference. Those results implicate potential consequences for their functional role in forests in relation to the distance to the trees.

**Keywords:** Araneae, Beech-spruce, Douglas fir, Forest ecosystems, Oak-beech, Pitfall traps, Small-scale distribution, Spruce.

**Nomenclature** for spiders: Platnick (2011)

### 3.2 Introduction

Temperate forests provide habitat for a considerable number of arthropods due to a wide variety of spatio-temporal heterogeneity and the complexity of their environments (Langellotto and Denno 2004; Oxbrough et al. 2005). There is evidence that a number of species of diverse arthropod taxa are non-randomly dispersed at the forest floor following microclimatic and structural habitat conditions (e.g., ground beetles, spiders or rove beetles: Niemelä et al. 1996; Bonn and Schröder 2001; Ziesche and Roth 2008). It is widely postulated in this context that the tessellated habitat structure of a forest ecosystem cares for increased ecological niche differentiation, and thus, for a heterogeneous patchy distribution of the species (Begon et al. 1996).

Spiders are commonly used as indicators of habitat quality, as the small-scale distribution of species is determined by strictly defined ecological requirements and the given properties and gradients of environmental habitat parameters (Churchill and Arthur 1999; Legendre et al. 2002). Species are known to follow distinct environmental conditions provided by the structure and cover of vegetation, litter layer, temperature, humidity, or light intensity (Wise 1993). Beside the preference for beneficial structural and microclimatic conditions, there is evidence that microhabitat selection is affected by the size or diversity of a community (Marshall and Rypstra 1999) as well as by food availability (Wagner and Wise 1997; Toft and Wise 1999). In addition, there is often a shift of habitat utilization caused by changing requirements of the species due to seasonality, reproduction, or life cycles (Hendrickx and Maelfait 2003; Berg and Bengtsson 2007). Hence, microhabitat heterogeneity and its spatial and temporal dynamic play an important role in determining the local spider distribution pattern, as well as the closely related population and ecosystem processes (Tilman and Kareiva 1997; Leibold et al. 2004). Basic knowledge about the small-scale distribution of species is, thus, essential for the understanding of the functional role of arthropods (Niemelä et al. 1996), their relevance for habitat suitability analyses, biodiversity assessment, and the effects of forest management. In addition, the non-random

distribution of species on a small spatial scale is likely to determine the experimental design for any quantitative approach to community structure and population dynamic analysis, and is thus a prerequisite for data quality in ecological research (Dajoz 2000).

At the forest floor, the spatial arrangement of diverse microhabitats is primarily affected by the arrangement and habitus of trees, due to variation in canopy closure, and thus, the incidence of light as well as interrelated microclimatic parameters. It has also been recognized that the activity of diverse herbivorous communities in the crown strata is likely to initiate effects on the floor below (Parker et al. 1989), combined with correlated differences in microbiological activity and soil macrofauna (Scheu and Poser 1996, Prescott 2002). No knowledge exists about the effects of this spatial pattern on soil-dwelling predatory arthropods. A difference in the composition of species assemblages close and distant to the stem may affect the role of spiders as regulators of detritivorous food webs and as natural enemies of herbivorous pest species (Wise 1993; Dajoz 2000), because herbivores often show a close relationship to the area adjacent to the stems (e. g. defoliators with soil dwelling developmental stages; Majunke et al. 1999).

Therefore, our study focuses on whether the composition of ground-dwelling spider communities is affected by the distance to the trees. The main research questions are: (i) Are spider activity density and species richness affected by the distance to tree? (ii) Which are the main environmental factors explaining tree distance-related differences in species distribution? (iii) Is the effect of tree distance on the assemblage of spider species influenced by the tree species?

### **3.3 Materials and Methods**

#### **Study sites**

The investigation was conducted in a historically well-forested region of South Germany (48°19′/11°06′; Central Bavaria). We studied four mature stands (size 1

ha; Table 1) of different tree species composition: pure stand of spruce (*Picea abies*) and Douglas fir (*Pseudotsuga menziesii*), as well as mixed stand of beech-spruce (*Fagus sylvatica*, *Picea abies*) and oak-beech (*Quercus robur*, *Fagus sylvatica*). The forest stands were similar in age class, soil parameters, climatic conditions, landscape features, and number of mature trees. The region is predominantly characterized by sub-Atlantic climate with mean annual temperatures of 7.5 °C to 8.0 °C. Mean annual precipitation ranges between 700 and 900 mm. The soils developed on these sites are fertile brown and parabraun earths. They originate from sediments of the Upper Miocene, overlaid by a fine, more or less mighty loam layer, which is derived from loess loam. The distance between the four stands covered approximately 20 km.

At the center of each stand, a study site with a size of 50 m x 50 m was established, which was representative for the stand type with respect to tree size and stem interspace (Fig. 1). In order to avoid neighboring effects, each study site was surrounded by a belt (>25 m) of the same stand type and, beyond that, by further woodlands.

### **Sampling design**

We collected ground-dwelling spiders by pitfall trapping (Spence and Niemelä 1994). Pitfall traps could have two trap positions: either (i) close to the stem base (in the following named – stem-close: 20-30 cm distance to trees), or (ii) at a maximum distance between surrounding stems (stem-distant: 2 m average distance to trees). Overall, 4 trap pairs, each consisting of one stem-distant and one stem-close pitfall trap, were arranged on each site, resulting in 8 pitfall traps per study site. The distance between the traps of a pair averaged 5 to 7 m, the distance between the trap pairs at least 20 m (Fig. 1). The selection of the trees, regarding the position of stem-close and stem-distant traps, was based on random selection, although sampled trees had to be similar in height and stem diameter ( $\varnothing=36-61$  cm at ground level,  $\varnothing=36-43$  cm at 2 m above the floor level).

All pitfall traps (glass cup,  $\varnothing=7.5$  cm) contained a solution of saturated benzoic acid with detergent as preservative agent. Sampling was carried out between 12 April and 22 October in 2002, and the traps were emptied every 4-wk. The determination of spider species followed the identification keys of Wiehle (1956, 1960), Roberts (1985, 1987, 1998), and Heimer and Nentwig (1991), Nentwig et al. (2003). The ecological characterization was based on Martin (1991), and Maurer and Hänggi (1990). The nomenclature of spiders followed Platnick (2011).

### **Environmental variables**

Nine environmental parameters were surveyed during the investigation period. Soil surface temperature was measured continuously every 45 min at each pitfall trap (1 cm in the litter layer above the mineral soil) using a data logger (Tinytalk II/TK-0023, Spectra Computersysteme, Leinfelden-Echterdingen). The depth of the litter layer above the mineral soil was measured every 4 weeks at four randomly chosen locations around each trap to estimate mean thickness. Soil and litter samples for the determination of water content (Scheffer and Schachtschnabel 1992) and pH (H<sub>2</sub>O) were taken in the spring (9 April), summer (30 July), and fall (24 September) within a radius of 0.8 m around each trap (n=4-6). The degree of canopy closure, the cover value of natural regeneration, herb, grass, and moss were assessed according to Braun-Blanquet (Mühlenberg 1989) around each trap following the 4-wk intervals of pitfall trap sampling.

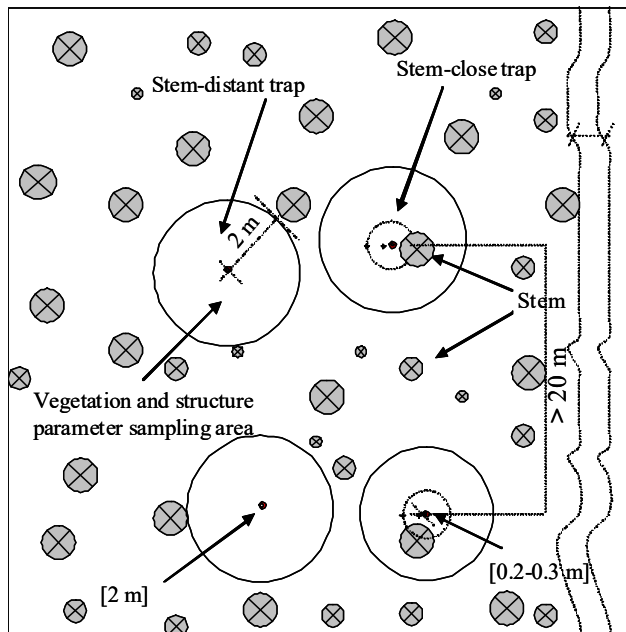
### **Statistical analyses**

A paired Mann-Whitney-*U* test (Wilcoxon) was applied to evaluate the effect of trap position on species and individual numbers. Ecological preferences of the species, the proportional abundance of families, and the distribution of size classes were used by site (Maurer and Hänggi 1990; Heimer and Nentwig 1991; Platen et al. 1999).

Permutational multivariate analysis of variance (PERMANOVA, Anderson 2001) based on Bray-Curtis dissimilarities (Bray and Curtis 1957) of square-root transformed data (32 samples and 52 variables) was used to estimate the relevance of trap position for the composition of spider assemblages (Anderson 2004). We used square-root transformation to lessen the influence of prevalent species and to increase the weight of rare species. The DISTLIM extension of the PERMANOVA package (distance-based multivariate analysis for a linear model; McArdle and Anderson 2001) was used to analyze environmental factors associated with trap position and controlling for the factor site, because the extension accommodates within-subject design. Differences in species assemblages of stem-close and stem-distant samplings were visualized by DCA (Hill 1979) using CANOCO 4.5 software (Leps and Smilauer 2003).

In order to detect effects of trap position on the species composition of spiders, TWINSpan analysis (Hill 1979) was carried out. This ordination method is a useful technique for the classification of species assemblages. It classifies trap position (site specific trap position end groups, SSTP) as well as species into groups (species end groups, SG). For each dichotomous site division, the ordination assigns differential species, as shown in the dendrogram in the header (Fig. 6). For each site, the catch results of the stem-close pitfall traps of two randomly chosen pairs were pooled to create two stem-close groups; likewise, the stem-distant trap data of the same pairs were pooled to create two stem-distant groups. Regarding the difficulties of interpretation of pitfall trap catches, we therefore worked only with relative abundance data. For this analysis, we included only species with >2 individuals in the total catch. Subsequently, with the same data base, an Indicator Species Analysis (Dufréne and Legendre 1997) was performed to classify the data set of spider species according to their indicator value for trap position and SSTP.

A Canonical Correspondence Analysis (CCA) was conducted to display associations of environmental conditions and species distribution, using the pooled data of the TWINSpan analysis. Statistical analyses were performed using the software CANOCO 4.5 (CCA) and PCORD 4.5 (IndVal).



**Fig. 1** Placement of pitfall traps at a study site. Stem-close: pitfall trap near stem (0.2-0.3 m); Stem-distant: pitfall trap distant to stem (2 m). At a site in total 4 trap pairs were placed, here only half of them are depicted.

**Table 1**

Characteristics of the studied forest sites.

Stand	Spruce	Douglas fir	Beech-spruce	Oak-beech
Stand structure	Pure stand	Pure stand	Mixed stand	Mixed stand
Tree species	<i>Picea abies</i>	<i>Pseudotsuga menziesii</i>	<i>Fagus sylvatica</i> / <i>Picea abies</i>	<i>Quercus robur</i> / <i>Fagus sylvatica</i>
Stand age (y)	62	83	73	75
Canopy closure in summer (%)	50-53	38-43	58-69 49-50	76-83
Trees / ha (n)	680	314	618	1564
Medium height (m)	26-28	37-39	29-31	32-33
Vegetation cover (%)	10.6	86.9	10.1	23.8

### 3.4 Results

#### Small-scale distribution pattern

A total of 3440 adult and 2164 juvenile spiders were collected representing 92 species. The spider community of all study sites was numerically dominated by Linyphiidae, Hahniidae, Amaurobiidae, Tetragnathidae, Dysderidae and, to a lower extent, by diurnal running spiders (Lycosidae).

Except for the pure Douglas fir stand with an outstandingly high number of species (58) and individuals (1799), the spider communities of the study sites comprised similar numbers of species (spruce: 42, beech-spruce: 46, oak-beech: 45) and individuals (spruce: 442, beech-spruce: 606, oak-beech: 593). The same applied to the total catch result of all stem-distant (1788 specimen, 73 species) and stem-close (1652 specimen, 66 species) pitfall traps. However, within the sites, spatial differences in species composition due to trap position were obvious. Compared to stem-distant traps, the number of species in the stem-close traps was significantly higher for Douglas fir and significantly lower for beech-spruce (Table 2). In addition, the count of spiders of the stem-close traps was significantly lower for pure spruce and beech-spruce, whereas the relative abundance did not differ considerably according to trap position within oak-beech and Douglas fir (Table 2).



**Table 2**

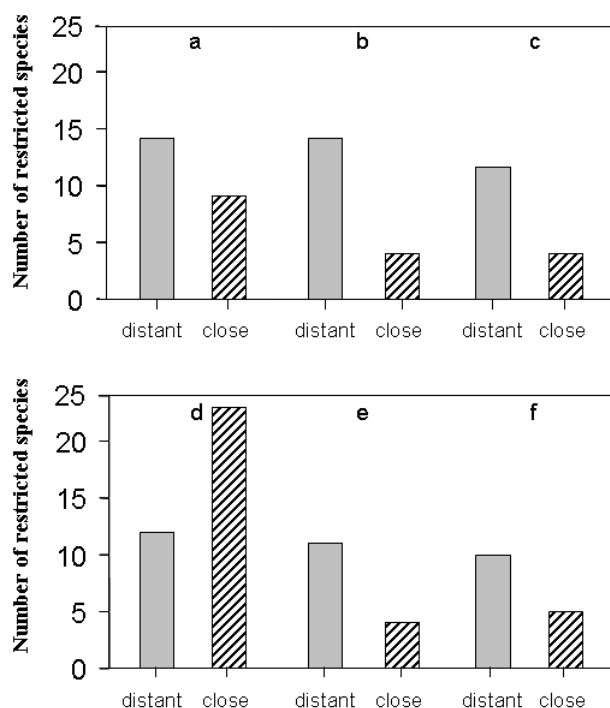
Number of species and adult specimens caught in stem-distant and stem-close pitfall traps by study sites. The letters A and B indicate significant difference [Man-Whitney  $U$  (Wilcoxon) Test;  $P < 0.05$ ].

	Species			Individuals		
	Stem-distant	Stem-close	$P$	Stem-distant	Stem-close	$P$
Spruce	16.51 + 1.29	14.03 + 3.74	0.243	63.75 + 7.91	46.75 + 17.7	0.021*
Douglas fir	21.01 + 2.03	26.01 + 1.63	0.025*	222.5 + 26.5	227.3 + 61.3	0.767
Beech-spruce	18.75 + 2.87	14.52 + 2.88	0.018*	83.75 + 14.1	67.75 + 23.7	0.028*
Oak-beech	20.25 + 2.63	18.25 + 1.71	0.304	77.01 + 13.1	71.25 + 8.05	0.243

A good indicator for differences in spider assemblage composition was the restriction of species with respect to the trap position. These effects were obvious for each study site (Fig. 2). In spruce, beech-spruce, and oak-beech, the number of species only present in the stem-distant pitfall traps was significantly higher compared to stem-close traps. The Douglas fir stand revealed the opposite pattern.

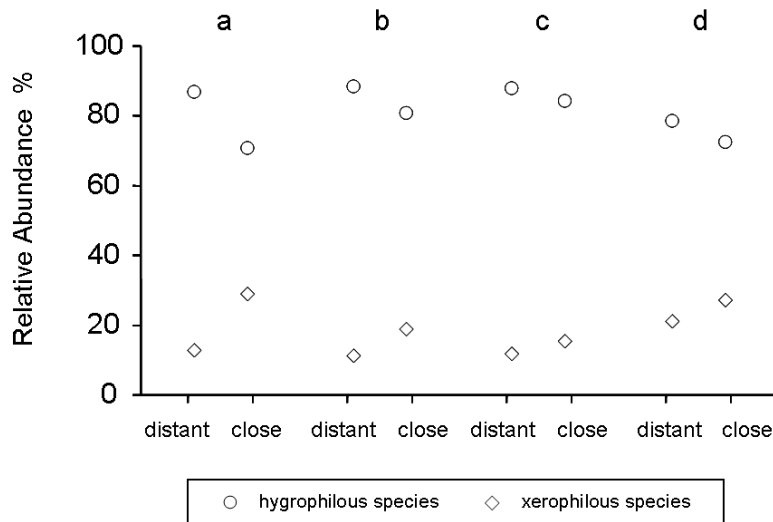
PERMANOVA revealed marked differences between species assemblages of the sites ( $F_{1,3} = 5.57$ ,  $P = 0.0001$ ). Spider assemblages of the oak-beech site were significantly different from the spruce site ( $P = 0.049$ ) and the Douglas fir site ( $P = 0.0291$ ). Deviations were also significant for beech-spruce and spruce ( $P = 0.0255$ ), or beech-spruce and Douglas fir ( $P = 0.0441$ ).

The composition of spider communities differed highly significantly with regard to trap position in stand types overall ( $F_{1,3} = 20.24$ ,  $P = 0.0001$ ). Beside deviation in spider species assemblages of coniferous from deciduous stands (Fig. 8), catches of stem-close pitfall traps distinguished from stem-distant ones in sites. Deviations in spider species composition of trap positions were also confirmed by an analysis based on paired data within each site showing significant variation in spruce ( $F_{1,6} = 2.42$ ,  $P = 0.031$ ), Douglas fir ( $F_{1,6} = 3.84$ ,  $P = 0.014$ ), and oak-beech ( $F_{1,6} = 2.95$ ,  $P = 0.032$ ). Results were not significant for the beech-spruce stand ( $F_{1,6} = 1.95$ ,  $P = 0.088$ ).



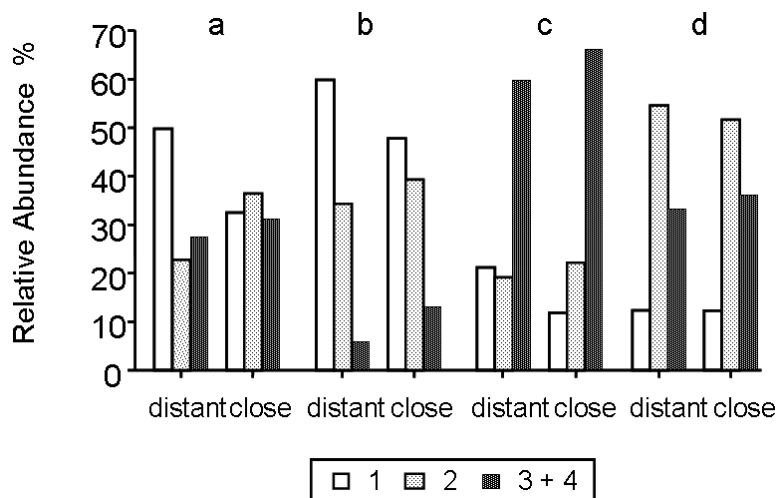
**Fig. 2** Number of spider species restricted to stem-distant and stem-close pitfall traps by tree species: (a) spruce, (b) spruce (in beech-spruce), (c) beech (in beech-spruce), (d) Douglas fir, (e) oak (in oak-beech), (f) beech (in oak-beech).

The classification of species according to their ecological preferences revealed, on all study sites, a higher proportion of xerophilous species in stem-close pitfall traps and a higher proportion of hygrophilous species in stem-distant ones (Fig. 3, not significant). The spider community was dominated in the Douglas fir stand by small-sized (1-2 mm), in the beech-spruce stand by bigger-sized (3.4–8 mm), and in oak-beech stand by intermediate-sized (2.1–3.3 mm) species (Fig. 4). Differences in spider size class proportion of trap position were obvious for spruce, Douglas fir, and beech-spruce, with a higher share of bigger-sized species close to the stem (Fig. 4).

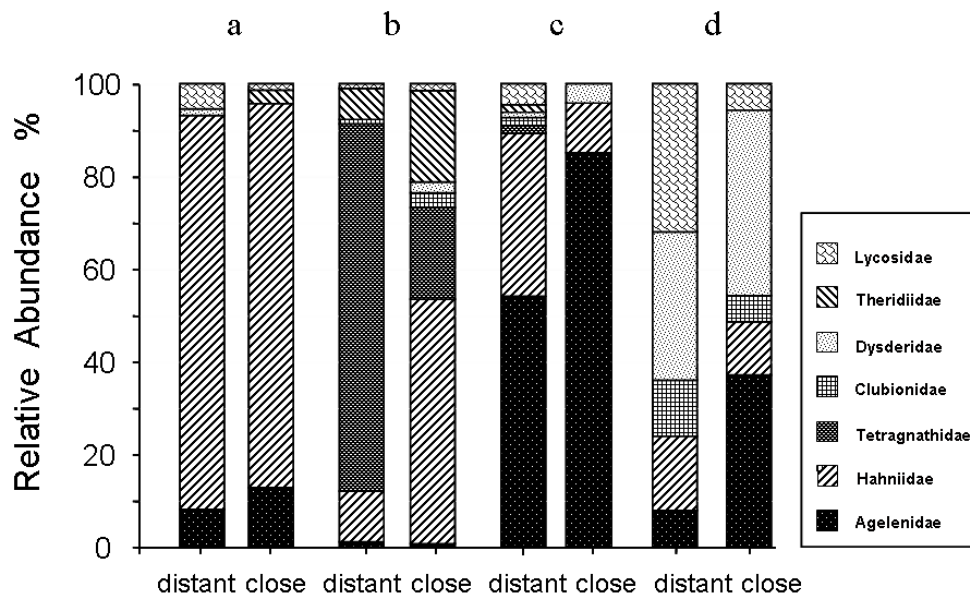


**Fig. 3** Distribution of spiders according to their ecological preferences (Maurer and Hänggi 1990) in stem-distant and stem-close pitfall traps by study site: (a) spruce, (b) Douglas fir, (c) beech-spruce, (d) oak-beech.

Preferences for trap position became obvious on the taxonomic level of spider families (Fig. 5). Thus, in spruce, beech-spruce and oak-beech, Agelenidae preferred stem-close positions, whereas the Lycosidae dominated in stem-distant traps. In the Douglas fir stand, Tetragnathidae were significantly more numerous in stem-distant traps, whereas the Hahniidae were more abundant in stem-close ones. Only the Linyphiidae and Amaurobiidae appeared evenly distributed at the forest floor of the sites in terms of individual numbers.



**Fig. 4** Relative abundance of spider species of different sizes (size class 1=1–2 mm; 2=2.1–3.3 mm; 3=3.4–4.7 mm; 4=4.8–8 mm) in stem-close and stem-distant pitfall traps by study sites: (a) spruce, (b) Douglas fir, (c) beech-spruce, (d) oak-beech stands.



**Fig. 5** Relative abundance of spider families in stem-distant (2.0 m) and stem-close (0.2–0.3 m) traps at the sites: (a) spruce, (b) Douglas fir, (c) beech-spruce, (d) oak-beech. *Linyphiidae* and *Amaurobiidae* were excluded because they exhibited similar proportions everywhere.

The TWINSPLAN analysis of spider assemblages of trap position of stand types defined 8 site-specific trap position end groups (Fig. 6, SSTP) and 14 species end groups (SG). The species distribution differentiated clearly between the stand type and the trap position, and accordingly, the composition of spider assemblage of SSTP segregated. Apart from eurytopic species (species end group 3), which were present in almost every stand type, numerous stenotopic species are predominantly present in stand types and/or trap positions. For the first, second, and third levels, the arrangement of SSTP referred significantly to the respective stand type covering the ground. Thus, stem-close and stem-distant traps of the same tree species were grouped together: Douglas fir (SSTP: 7, 8; SG: 10, 11, 12, 13, 14), oak-beech (SSTP: 1, 2; SG: 1, 2, 13, 14), beech-spruce (SSTP: 3, 4; SG: 4, 7) and spruce stand (SSTP: 5, 6; SG: 5, 9). Representatives of the Douglas fir stand were predominantly hygrophilous forest species, whereas catch results of the oak-beech stand comprised several xerophilous species. Finally, further analysis revealed separated species composition at the stem-close and stem-distant positions within each stand type. The analysis identified single differential species for the division separating trap positions at each stand (dendrogram in Fig. 6: e.g., stem distant traps: *Clubiona terrestris* for oak-beech, *Palliduphantes pallidus* for beech-spruce, *Hahnia helveola* or *Troxochrus nasutus* for spruce, and *Ceratinella brevis* for Douglas fir).

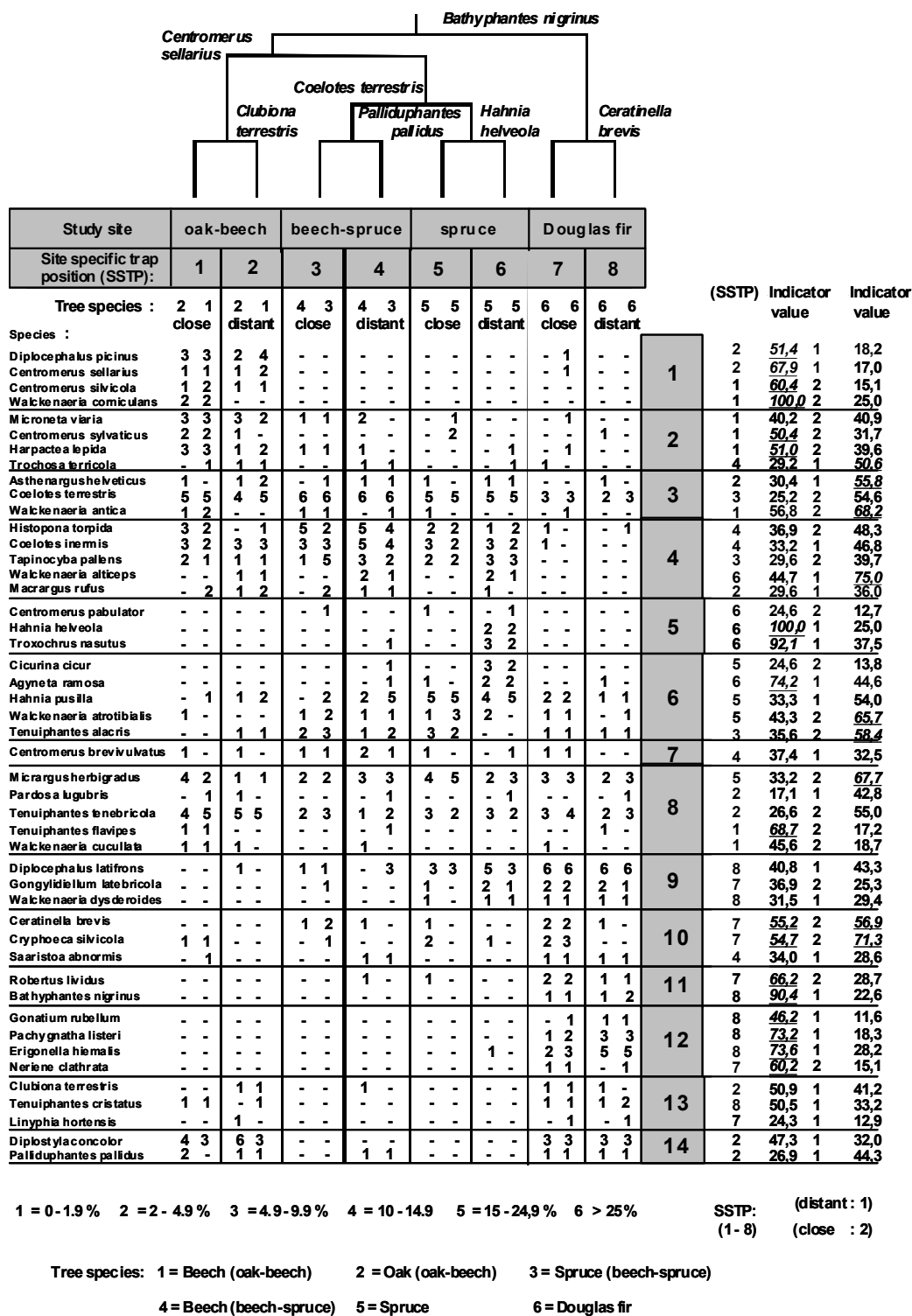


Fig. 6 TWINSpan classification of spider assemblages. The dendrogram indicates the separation by trap position and by stand type. The separation of site-specific trap position end groups (SSTP: 1–8) is given in gray boxes at the top. The separation of species end groups (SG: 1–14) is given in gray box at the right. The relative frequency of each species is indicated by numbers from 1 to 6. Indicator values (to the right) for site specific trap position (1–8) and trap position (stem–distant: 1; stem–close: 2). Indicator species for the separations are given in italics beneath the dendrogram.

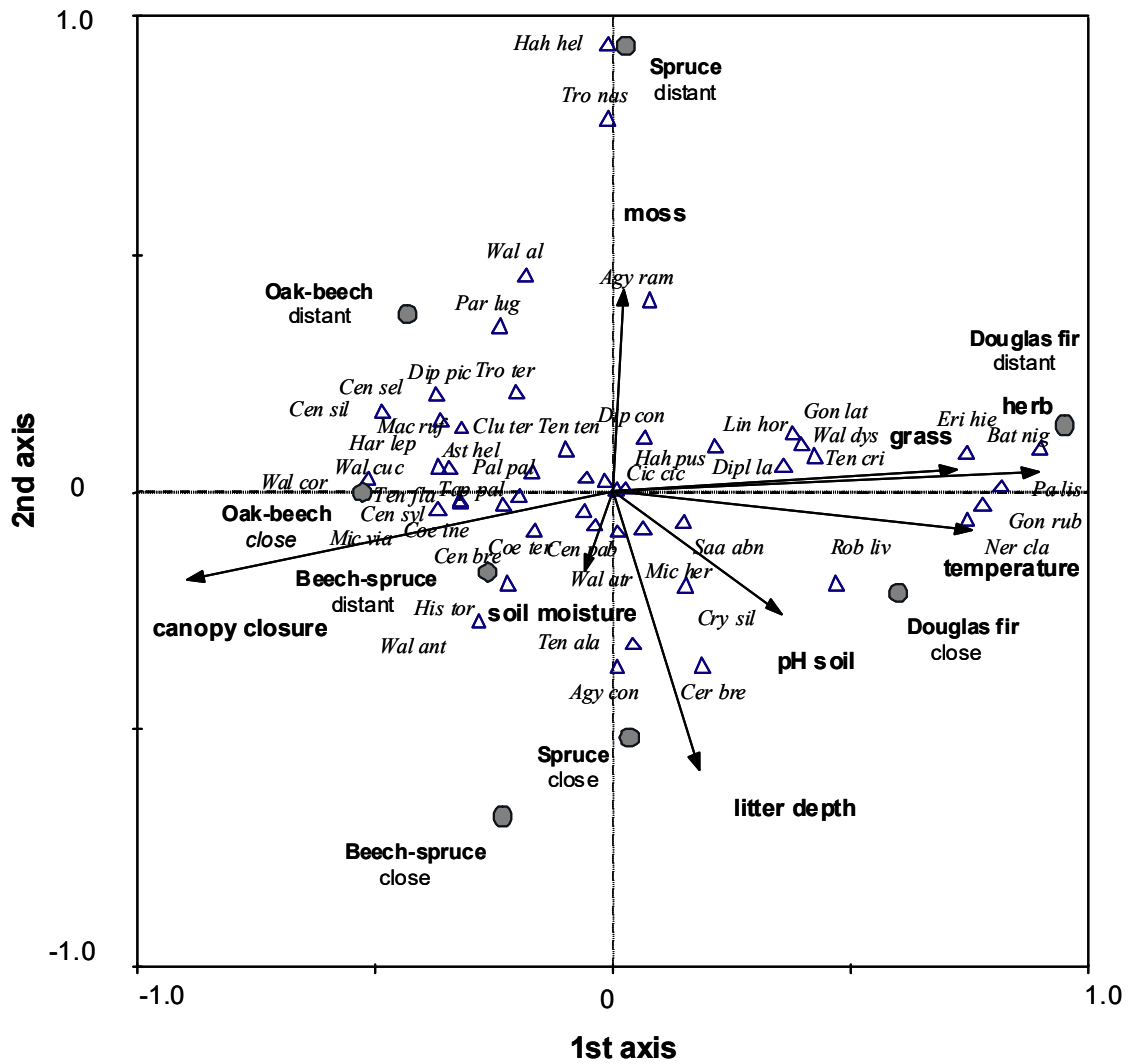
Comparing catches of all stands, singleton species showed a non-uniform distribution with regard to their occurrence at stands and/or trap positions. This was reflected in the presence or relative frequency of single species (e.g., oak-beech: *Walckenaeria corniculans*, *Centromerus sylvaticus*, *Harpactea lepida*; beech-spruce: *Trochosa terricola*, *Walckenaeria antica*, *Walckenaeria alticeps*; spruce: *Walckenaeria alticeps*, *Cicurina cicur*, *Agyneta ramosa*, *Tenuiphantes alacris*; Douglas fir: *Centromerus brevivulvatus*, *Cryphoeca silvicola*).

Several species obtained high indicator values (Fig. 6), documenting a preference for stem-distant (*W. alticeps*, *Asthenargus helveticus*, *T. terricola*, *P. pallidus*) or stem-close (*W. antica*, *Hahnina pusilla*, *Walckenaeria atrotibialis*, *T. alacris*, *Micrargus herbigradus*, *C. silvicola*, *Coelotes terrestris*) traps. According to TWINSpan analysis, the occurrence of 5 spider species was almost restricted to stem-distant pitfall traps. In a total of 25 species, a high indicator value to stem-distant pitfall traps was observed (Fig. 6). Four species were restricted to stem-close pitfall traps and, in total, 19 species showed a high indicator value to stem-close traps (Fig. 6). In addition, single species groupings were predominantly collected in stem-distant (SG 5) or stem-close traps (SG 10).

### **Environmental habitat parameters**

The investigation of environmental parameters showed considerable variation according to the trap position in sites (Fig. 7). The litter depth in spruce, Douglas fir, and beech-spruce, as well as the degree of canopy closure of all stand types, was higher at stem-close traps (Fig. 7). Moreover, the soil moisture at stem-close traps exceeded those at the stem-distant ones, with the exception of the spruce stand. The vegetation cover was considerably lower at stem-close traps except for the grass cover of Douglas fir. Besides, in coniferous stands, the temperature at stem-close traps was higher, whereas the opposite pattern was obvious for deciduous stands. According to the results of CCA (Fig. 7) and DCA (Fig. 8),

environmental conditions were attributed to the stand type as well as to the trap location within the site.



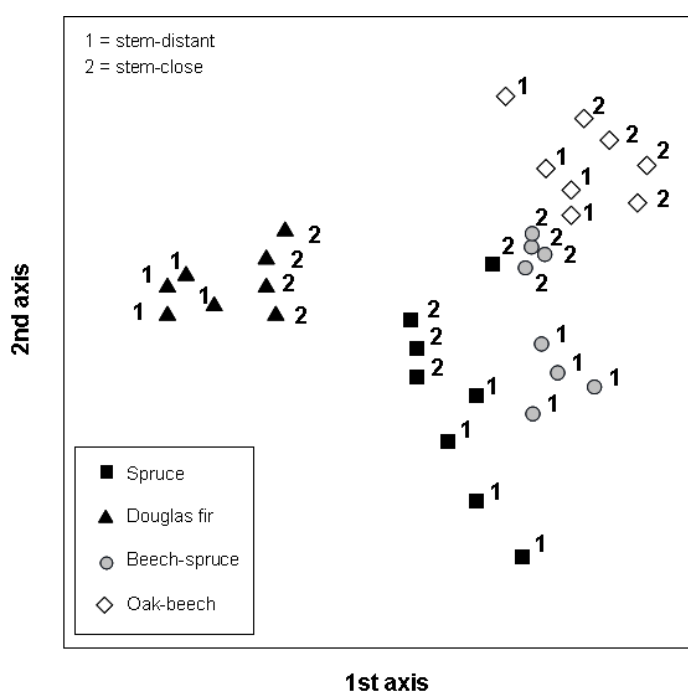
**Fig. 7** CCA biplot depicting the relationship between significant environmental microhabitat factors and the catches of stem-close and stem-distant pitfall traps of the four sites. The biplot also depicts the associations of individual species.



### 3.5 Discussion

#### Parameters influencing the small-scale distribution of soil-dwelling spiders

The investigation of coniferous pure and deciduous mixed mature forests documented a species-rich spider fauna and each stand type affirmed its characteristic species community. With the comparison of stem-close and stem-distant trap positions, we demonstrated an important small-scale spatial distribution pattern of a broad variety of spider species in forests. Species assemblages of different trap position were shown to be significantly different in stands. Many species were strongly associated with or even restricted to traps close or distant to the stem.



**Fig. 8** DCA ordination of assemblages sampled by stem-close and stem-distant pitfall traps in each of four sites. The first axis separates sites by stand type [e.g., needle stands (left) from deciduous stands (right)].

Nevertheless, the dissimilarity in species assemblage composition referring to the position to trees was not uniform among stand types. Because spider species preference for microhabitats at the forest floor is attributed to environmental requirements of species (Wise 1993; Lensing et al. 2005), the stand type or tree species-specific differences in microhabitat conditions close and distant to the stems have to be regarded as drivers of community structure. Trap position differed in a number of environmental parameters, such as the shading effect of the crown canopy, litter depth, or vegetation cover (i.e., grass, herb, moss, and natural regeneration). Moreover, gradients of several non-significant factors were measured referring to the distance to stems, namely, temperature, moisture, and pH of the soil or litter. Especially for the coniferous stands, the litter layer proved to be significantly deeper near the stem, whereas deciduous sites appeared evenly structured in this respect. Apparently, the presence of several spider species is influenced by the thickness, structure, and composition of the litter layer (Bultmann and Uetz 1984). Bultman et al. (1982) found that the species diversity of free hunters (Lycosidae) increased with the depth of the litter for mature stands. Huhta (1971) documented an increase of spider abundance along with litter accumulation during sequential development of stands. Within the litter, structural components are used for the construction of webs, in addition to adequate moisture and temperature conditions that promote several Linyphiid and Hahniid spiders.

Temperature and soil moisture, which are closely related to the degree of canopy closure, play a major role in the microhabitat selection of spiders. Frick et al. (2007) detected a particular distribution pattern in a free hunting wolf spider (*Pardosa riparia*, Lycosidae), which avoids the immediate surroundings of the tree trunks due to distinct temperature preferences. The authors concluded that the microhabitat selection for a number of species could be affected by stem distance (Maurer and Hänggi 1990). Studying the small-scale distribution of spiders in spruce stands, Pearce et al. (2005) observed higher abundance of open habitat specialists in patches having a low degree of canopy closure. Several species are

known to orient themselves toward light gradients and have interrelated environmental parameters in forests (Ziesche and Roth 2008).

There is also experimental evidence that spider density increases with enhanced density of their litter roaming fungivore and detritivore prey (Chen and Wise 1999), which is similarly affected by moisture and temperature conditions of litter and soil (Wagner et al. 2003; Berg and Bengtsson 2007). Schwerdtfeger (1949) described an accumulation of larvae of *Dendrolimus pini* (Lepidoptera) close to the tree during wintertime. The same applies to the pine sawfly (*Diprion pini*, Majunke et al. 1999) or the winter moth (*Operophtera brumata*, Frank 1967). Scheu and Poser (1996) detected significant variation in the community structure of the soil macrofauna, and even differences in bioturbation by earthworm communities, with regard to the distance to stems in a beech forest. They explained it by the influence of water flowing on stems and affecting stem-close patches. Additionally, moisture has been shown to affect the interactions between spiders and Collembola (Shultz et al. 2006). Moreover, investigations show that single trees of different tree species affect soil microbiological processes (Menyailo et al. 2002) or soil properties and nutrient concentrations near the tree trunk (Boettcher and Kalisz 1990). Humus profiles near the trunk base (Deschaseaux and Ponge 2001) or variation in soil nutrients below the crown due to tree growth and leaching processes (Hornschurch and Riek 2008) likewise influence the presence of litter decomposers. There is also knowledge about a number of bark-dwelling Oribatid mites and Collembola reaching high abundance at the trunk and the lower stem (Erdmann et al. 2006). These species present potential prey of spider species (Nentwig 1987).

Moreover, previous studies demonstrated that spiders respond to vegetation aspects (Hatley and Macmahon 1980; Ziesche and Roth 2008). Higher plant diversity is generally associated with enhanced diversity of spiders (McNett and Rypstra 2000; Symstad et al. 2000). Microhabitats with well-structured ground vegetation occur at illuminated places, which are more frequently located at stem-distant sites as documented in our study. Spiders are particularly susceptible to vegetation features due to specific spatial requirements for the web arrangement

(Riechert and Gillespie 1986) and due to distinct microclimatic conditions provided by vegetation cover. Moreover, well-developed and heterogeneous vegetation is often combined with an increase in herbivorous prey for spiders, which potentially decreases the level of competition. Thus, heterogeneous vegetation cover in forests may contribute to heterogeneous spider distribution due to stem-distance as well.

Spiders may as well occupy stem-close microhabitats as a consequence of structure provision by the stem base or stem bark. Several species are known to depend on structural complexity combining plants, litter, and debris as web and hiding substrates (Castro and Wise 2009). Wise (1993) resumed that the enhancement in structural diversity in a habitat can maintain diverse spider assemblages significantly.

Consequently, our results document that spider species composition in a forest is heterogeneous and depends on the distance to the stem. Studies focusing on a complete species inventory should consider the small-scale distribution pattern of spiders caused by the diverse microhabitat patches in forests attributed to the stem distance.

### **Functional aspects of spiders in forests**

Sunderland and Samu (2000) hypothesized a considerable resistance of spiders to move from a preferred microhabitat to less suitable patches, as was shown in several further studies. Moreover, Wise (1993) described that territoriality in spiders is an evolved behaviour that is tightly linked to competition among adults and results in restricted spatial distribution. In addition, spatial variation has been recognized as an important component in ecological processes (Reynolds and Crossley 1997). Langellotto and Denno (2004) demonstrated that diverse habitat structure resulted in a large and significant increase in natural enemy abundance for a large number of taxa. Many guilds of natural enemies were, to a great extent, affected by alteration in structural complexity. Spiders, in particular, were more abundant under conditions of increased habitat complexity.

Our data demonstrated the occurrence of bigger-sized spider species close to trees. Because the size of prey is closely related to the size of spiders (Nentwig 1982; Wise 1993), differences in their foraging pattern have to be expected near the stem. Lycosids are known to feed on larger prey items (Nyffeler 1999), whereas most Linyphiids depend on smaller prey-like springtails (Collembola).

Spiders are known to play a major role as natural enemies of pest species in several environments (Marc et al. 1999), and the abundance of spiders in forests suggests that they may contribute to maintain low pest densities even at the forest floor (Wise 1993). This also applies to their role as antagonists of defoliators, as stages of several crown living arthropods develop in the ground or endure the winter time within the litter layer or the soil near the stem (Dajoz 2000). Several investigations confirm the relevance of pupal stages as prey for predacious invertebrates (e.g. spiders) at the forest floor (Frank 1967).

Referring to the results of spider assemblages close to trees, the importance of the canopy as stratum between the atmosphere and the floor has widely been recognized (Parker et al. 1989, Dajoz 2000). Canopy arthropods make up an important component of the forest community (Nadkarni and Parker 1994). Hence, herbivores are likely to initiate effects on the floor area below the canopy, playing a role in the regulation of ecosystem nutrient cycling (Schowalter et al. 1986), and thus, in the food web of forests. Waltz and Whitham (1997) demonstrated that alterations in the composition of common herbivores of upper tree canopies affected the abundance and diversity of arthropod communities below the crown during successional plant development. Consequently, the canopy and the floor area below are interrelated, affecting the abundance of species close to the stem, and thus, directly influencing the dominance structure of spider assemblages. Further investigation is needed to determine how the stem distance-dependent distribution of spiders affects the role of spiders as regulators of detritivore food webs, as well as of natural enemies of invertebrate forest pests.

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## **4 The impacts of seasonality, forest type and succession on the community structure of temperate-forest ground beetles**

### **4.1 Abstract**

Tree species composition and stand structure is a dominant factor that controls forest biodiversity and affects intrinsic heterogeneity and environmental conditions crucial for species distribution, interaction and finally functional roles. Research on the microspatial distribution of indicator species while critically examining the impact of the covering tree layer is still rare. Therefore, this study emphasized on soil dwelling carabid beetle communities of four stand types of forests (pure stands: spruce, Douglas fir; mixed stands: beech-spruce, oak-beech) along a successional gradient (four age classes: 15–112 yr) to show the effects of small-scale microhabitat heterogeneity on the composition of species assemblages. Ground beetles were collected by pitfall traps ( $n = 96$ ) in 4-wk intervals. To reveal key environmental factors that affect carabid communities, abiotic and biotic habitat parameters (e.g. temperature, air humidity, soil characteristics, and vegetation parameters) were systematically assessed around each pitfall trap ( $r=5$  m). Species showed a small-scale distribution pattern on the forest floor, significantly affected by vegetation cover of herb, moss, grass and natural regeneration, canopy closure, litter type, soil-pH as well as temperature and humidity parameters according to discriminant analysis and ordinations. The relevance of habitat parameters changed with the growing season. While many species were correlated to vegetation cover overall and temperature aspects in spring, the influence of soil pH, litter parameters and the canopy closure prevailed during summer. The species assemblages assessed in the four forest types of different age classes indicate that the covering tree species has a profound influence on the small-scale distribution of ground beetle species expressed by environmental and seasonal characteristics. Nevertheless, the high similarity in

the composition of species assemblages of different stand types but with similar formations of ground vegetation, microclimatic parameter and canopy closure displayed a considerable impact of environmental factors not necessarily bound to the stand type itself.

**Keywords:** Biodiversity; Carabus; Managed forest; Microhabitat selection; Spatial heterogeneity

## 4.2 Introduction

Due to economical drivers, temperate forests are strongly affected by human over long periods of time. European forests are among the most intensively managed forests and biodiversity aspects have been neglected in many respects in the past (Brockerhoff et al. 2008). Thus, with regard to recurrent and forthcoming risks displayed in climate scenarios (Moss et al. 2010) biodiversity aspects might gain increasing importance.

Moreover, recently there is recognized agreement about the necessity of biodiversity preservation and enhancement also to take potential functional traits into account that rely on species richness. While forests are generally among the most species-rich terrestrial ecosystems and to address to the maintenance of biodiversity, it is desirable to assess key factors that make production forest ecosystems suitable habitats for a large number of taxa. Moreover, the identification of key variables structuring communities provides insight in the effects of management practices on forest invertebrates (Eyre and Rushton 1989; Ferris and Humphrey 1999).

In general, forestry expresses effects on the ecosystem level including selective cutting at certain intervals depending on the tree species and growth conditions (Otto 1994). The decision for the tree species and habitat modification by means of selective felling or the implementation of forest harvesting trails are likely to cause effects on the species community level simply through micro-environmental variation (Buckley et al. 2003). This applies particularly to invertebrates including insects. However, it seems crucial to disentangle the significant drivers that affect or even form invertebrate species assemblages and allocate them to the management or tree species effect. In forests, factors such as stand structure, tree species composition and age have been shown to influence invertebrate assemblages to some extent (Brouat et al. 2004; Irmiler et al. 1996; Humphrey et al. 1999) and many environmental parameters like ground vegetation, litter layer, canopy structure, dead wood and soil characteristics result in a diverse

microhabitat mosaic on the forest floor (Burel 1989; Grüm 1971; Niemelä et al. 1992).

In this context, carabid beetles as ecological well investigated group are proved to respond to environmental changes on a spatial scale. Known for their distinct distribution patterns, they show a high ecological diversity and environmental adhesions. Furthermore, many species rely on the epigeic stratum showing indicating potential of many environmental characteristics and qualitative changes of their environment (Baguette 1993; Downie et al. 1995; Langor et al. 1994; Scheidler 1990). This applies also to alterations of environmental heterogeneity due to intensive forest management resulting in significant changes of the microclimate at the forest floor (Grenberg and Thomas 1995). While those influences are reflected in the composition of vegetational and faunistic species assemblages (Oxbrough et al. 2006) the exact causes of small-scale distribution patterns in forest dwelling carabids within habitats are largely unclear (Niemelä et al. 1994 a, b).

The defined knowledge of microspatial distribution in forest stands is also significant for the understanding of drivers of ecosystem functions and the estimation of effects following active forest management. We should basically know which structures and processes are essential in maintaining the diversity of different assemblage groupings and how these features can be preserved in practical forestry operations. Finally, there is no doubt at all that integrated pest management in forestry is based on prevention after all (Watt et al. 1997).

Our aim was to examine the effects of small scale spatial heterogeneity in representative deciduous and coniferous forests of southern Germany on forest dwelling ground beetles. The investigation comprises different age classes to reach a wide span in heterogeneity and to establish knowledge of characteristics during the forestry cycle.

The study design was addressed to three questions: (1) What influence has the specific tree species or tree species composition and its intrinsic features on the ground beetle fauna of the forest floor in different common production forest types? (2) Which are the main environmental factors leading to a separation of

carabid species assemblages? (3) Are those key factors controlling the microspatial distribution of species assemblages stronger or even independent from the tree species?

### 4.3 Methods and materials

#### Study sites and sampling

The investigation was carried out in the cultural landscape around Augsburg, a historically well-forested area of south Germany (Central Bavaria, 48° 19′/11° 06′). The study sites comprised pure stands of spruce (*Picea abies*) and Douglas fir (*Pseudotsuga menziesii*), mixed stands of beech-spruce (*Fagus sylvatica* – *P. abies*) and oak-beech (*Quercus robur* – *F. sylvatica*). We chose 12 study sites (100 x 100 m) that represented four age classes of these stand types to define comparable forest successional stages: young stand (YS), mature stand (MS), mature stand with upcoming (MR), and established regeneration (eMR) (Table 1). The age classes referred to silvicultural thinning measures representative of forestry practice. Age classes of the respective forest type that were not integrated in the study design were not present in the study area (i.e., oak-beech, MS; Douglas fir, MS).

The study sites correspond in terms of soil conditions, altitude (510–545 m above sea level) and the subatlantic climatic conditions. Annual mean temperatures varied between 7.5 and 8.0 °C, average of annual precipitation ranged between 700 and 900 mm. The soils on these sites were fertile brown and parabrown earths.

To exclude side effects from adjacent forests, a core investigation area of 50 x 50 m was established in the center of each study site for the sampling of ground beetles and the assessment of environmental parameters (Fig. 1). The core area of each study site was surrounded by a belt (width: at least 25 m) of the same stand type representing a buffer zone (Molnar et al. 2001) and beyond that by further



forest ecosystems up to a distance of several kilometers. The distance between the study sites, varied between 150m and 25 km. The distance between the age classes within a stand type covered 1–2km on average.

In contrast to the oak-beech stands with a homogeneous mixture of deciduous trees, the beech-spruce stands consisted of beech groups, separated from areas covered with pure spruce. Hence, in beech-spruce stands, the core area was established: one half was covered with spruce, the other with beech.

**Table 1**

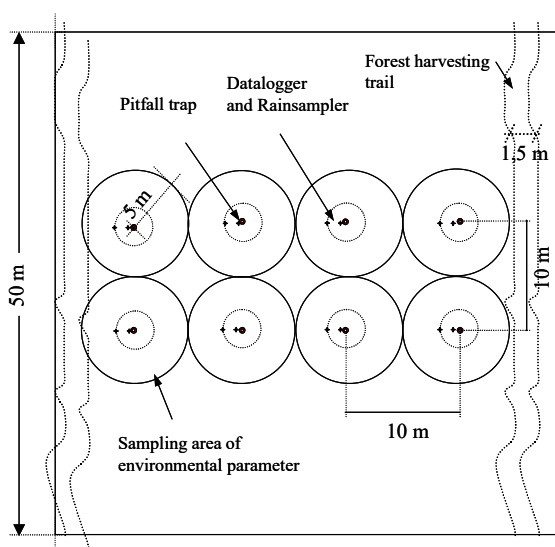
Characteristics of the 12 forest study sites

Study site	Stand type	Age [yr]	Trees per ha [n]	Medium height [m]	Pitfall group	
					A	B
Ps - YS	Douglas fir	15	938	13-14	D2	D1
Ps - MR	Douglas fir	80	314	37-39	D4	D3
Pi - YR	Spruce	30	1852	12-13	P2	P1
Pi - MS	Spruce	62	680	26-28	P4	P3
Pi - MR	Spruce	89	432	34-36	P6	P5
FaPi - YS	Beech-spruce	38	1604	12-16	F2	F1
FaPi - MS	Beech-spruce	73	618	29-31	F3	F4
FaPi - MR	Beech-spruce	89	404	31-33	F5	F6
FaPi - eMR	Beech-spruce	105	312	32-34	F7	F8
QuFa - YS	Oak-beech	28	1564	13-14	Q1	Q2
QuFa - MS	Oak-beech	75	1058	32-33	Q3	Q4
QuFa - eMR	Oak-beech	112	234	36-37	Q6	Q5

YS: Young stand; MS: mature stand; MR: mature stand with upcoming regeneration; eMR: mature stand with established regeneration. Grouping of four pitfall locations (i.e., microhabitat) according to degree of canopy closure within the study sites: pitfall trap locations with a high (A) and low (B) degree of canopy closure during the period of complete foliation.

We collected carabid beetles by pitfall trapping (glass jar,  $\varnothing=7.5$  cm, fixing agent: solution of saturated benzoic acid and detergent), since they sample a high number of ground- and litter-dwelling species (Niemelä et al., 1994c), while

measuring the activity density of species at the floor (Baars, 1979). The method is common and proven in ecological research (Eyre and Luff, 1990; Spence and Niemelä, 1994). Eight traps in two linear transects with four traps each were arranged within the core area of each study site (Fig. 1). The distance of the traps between and within the transects covered 10 m.



**Fig. 1** Design of data sampling in the core investigation area (50 m x 50 m) within each study site (1 ha).

Each core area offered a gradient in the degree of canopy closure due to harvesting trails (width <math>< 1.5\text{ m}</math>) located at two sides of the core area (Fig. 1). This degree of canopy closure was reflected along the transects of pitfall traps, providing the opportunity to define microhabitats (with four pitfall traps, each) with a high (pitfall group A) and low (pitfall group B) degree of canopy closure at each study site (Table 1). In the beech-spruce stands, one transect of four pitfall traps was established under beech (microhabitats: F1, F3, F5 and F7), the other transect under spruce (microhabitats: F2, F4, F6 and F8; Table 1).

The traps were emptied every 4-wk between 18 March and 22 October of 2002. The determination of carabid species followed the identification keys of

Freude et al. (1976). The ecological characterization was based on Thiele (1977). The nomenclature of carabid beetles followed Lindroth (1985, 1986).

### Environmental microclimate variables

Overall, we surveyed twenty-five environmental parameters during the investigation period (Table 2). Soil surface temperature was measured continuously every 45 min at each pitfall trap (at a depth of 1 cm in the litter layer) by data logger (Tinytalk II/TK-0023, Spectra Computersysteme, Leinfelden-Echterdingen). Air temperature and relative humidity values were taken every 90 min twice in a trap line (80 cm above the ground) by Tinytags Ultra (TGU 1500, Spectra Computersysteme, Leinfelden-Echterdingen). For climatic parameters calculated from the recorded data see Table 2. The seasonal (spring, summer and fall) averages were calculated from the daily data.

**Table 2**

Environmental factors surveyed at each pitfall trap

	Vegetation cover (%)	pH of litter layer
	Degree of canopy closure	Litter type
	Natural regeneration	Litter depth
	Herbs	Litter cover
	Grass	Microclimate
	Moss	Air humidity (%)
	Total standing vegetation	Precipitation per trap (ml)
Vegetation hight (cm)		Soil surface temperature (C°)
	Natural regeneration	<i>t</i> – min soil surface
	Grass layer	<i>t</i> – max soil surface
	Herb layer	<i>t</i> – variation
Soil characteristic		Mean temperature per year/season
	Soil moisture (%)	Temperature – air
	pH of the soil	Days above 8°C, <i>n</i>
	Moisture of litter layer	

The depth of the litter layer above the mineral soil was measured every 4 weeks at four randomly chosen locations around each trap (diameter of 2 m) to

estimate mean thickness. Precipitation was measured at each pitfall trap by rain samplers in a distance of 80 cm (funnel diameter: 7.6 cm), gathering the precipitation of 4-week intervals. Soil and litter samples for the determination of moisture (Scheffer and Schachtschnabel, 1989) and pH (H<sub>2</sub>O) were taken in spring (9 April), summer (30 July), and fall (24 September) within a radius of 1 m around each trap. The degree of canopy closure, the cover value of natural regeneration, herb, grass, moss, and litter were assessed according to Braun-Blanquet (Mühlenberg, 1989), within a radius of 5 m around each trap following the 4-week intervals of pitfall trap sampling. Litter type was also assessed every 4 weeks as the proportion of the tree species-specific litter covering the soil (in mixed stands, according to the predominating litter type) within a radius of 5 m around each trap (classification of litter types in ascending order: Douglas fir, spruce, spruce-beech, beech-spruce, beech, beech-oak, oak-beech, oak).

We distinguished three time periods to assess the effects of seasonal habitat alterations on the carabid community, mainly based on the development of the crown canopy and the ground vegetation. Spring was defined as the time period from the beginning of the study until the foliation of the deciduous trees was completed (18 March-5 June). Summer season was the time period when trees have a fully developed crown canopy and when mean temperatures were higher than those in spring (6 June-28 August). Fall season started with the beginning of the leaf fall accompanied by dropping temperatures (29 August-22 October).

### **Statistical analysis**

To compensate possible differences in catch results of pitfall traps due to different levels of activity density between the 24 microhabitats we used relative abundance data (dominance in %) for statistical analyses (Honek 1988), to emphasise differences in the assessed species composition.

TWINSPAN analyses (Hill 1979) were carried out to detect corresponding and deviating patterns in the composition of ground beetle assemblages of microhabitats (i.e., grouping of four pitfall traps with a similar degree of canopy

closure and tree species composition;  $n = 24$ , Table 1). This hierarchical ordination method classifies microhabitats based on structural parameters of species assemblages (e.g., species spectrum, dominance position) and combines corresponding ground beetle assemblages of microhabitats to microhabitat groupings. Additionally, the analysis identifies character species for each classified division of microhabitats that may be present in low numbers in other microhabitats.

We used discriminant analyses (DA) to reveal significant environmental factors that contribute to the explanation of the ground beetle assemblage classification in the TWINSPAN analyses. Applying a forward stepwise procedure, the DA determined those environmental key parameters that discriminate best between the TWINSPAN microhabitat groupings of the spring, summer, and fall aspects, respectively. Subsequently, all seasonal environmental parameters of microhabitats were examined by DA to evaluate the effects of intrinsic characteristics of the tree species composition. Therefore, all age classes of the same stand type (Douglas fir, spruce, beech-spruce, Oak-beech) were pooled in the statistical procedure.

To reveal correlations between the distribution pattern of carabid species and environmental conditions the catch results of species of each single trap ( $n = 96$ ) were related with environmental parameters (Spearman rank, SPSS 12.0) assessed in the surrounding of each trap.

A species-centred principal component analysis (PCA) was run to determine the main environmental parameters affecting the distribution pattern of carabid species and microhabitats during spring, summer, and fall. Finally, a redundancy analysis (RDA) (stepwise forward selection,  $p < 0.05$ , unrestricted Monte Carlo permutations;  $n = 9999$ , CANOCO 4.5) was performed for the graphical ordination of the environmental key parameters that contribute best to the characteristic pattern of ground beetle assemblages (Legendre and Anderson 1999; ter Braak and Smilauer 2002; Jongman et al. 1995). Analyses separate species and sites according to an indirect gradient (PCA) and additionally give

indication of the main environmental parameters involved in the partition of species assemblages (RDA).

To reduce the pitfall method specific overestimation of the most active species, the activity density data of the 24 microhabitats were log-normal transformed. A preliminary detrended correspondence analysis (DCA) indicated a strong linear response of the species variance to the environmental parameters (Hill and Gauch 1980), which is common with proportional data. Thus, we used PCA and subsequent RDA (Leps and Smilauer 2003). The results of the PCA and RDA environmental variables were tested on multicollinearity. All analyses comprised only species with >3 individuals in total catch of each season.

Because litter type was only assessed as a qualitative parameter, not representing a linear gradient, this environmental parameter was excluded from the PCA and RDA.

#### 4.4 Results

A total of 4431 ground beetles were assessed from 48 species. The activity density of beetles remained at a similar level for the spring (1934 adult carabids and 38 species, 18 species > 3 individuals) and summer period (1874 adult specimen and 35 species, 21 species > 3 individuals) according to the pitfall trap recordings. In contrast the relative abundance of the fall period decreased to 623 adult carabids and 22 species (12 species > 3 individuals). Beside *Abax carinatus*, which was restricted to one forest site, species indicated no particular preference to the respective tree species or age class. Only *Abax ovalis* was restricted to the deciduous and Douglas fir microsites (see TWINSPAN analyses).

Almost eighty five percent of the sampled species were commonly known forest (64.6 %) and forest edge species (20.8 %). Only 14.6 % of all the determined species were characteristic open-habitat species. These species were barely subject of statistical analyses, since they occurred in low individual numbers (50 individuals from 7 species).

## Classification of species assemblages

### Spring season

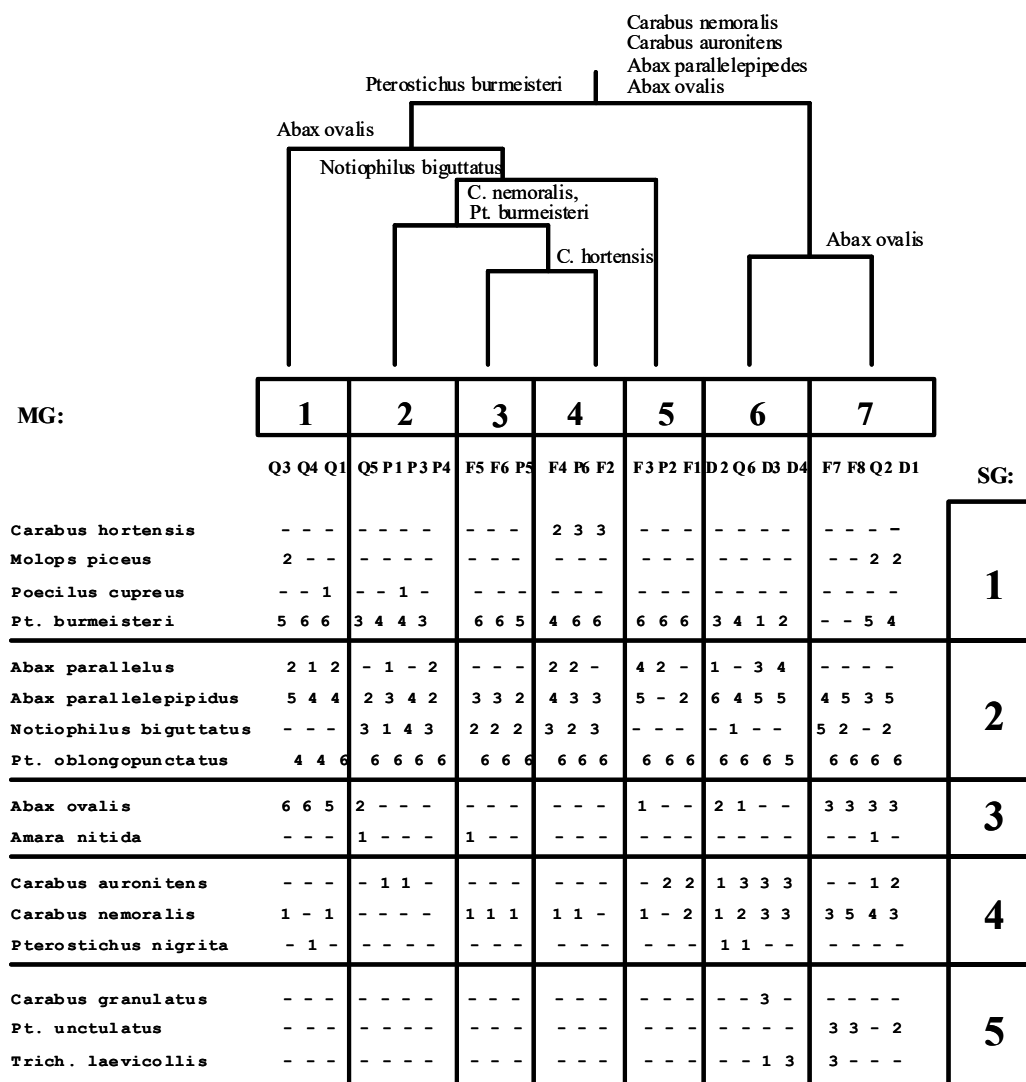
The TWINSpan classification for the spring aspect defined seven microhabitat groupings (MG) and five species groupings (SG, Fig. 2). Several species segregated in presence and abundance significantly between the sites. Nevertheless, three dominant species were recorded at almost every microsite with *P. oblongopunctatus*, *A. parallelepipedus* known as eurytopic forest species, and *P. burmeisteri* (species group 1-2).

The arrangement of microhabitat groupings in spring did not follow the respective tree species (stand type) covering the ground. The defined microhabitat types group along herb cover and vegetation composition gradients. Especially the spring herb cover and the canopy closure during spring were showing a clear characterisation of microhabitat groupings with respect to several carabid species of open sites on one side (MG 6–7; oak-beech, Douglas fir) and assemblages of predominantly true forest species on the other (MG 2–5; spruce, beech-spruce) as well as oak-beech with spring herb cover (MG 1).

The first division by TWINSpan separated 8 open hygrophilous microhabitats (MG 6–7) from microhabitats with close canopy and low herb cover (MG 2–5), as well as the oak-beech sites with a strong spring geophyt vegetation (MG 1, Fig. 2). Those 8 microhabitats comprise two different tree compositions (MG 6–7: Douglas fir and oak-beech). Here, for the first division the analysis defines four character species (SG 2–4) with *Carabus nemoralis*, *Carabus auronitens*, *A. parallelepipedus*, and *A. ovalis*. There was a high prevalence of hygrophilous species (SG 3–5) in this grouping (MG 6–7) with respect to the species *Carabus granulatus*, *P. unctulatus* and *Trichotichnus laevicollis*.

In the second division, all microhabitats of the spruce and beech-spruce stands (MG 2–5) and one oak-beech microhabitat (Q5; MG 2) were arranged and separated from the oak-beech sites with comprehensive spring vegetation (MG 1). For this division *A. ovalis* serves as a character species representing a cold

preferent, hygrophilous species, which is known as stenotopic. This species also characterises the separation of MG 6 and 7.



**Fig. 2** TWINSpan classification displaying the distribution pattern of carabid beetles in the forest study sites in spring. The dendrogram indicates the separation of microsites into groups (1-7). The separation of the species into groups is given by numbers (1-5). The relative frequency of each species is indicated by numbers from 1 to 6 (1 = 0–1.9%, 2 = 2–3.9%, 3 = 4–4.9%, 4 = 10–14.9%, 5 = 15–24.9%, 6 ≥ 25%). Microhabitats: spruce: = P1–P6, Douglas fir = D1–D4, beech-spruce = F1–F8 (beech: F1, F3, F5 and F7; spruce: =



F2, F4, F6 and F8), oak-beech = Q1–Q6. MG = microhabitat groupings; SG = species groupings.

The further division of microhabitat groupings (MG 2–5) displayed the young and mature beech microhabitat (MG 5: F1 and F3) and the young spruce (P2) marked by the absence of *Notiophilus biguttatus* (eurytopic species of dry and open forests). It was also characterised by the presence of species grouping 4 (eurytopic and hygrophilous forest species).

In the next division, the young and mature spruce and one oak covered microhabitat (MG 2: Q5) were separated from microhabitats covered by beech and mature spruce with upcoming regeneration (MG: 3, 4). This was reflected in the presence of *Carabus nemoralis* and increased activity of *P. burmeisteri* (dark and cold preferent, xerophilic forest species). The last division of microhabitats separated the spruce covered young and mature beech-spruce sites and the mature spruce with upcoming regeneration (MG 4) with the presence of *Carabus hortensis* from MG 3 (F5, F6 and P5).

### Summer season

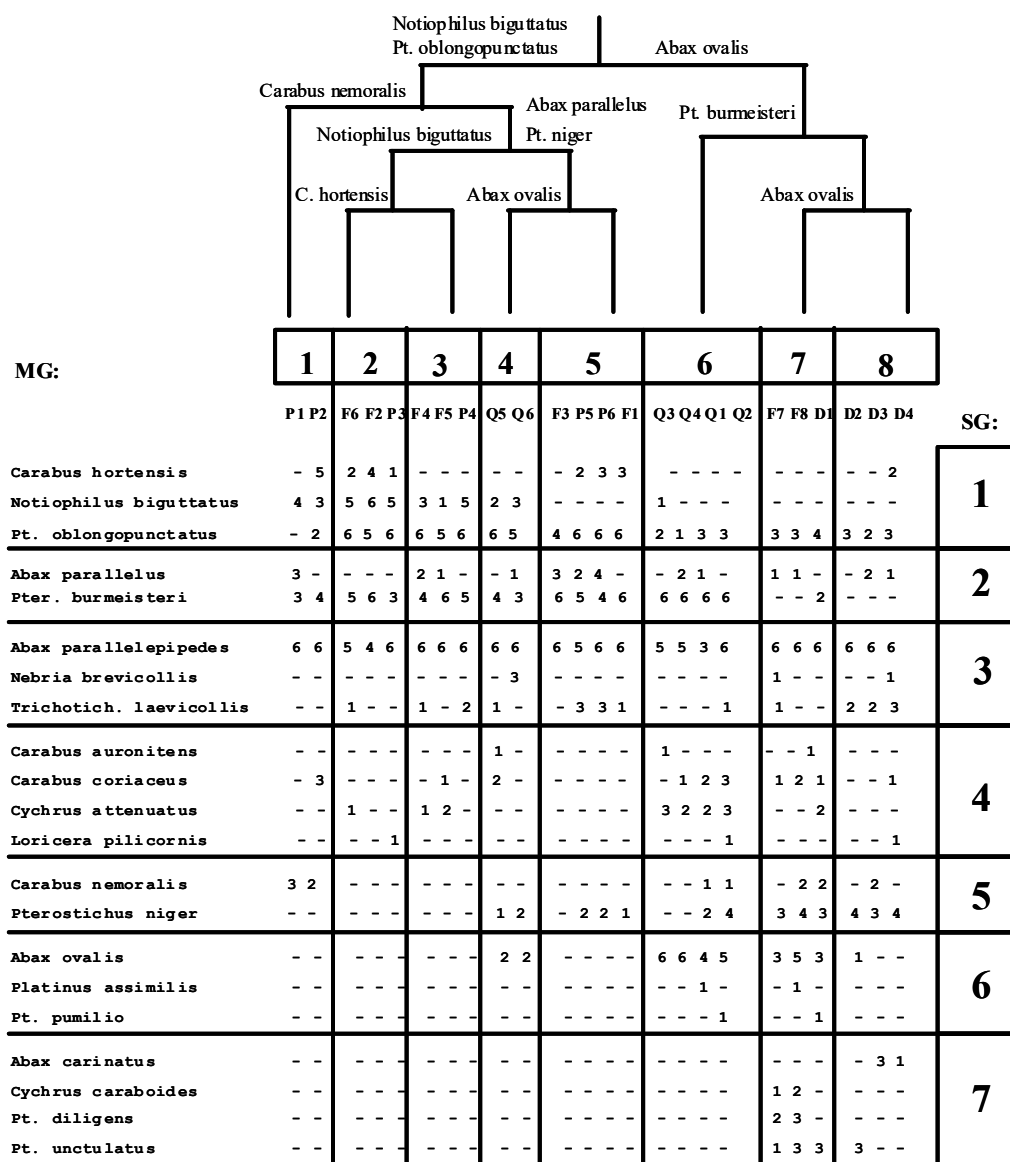
The TWINSpan classification for the summer aspect separated eight microhabitat groupings (MG) and seven species groupings (SG; Fig. 3). The composition of species assemblages in microhabitats differed significantly from the spring season. Meanwhile the deciduous canopy had fully developed, the spring vegetation nearly vanished, the summer vegetation succession had taken place and the soil moisture remained evenly low. With *A. parallelepipedus* and *P. oblongopunctatus* two dominant eurytopic forest species were sampled in almost every microhabitat. Besides, the species differentiate significantly between the sites. The activity density of the carabids increased in June and July for several microhabitats with increased temperatures and the development of shrub, grass and herb vegetation. Some species were sampled more frequently like *A. parallelepipedus*, *Pterostichus niger*, *Cychrus attenuatus*, *Carabus coriaceus* and

*Cychrus caraboides*, while other species were less abundant in total catch like *C. auronitens*, *C. nemoralis* or *P. oblongopunctatus*.

The different microhabitat types of the TWINSPAN analysis were not as strictly arranged along the spring vegetation cover and temperature anymore, but rather similar humidity conditions of soil and litter, and ground vegetation characteristics, including the cover and depth of the surface litter were obvious within the first three levels. The effect of the canopy cover is stronger than for the spring season, while the correlation of single species to the litter type increased.

For the first division microhabitats of young and mature oak-beech (MG 6), beech-spruce with established regeneration and the Douglas fir microhabitats (MG 7–8) separated clearly. Low density of *P. oblongopunctatus* and the absence of *N. biguttatus* or the presence of *P. niger* characterise this cluster of microhabitat groupings. The hygrophilous forest species *Abax ovalis* serves as a character species. Common to those microhabitat groupings (MG 6-8) is a still present herb cover, increased pH of the soil and level of precipitation, as well as a low soil moisture and litter depth. Moreover, the common parameter in this grouping was a high level of air humidity (80–90%), being only temporally interrupted in the oak-beech (MG 6) and the young stand of the Douglas fir (MG 8). These microhabitat groupings (MG 6-8) were characterised by the presence of hygrophilous species (SG 4–6) like *Carabus coriaceus* or *Cychrus attenuatus*.

The second TWINSPAN division separates microhabitats of the young spruce stand (MG 1) from the microhabitats of mature spruce, the young and mature beech-spruce and oak-beech with established regeneration (MG 2-5). The second division also separates the young and mature oak-beech microhabitats (MG 6) from the Douglas fir and beech-spruce with established regeneration (MG 7-8) in the second subcluster. This was due to obvious deviations of the species composition (SG 7) and the presence of *P. burmeisteri* and *C. attenuatus*, both stenotopic forest species and dark preferent.



**Fig. 3** TWINSpan classification displaying the distribution pattern of carabid beetles in the forest study sites in summer. The dendrogram indicates the separation of microsites into groups (1-7). The separation of the species into groups is given by numbers (1-5). The relative frequency of each species is indicated by numbers from 1 to 6 (1 = 0–1.9%, 2 = 2–3.9%, 3 = 4–4.9%, 4 = 10–14.9%, 5 = 15–24.9%, 6 ≥ 25%). Microhabitats: spruce = P1-P6, Douglas fir = D1–D4, beech-spruce = F1–F8 (beech: F1, F3, F5 and F7; spruce:

F2, F4, F6 and F8), oak-beech = Q1–Q6. MG = microhabitat groupings; SG = species groupings.

For the third division the species assemblages of the predominantly spruce canopied microhabitats (MG 2-3) distinguished from the beech, oak-beech with established regeneration and the mature spruce site with upcoming regeneration (SG 4-5). *P. niger* and *A. parallelus*, a hygrophilous stenotopic forest species, serve as character species for this microhabitat grouping. In the third division, the beetle assemblages of the mature beech-spruce microhabitats with established regeneration and the more open Douglas fir microhabitat (MG 7) were separated from the Douglas fir (MG 8) with significant differences in the species grouping 6 and 7.

### **Fall season**

In fall, the overall activity density of carabids has decreased. In total 22 species were caught and only 12 species reached individual numbers, adequate for statistical analyses ( $N > 3$  individuals). The TWINSpan analysis of the ground beetle assemblages revealed 10 microhabitat groupings and 5 species groupings with a species distribution pattern deviating from the spring and summer aspect. Effects of the stand type or tree species on the TWINSpan divisions were less evident than in summer.

### **Discriminant analyses (DA) - Environmental factors explaining the TWINSpan classification of ground beetle assemblages**

The stepwise forward DA showed significant discriminant functions explaining the arrangement of the TWINSpan microhabitat groupings for the spring, summer and fall season. The results of seasonal aspects indicate a shift in significant environmental factors that affected the distribution pattern of species assemblages.

The spring aspect was defined by a strong gradient in the degree of canopy closure between evergreen coniferous stands and stands with deciduous trees, starting with the leaf formation in May. Also, a gradient of canopy closure was obvious within the coniferous stands due to their differences in age and as a consequence of silvicultural practice. This apparent feature was reflected by recorded environmental conditions affecting the carabid species distribution significantly.

For the spring aspect, the only significant discriminating variable explaining the classification of TWINSPAN groupings ( $n = 7$ ) in forward stepwise analysis was the vegetation cover overall ( $F = 14.85$ ,  $p < 0.001$ ).

The summer aspect was visually characterised by deciduous trees with fully developed foliage, shading the forest floor. The spring vegetation nearly vanished and the summer vegetation succession has taken place. These alterations were accompanied by changes in the significance of the variables.

Accordingly changes the significance of variables for the summer season. The litter type ( $F = 18.6$ ,  $p < 0.001$ ) is the first significant discriminating factor for the separation of microhabitat groupings identified from the TWINSPAN classification. It was followed by litter cover ( $F = 10.22$ ,  $p < 0.001$ ), litter depth ( $F = 7.25$ ,  $p < 0.05$ ), the cover of natural regeneration ( $F = 8.5$ ,  $p < 0.05$ ), and the mean temperature of the season ( $F = 5.99$ ,  $p < 0.05$ ) were also significant factors in the separation of microhabitat groupings ( $n = 8$ ).

The fall aspect was characterised by the defoliation of deciduous trees but still by a fully developed herb and grass vegetation. The only significant variable in fall contributing to a separation of microhabitat groupings in the TWINSPAN analysis appeared to be soil moisture ( $F = 5.26$ ,  $p < 0.001$ ), followed by seasonal mean temperature ( $F = 4.23$ ,  $p < 0.05$ ).

To judge whether these discriminating factors were intrinsic features of the tree species covering the ground, a forward stepwise DA was conducted, combining all microhabitats ( $n = 24$ ) of the same stand type. In spring, the different stand types were separated by the litter type ( $F = 57.412$ ,  $p < 0.001$ ) and the cover value of natural regeneration ( $F = 25.211$ ,  $p < 0.001$ ). The pH of the soil ( $F = 16.606$ ,  $p$

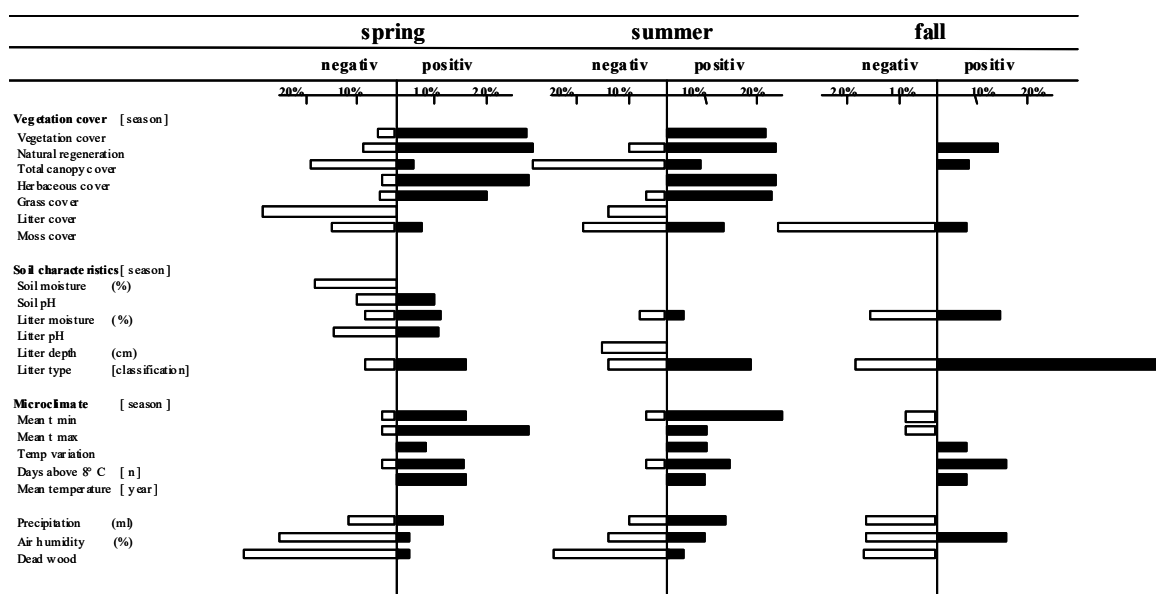
< 0.001) and canopy closure ( $F = 7.69$ ,  $p < 0.001$ ) represented further significant discriminating variables. In summer, still the litter type ( $F = 45.571$ ,  $p < 0.001$ ), the cover value of natural regeneration ( $F = 15.802$ ,  $p < 0.001$ ), as well as air humidity ( $F = 15.3$ ,  $p < 0.001$ ) and mean temperature of the season ( $F = 6.01$ ,  $p < 0.001$ ) differed most between the stand types. In fall, litter type ( $F = 90.401$ ,  $p < 0.001$ ), cover value of natural regeneration ( $F = 30.073$ ,  $p < 0.001$ ), and soil moisture ( $F = 10.61$ ,  $p < 0.001$ ) were the most important variables separating the stand types.

### **Spearman rank correlations - Environmental factors explaining the distribution pattern of single species**

Correlation analyses revealed strong causal relationships between single carabid species and environmental parameters assessed in spring, summer, and fall. Figure 4 summarizes the proportional correlations within the three studied seasons, combining significant positive and negative correlations ( $p < 0.05$ ). It became evident that for the spring season vegetation parameter like the vegetation cover overall, the cover of natural regeneration or the herb layer were significantly correlated with more than 24% of the carabid species, respectively. Next to these, the canopy closure was important, and almost 76 % of all species correlate significantly to the canopy closure, the herb and grass cover. Moreover, the maximum temperature (pos.), and the cover of litter (neg.), as well as the humidity of the air (neg.) are of relevance and about 60 % of all species show a significant correlation to those parameters in spring.

Meanwhile, the results of the Spearman rank correlation of the summer season displayed a shift in the relevance of environmental parameters (Fig. 4). When comparing those 18 species, assessed in spring and summer with more than 3 individuals, only a proportion of 49.5 % of all significant correlations stayed the same. There seems to be a shift in importance between spring and summer, and during summer a high number of species is significantly correlated to vegetational aspects like the cover of grass (27%), the moss cover (pos. / neg. = 32 %), a high

level of minimum temperature (28 %), or the canopy closure (neg. = 34 %) comprising almost 65% of all species. Herb cover and natural regeneration is like in spring significantly correlated to a number of species, just like litter depth as an additional factor. Many species were correlated to the litter type of namely beech and oak in summer. Furthermore, a decreased proportion of species showed significant correlations to moisture and pH of the soil and litter as well as the maximum temperature compared to the spring period.



**Fig. 4** Environmental parameters explaining the seasonal (spring, summer and fall) distribution pattern of ground beetle species in different types of forests: results of Spearman rank correlations expressed as the percentage of carabid species showing significantly negative (white bars) or positive (black bars) correlations to the respective microhabitat factors.

In fall, preferences of the species to the vegetation parameters decreased and many species were negatively correlated to the cover of moss. There was still a preference for moist litter conditions or a high relative air humidity and many

species showed strong adhesions to the deciduous leaf litter type surrounding the trap, thereby avoiding the soil-covering mosslayer. Altogether, the species responses to environmental factors subsided and the strength of correlations decreased significantly. The litter type, that covered the trap area ( $\varnothing=10$  m), showed highly significant positive correlations and thus represented a significant habitat factor influencing species distribution even more than in summer and spring.

### PCA/RDA ordinations

Multivariate analyses revealed a distinct distribution pattern of species and microhabitats (Fig. 5 and 6). The RDA in combination with PCA for the data sets of spring and summer resulted in a good separation of microhabitats as well as species. This corresponded with the results of the TWINSpan analysis. Thus, microhabitats were not strictly arranged according to the covering tree species but mainly in compliance with similar vegetational aspects. The first four PCA axes for the spring season explained 56.8% of the variance of the species, displayed in the biplot, and 97.2% of the correlations between species and environmental factors chosen in the RDA.

**Table 3**

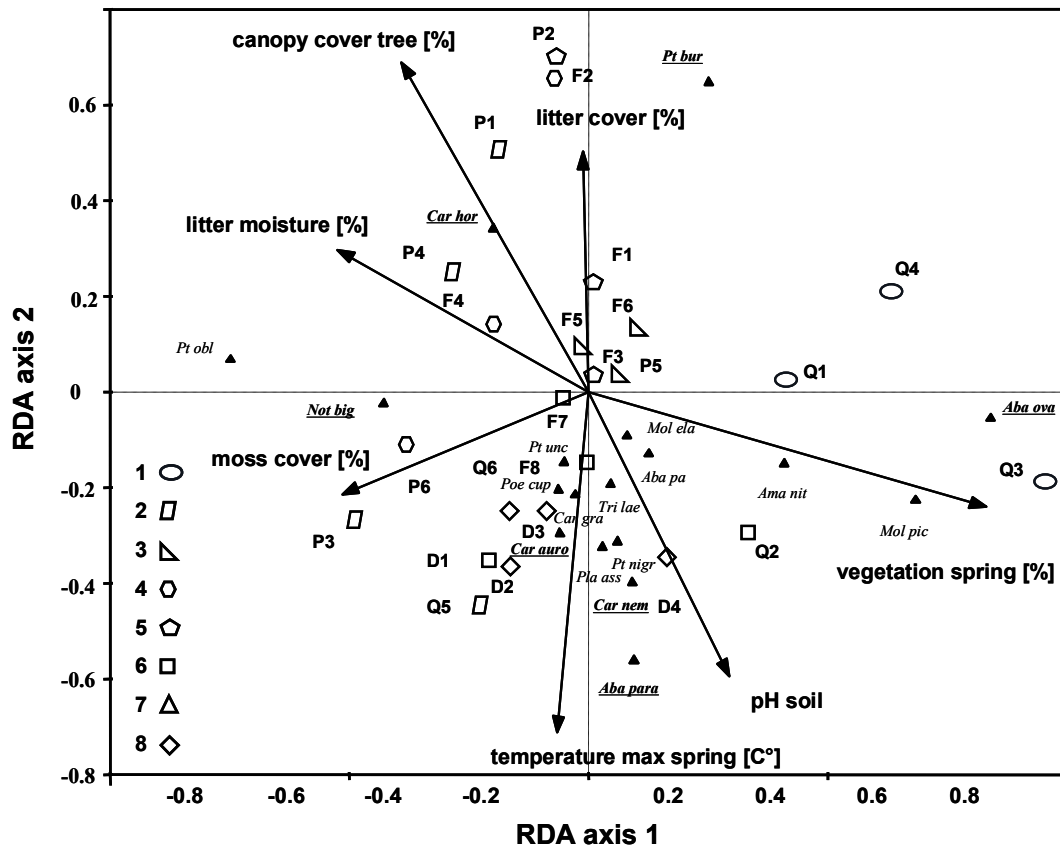
Comparison of results obtained by PCA and RDA for the spring and summer data set: species environment coefficients for the first four axes

Axis	1	2	3	4
Correlation coefficients				
Spring				
PCA	0.998	0.995	0.994	0.991
RDA	0.836	0.704	0.586	0.524
Summer				
PCA	0.883	0.878	0.974	0.906
RDA	0.774	0.691	0.736	0.778



In spring the first axis was mainly related to vegetation cover as well as moss cover and litter moisture, the second axis to canopy closure, the cover value of litter, maximum temperature as well as soil pH. This separation was reflected in a strong grouping of the microhabitats according to the canopy closure. Thus, the first axis separated the oak-beech (Q1–Q4) from the Douglas fir, beech-spruce and spruce microhabitats. Along the second axis, young and mature coniferous and beech-spruce microhabitats (above) were separated from the oak-beech, mature beech and spruce with established regeneration (P5, P6, F7 and F8) and Douglas fir-covered sites (D1–D4) distinguished by a more open character and vegetation cover (below). Besides, beech microsites (F1, F3 and F5) of the beech-spruce still separate from the spruce microsites (F2 and F4). At the lower central side of the biplot, we recognize a group of all Douglas fir-covered microhabitats and the microhabitats of the oldest oak-beech and beech-spruce stands (Q5, Q6, F7 and F8) with increased maximum temperature, pH of the soil, moisture and a low cover value of the canopy. At the lower left side of the biplot, spruce-covered microhabitats with a high cover value of moss (P3 and P6) were separated from the Douglas fir microhabitats characterised by a high soil pH and increased temperatures on the lower side (D1–D4).

Regarding species distribution pattern, three groups were obvious. At the upper left quadrant, species commonly known as dark and cold preferent species aggregated. At the upper right quadrant, cold preferent and hygrophilous species, which are common in deciduous forests grouped. The species group at the lower right and left quadrant of the biplot comprised character species of the TWINSPAN analysis, which are cold preferent and hygrophilous, and with *Carabus auronitens* adapted to moss cover.



**Fig. 5** RDA ordination triplot for the spring season (first and second axis). Species are represented by points to facilitate the readability of the graphic, environmental variables by arrows. The microhabitat types are represented as symbols according to TWINSpan analysis (legend left). The site endgroups defined by TWINSpan are indicated as different symbols, the character species are underlined. The microhabitat types are named according to the covering tree species (P: spruce, D: Douglas fir, F: beech-spruce (beech: F1, F3, F5 and F7; spruce: F2, F4, F6 and F8) and Q: oak-beech).

### Summer season

The multivariate analysis for the summer data set revealed a deviating pattern in the separation of microhabitats and species as has been documented by the

TWINSpan analysis. Together, the first four PCA axes explained 65.4% of the variance of the species data and 77.2% of the variance of the correlations between species and the environmental factors chosen in the RDA (Fig. 6). The eigenvalues of the RDA ordination axes were only slightly lower than in the PCA, and the species environment correlations were all very high. In summer the species assemblages showed a rather low correlation to the covering tree species, but arranged according to stand age characteristics and environmental factors.

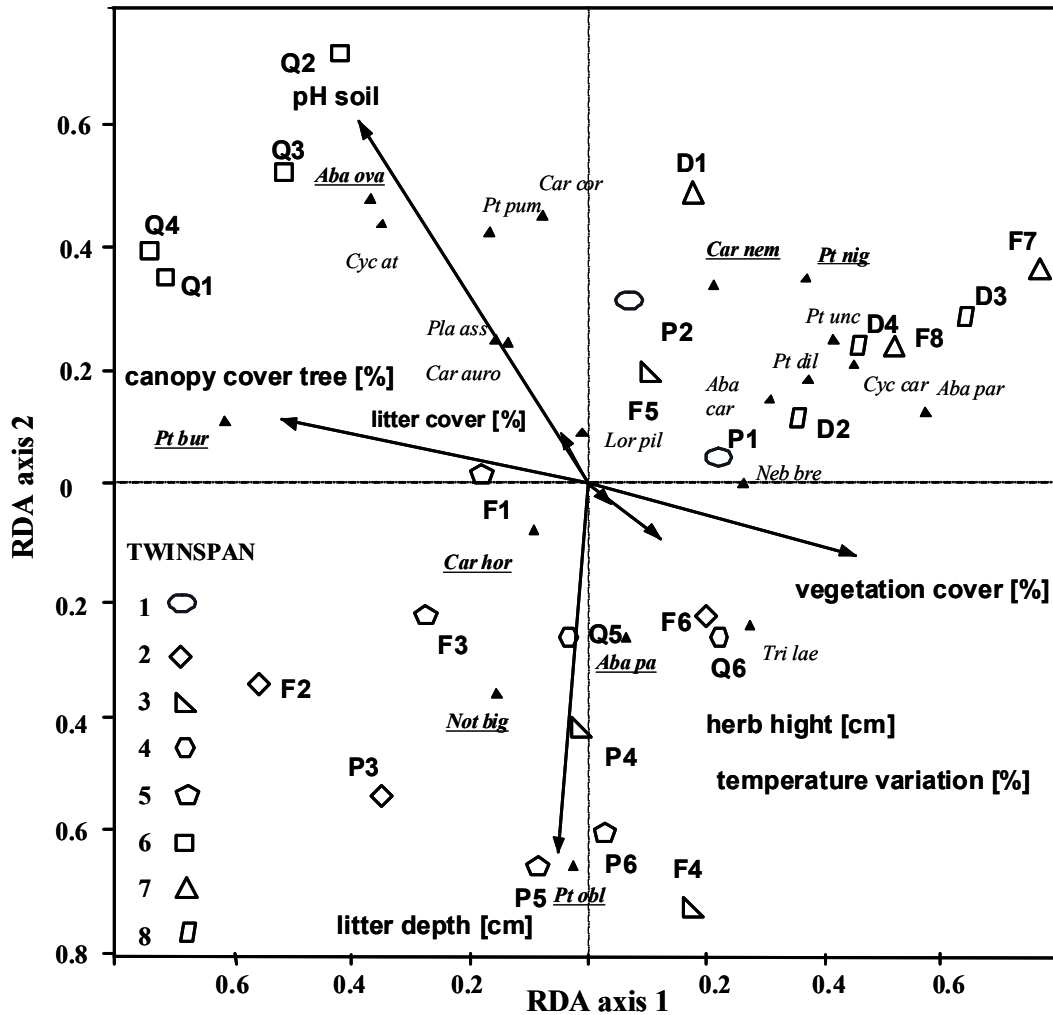
The first axis was mainly related to the covering of herbaceous layer and the canopy closure, whereas much of the variance of the second axis was explained by the pH of the soil and the depth of the litter (Table 5). Under the fully developed foliage in summer, shadowed microhabitats separated from the more open sites with and without a strong litter layer.

The oak-beech stands canopy has been developed and the spring geophyte vegetation has vanished for the summer season aspect defining microhabitats of young and mature oak-beech (Q1–Q4) at the upper left quadrant with hygrophilous species common in deciduous forests like *Carabus auronitens*, *Cychnus attenuatus* or with *Abax ovalis* a stenotopic hygrophilous forest species (TWINSpan: SG4 and SG6)

Along with increasing vegetation cover and lower canopy closure the microhabitats of the Douglas fir (D1–D4) and the oldest beech-spruce with established regeneration (F7 and F8) grouped at the upper right side of the biplot together with meso hygrophilous and eurytopic forest species. Several species typically found in more open forest under moist conditions were arranged in the upper right of the biplot e.g. *P. niger* and *C. nemoralis*, which were significantly enhanced by the ground vegetation and lower canopy.

The lower side of the biplot assembled microhabitats of oak-beech with established regeneration (Q5 and Q6) and beech (F1 and F3) as well as the oldest spruce with upcoming regeneration (P5 and P6) on one site and the spruce needle covered microsites with a dense canopy closure and increased litter depth (F2, F4, F5, F6, P3 and P4) on the other. Another group with the young spruce microsites

(P1 and P2) and thus a high canopy closure and low vegetation cover separated significantly (upper right).



**Fig. 6** RDA ordination for the summer season (first and second axes). Species are represented by points to facilitate the readability of the graphic, environmental variables by arrows. The microhabitat types are represented as symbols according to TWINSpan analysis (legend left). The site endgroups defined by TWINSpan are indicated as different symbols, the character species are underlined. The microhabitat types are named according to the covering tree species (P: spruce, D: Douglas fir, F: beech-spruce (beech: F1, F3, F5 and F7; spruce: F2, F4, F6 and F8) and Q: oak-beech).

## 4.5 Discussion

The investigation of temperate pure (spruce, Douglas fir) and mixed forests (beech-spruce, oak-beech) revealed a species-rich ground beetle fauna, including rare species (e.g. *A. carinatus*, *Diachromus germanus*, *P. diligens*, *P. unctulatus*). The different stand types and age classes of the production forests generated a high variation of microhabitat conditions shifting with the seasons. Age class forests of the forest cycle enabled us to focus on a large span of microspatial gradients within one stand type. Though the sampling scale of 4-week intervals resulted in a certain averaging, the broad spectrum of microhabitats allowed us to detect specific responses of species to a variety of micro-environmental parameter gradients and it revealed a very sensitive segregation of ground beetle assemblages. Many species proved to be nonrandomly distributed and especially the Douglas fir and oak-beech stands provided some specific and species rich carabid assemblages.

Environmental factors affecting ground beetle distribution have been described until now mostly at the stand level and regarding alluvial forests (e.g., Antvogel and Bonn 2001) or boreal forests (e.g., Niemelä et al. 1992) on the level of forest vegetation communities, but merely on that fine spatio-temporal scale. According to our results environmental factors and thus species distribution changed within a stand on a fine temporal and spatial scale.

The results of the DA confirmed defined characteristics of the stand type in measured habitat factors, while the distribution of carabids was not necessarily explained by stand type bound parameters. None of the carabid species were restricted to one stand type or age class, but many species preferred microsites with similar environmental conditions, shifting with distinct seasonal impacts. Generally, characteristic micro-environmental conditions in stand types were detected by the DA for each season like the litter type as the most obvious tree factor, the share of natural regeneration or pH of the soil (spring) and temperature values or humidity (summer). An intrinsic parameter of the tree species, affecting the composition of carabid assemblages, was the evergreen or deciduous character

of the stand type, determining the degree of foliation in spring. Among the strongest environmental factors contributing to the explanation of species distribution was the canopy closure for the spring aspect and for the summer season.

**Table 4**

Impact strength of environmental variables selected by unrestricted permutation (single and cumulative contribution of variables in forward stepwise analysis) in the PCA and RDA for the spring data set (intra-set correlation)

	Explained variance (%)			Correlation coefficients			
	Single	Cumulative	<i>p</i>	Axis 1	Axis 2	Axis 3	Axis 4
Standing vegetation	0.28	0.28	< 0.0001	- 0.67	0.08	- 0.12	0.19
Mean temperature max	0.10	0.38	< 0.0203	- 0.34	- 0.47	0.14	- 0.24
Moss cover	0.07	0.45	< 0.0604	- 0.38	- 0.50	- 0.15	0.33
pH of the soil	0.05	0.50	< 0.061	0.65	- 0.12	- 0.06	- 0.14
Canopy closure	0.02	0.52	< 0.067	- 0.21	0.26	- 0.13	0.61
Litter cover	0.02	0.54	< 0.0685	0.17	0.34	- 0.56	- 0.18
Litter moisture	0.02	0.56	< 0.072	0.16	0.28	- 0.05	0.04

**Table 5**

Impact strength of environmental variables selected by unrestricted permutation (single and cumulative contribution of variables in forward stepwise analysis) in the PCA and RDA for the summer data set (intra-set correlation)

	Explained variance (%)			Correlation coefficients			
	Single	Cumulative	<i>p</i>	Axis 1	Axis 2	Axis 3	Axis 4
pH of the soil	0.19	0.19	< 0.0094	0.55	- 0.11	0.29	0.55
Canopy closure	0.12	0.31	< 0.003	- 0.24	- 0.51	- 0.40	- 0.44
Litter depth	0.10	0.41	< 0.0272	0.27	0.38	- 0.38	- 0.51
Litter cover	0.08	0.49	< 0.047	0.08	- 0.35	- 0.54	- 0.02
Temperature variation	0.08	0.57	< 0.0322	0.30	- 0.49	- 0.34	- 0.45
Standing vegetation	0.03	0.60	< 0.0373	- 0.39	0.14	- 0.17	- 0.06
Vegetation height	0.01	0.61	< 0.0574	- 0.39	0.14	- 0.17	- 0.06

One stand type characteristic, the litter type, is influencing the microhabitat conditions in a diverse way (Welke and Hope 2005; McIver et al. 1992). It provides distinct environmental conditions due to humidity, pH, structural components, and the spectrum and availability of prey (Vargas 2000; Facelli and Pickett 1991; Magura et al. 2004). Nevertheless, the litter type did not prove to be significant in the distribution of carabid species during spring (DA, RDA) as has been shown for spider species before (Ziesche and Roth 2008). However, the litter type at each trap revealed strong importance for some species for the summer aspect as recognised by the Spearman rank correlations. A significant influence of leaf litter on carabid abundance and distribution can be attributed to abiotic factors controlling the micro-environmental conditions such as humidity, temperature and acidity (pH) as well as biotic ones like the provision of niche structures and improved food supply (Koivula et al. 1999). The amount of food is one of the most important biotic factors affecting carabid distributions (Niemelä 1990; Thiele 1977). Leaf litter accumulation may enable more species to coexist, by offering a variety of niches favoring a diverse community in a given stand (Giller 1984). Koivula et al. (1999) found litter accumulations and complexity appearing to influence the community structure of carabids and the removing of litter from plots resulted in an increased dominance of several species, which leads to distinct aggregation patterns of different carabid species at a forest stand level (Niemelä et al. 1997). Despite some species known to be strongly associated with a litter type it is difficult to separate the preference on litter structure or habitat factors, which they favour in the litter, namely prey, protection from desiccation or extreme temperatures.

Nevertheless, we found species preferring the deciduous microsites as *C. attenuatus* and *A. parallelus* and with *A. carinatus* even one species assessed only in the Douglas fir old stand, but the affinity to single habitat parameter explained most of the distribution of those species.

Among the key habitat factors affecting the microhabitat distribution of carabids were strongly abiotic parameters such as irradiation, soil pH, temperature, air humidity, and water content of the litter, respectively. Those factors explained

a great part of the species variation as determined by the discriminant, correlation and ordination (PCA, RDA) analyses. Strong gradients of these microspatial conditions became obvious during summer with the foliation of the deciduous trees and during fall with the fully developed ground vegetation. The impact of those microhabitat parameters that were not strictly attributed to the tree species itself increased during the growing season, while the covering tree species exerted its influence at all times.

Obviously, the conditions of several abiotic microhabitat parameters were affected by the degree of canopy closure, which is a result of the tree species specific crown architecture and silvicultural practice. Canopy closure has been regarded an important factor in forests, because it affects the microclimatic conditions of the lower forest strata in a diverse way (Lindh and Muir 2004; Pearce and Venier 2006; Mc Iver et al. 1992). In our study it was proven to have a profound influence on the small-scale regime of climatic conditions at the forest floor.

In our study, an increase in irradiation caused by a decrease of canopy closure was connected with a rise in temperature and air humidity. In spring the maximum temperature was a key habitat factor explaining the variance of species distribution by the RDA. The effect of the temperature decreased with the overall rising temperature from spring to summer. Thus, only the temperature variation of the summer season reflected a significant influence on the assemblage classification of microhabitat groupings anymore. Accordingly, we assume that the temperature conditions during summer season reached a satisfactory level for a number of forest species, while increased temperature variation displays more open sites with a characteristic cooling at night. Temperature and humidity have been shown to influence the abundance and distribution of carabids across habitats (Koivula et al. 1999; Magura et al. 2004). The Spearman rank correlations revealed few significant relations of ground beetle species to air humidity during summer, while many species preferred dry microhabitats in spring, e.g. areas under deciduous trees.



The results also indicate that the composition and cover of ground vegetation were of major importance. This matches the findings of ter Braak (1987) and Ysnel and Canard (2000) who derived close correlations between vegetation structure of the habitat and carabids assemblages. The share of herbs, grasses and moss covering the ground contributed significantly to the explanation of the variance (DA, RDA, Spearman rank correlations) in species composition, regardless of the covering tree species of the microhabitat groupings. The ground vegetation aspect expressed strong effects on the distribution of several species at all times, while the strong effect during spring decreased significantly for the autumn aspect ( $P < 0.01$ ), thus reflecting a seasonal shifting key factor (Hatley and Macmahon 1980; Niemelä et al. 1994a). Taxonomic diversity of ground beetles was shown to parallel that of plant diversity in successions by Southwood et al. (1979). Despite microspatial heterogeneity, habitat complexity is generally positively associated with the richness of fauna at the range of spatial scale (Uetz 1979; Humphrey et al. 1999; Hansen 2000) and recovers a diverse supply of nutrient balance, since one factor of species richness is always a resource-demanding task.

Higher vegetational diversity was found in our investigation to be correlated with higher temperature parameter throughout the season, enabling stronger decomposition rates and activity. However, there is considerable variation in the richness and abundance of understory plants among planted forest stands affected by the degree of canopy closure (Hurd and Fagan 1992; Watt et al. 1997; Wilson and Puettmann 2007) and thus by forestry management (Schowalter et al. 1986; Khanina et al. 2007). Some of this variation can be attributed to the amount of light available to understory plants (Cannell 1999). Particular dense stands of spruce and Douglas fir can cast so much shade that they appear to literally shade out the understory vegetation (Humphrey et al. 2002).

We found the moss cover influencing the distribution of species in a strong manner. While many species avoided moss-covered microsites in spring this pattern reversed during summer. This niche occupation was often promoted by humid conditions within the moss layer and even in the litter layer below.

Moreover, many species seem to adapt to the portion of natural regeneration (i.e., shrub layer), which offers possible protection from predation (Gunnarsson 1996). This applies in our study in spring, probably also for the grass cover remaining from the previous year. Thus, several species were associated to those grass patches (Fig. 4), indicating a relationship between the carabid species spectrum and the structure of plant communities, as suggested by Southwood et al. (1979) and Gunnarsson (1990).

	Stand type																							
	Douglas fir ( <i>P. mentziesii</i> )				Spruce ( <i>Picea abies</i> )						beech-spruce ( <i>Fagus sylv. – Picea abies</i> )								Oak-beech ( <i>Quercus r.-Fagus sylv.</i> )					
	YS <sup>a</sup>		MR <sup>a</sup>		YS <sup>a</sup>		MS <sup>a</sup>		MR <sup>a</sup>		YS <sup>a</sup>		MS <sup>a</sup>		MR <sup>a</sup>		eMR <sup>a</sup>		YS <sup>a</sup>		MR <sup>a</sup>		eMR <sup>a</sup>	
	D1 <sup>b</sup>	D2 <sup>b</sup>	D3 <sup>b</sup>	D4 <sup>b</sup>	P1 <sup>b</sup>	P2 <sup>b</sup>	P3 <sup>b</sup>	P4 <sup>b</sup>	P5 <sup>b</sup>	P6 <sup>b</sup>	F1 <sup>b</sup>	F2 <sup>b</sup>	F3 <sup>b</sup>	F4 <sup>b</sup>	F5 <sup>b</sup>	F6 <sup>b</sup>	F7 <sup>b</sup>	F8 <sup>b</sup>	Q1 <sup>b</sup>	Q2 <sup>b</sup>	Q3 <sup>b</sup>	Q4 <sup>b</sup>	Q5 <sup>b</sup>	Q6 <sup>b</sup>
<b>Spring</b>																								
Soil moisture	31.38	30.74	26.10	25.28	31.28	35.67	38.32	38.11	38.32	42.93	33.67	36.51	33.29	34.31	39.15	42.80	39.77	38.51	28.84	32.78	33.69	37.67	29.97	28.67
Canopy closure	46.25	42.50	40.00	40.00	78.50	69.00	50.00	52.50	38.50	50.00	45.00	67.50	42.50	45.00	40.00	49.00	31.25	41.25	41.25	30.00	38.75	35.00	44.00	38.75
Moss cover	75.00	97.50	21.25	8.75	3.75	18.75	60.00	71.25	57.50	81.25	0.00	6.25	7.50	43.75	2.50	43.75	16.25	20.00	0.00	0.00	2.50	2.50	2.50	0.00
Old grass cover	3.50	7.50	48.75	20.00	0.00	1.25	6.25	0.00	18.75	2.50	0.00	0.00	0.00	0.00	23.75	1.25	0.00	2.50	11.25	35.00	1.25	30.00	11.25	2.50
Regeneration	0.00	0.00	0.00	0.00	0.00	0.00	1.25	0.00	11.25	6.25	0.00	0.00	17.50	21.25	23.75	15.00	76.25	53.75	5.00	3.75	10.00	5.00	6.25	0.00
Herb cover	8.75	21.25	15.00	27.50	3.75	3.75	7.50	7.50	28.75	16.25	0.00	1.25	13.75	7.50	13.75	35.00	7.50	20.00	26.25	22.50	67.50	46.25	6.25	3.75
Temperature	6.92	6.46	7.41	7.78	6.49	6.63	7.04	6.86	7.18	7.00	7.19	6.33	7.00	7.08	7.53	10.10	8.04	8.33	8.25	8.54	8.30	8.03	7.46	7.66
<b>Summer</b>																								
Canopy closure	46.00	43.75	38.50	38.00	69.25	78.75	50.00	52.50	39.00	49.25	75.00	77.50	70.75	53.75	64.50	49.50	45.00	37.50	64.00	54.25	76.25	65.75	59.50	58.75
Moss cover	75.00	97.50	21.25	8.75	18.75	3.75	90.00	97.50	75.00	87.50	0.00	6.25	7.50	62.50	2.50	55.00	16.25	20.00	0.00	0.00	2.50	2.50	2.50	0.00
Regeneration	0.00	0.00	0.00	0.00	0.00	0.00	1.25	0.00	11.25	5.00	0.00	0.00	22.50	15.00	23.75	11.25	75.00	53.75	5.00	3.75	10.00	5.00	6.25	0.00
Soil moisture	41.70	38.56	33.69	37.67	51.93	48.45	40.03	52.61	47.16	40.42	47.13	41.52	34.65	33.85	51.43	43.55	45.02	52.06	31.65	33.00	34.16	32.64	32.04	32.58
Litter moisture	60.27	69.06	57.95	54.71	65.31	62.85	64.19	67.52	68.86	67.59	58.23	60.47	65.25	64.83	69.55	70.35	67.83	61.50	55.99	46.91	52.95	60.08	55.88	63.43
Herb cover	8.75	21.25	21.25	63.75	3.75	3.75	7.50	7.50	31.25	18.75	0.00	1.25	12.50	7.50	13.75	22.50	7.50	20.00	8.75	17.50	7.50	8.75	6.25	3.75
Grass cover	3.50	7.50	48.75	20.00	1.25	0.00	6.25	0.00	16.25	2.50	0.00	0.00	0.00	0.00	23.75	2.50	0.00	5.00	11.25	31.25	1.25	30.00	11.25	2.50

Spring	Soil moisture	Canopy closure	Moss cover	Old grass cover	Regeneration	Herb cover	Temp max
Soil moisture	1						
Canopy closure		-0.028					
Moss cover		0.194	0.2				
Old grass cover		-0.131	-.375**	-0.145	1		
Regeneration		.310**	-.325**	-0.009	-0.02	1	
Herb cover		-0.066	-.372**	0.061	.361**	-.363**	1
Temperature max		0.065	-.420**	-.310**	.291**	.422**	.444**

Summer	Canopy closure	Moss cover	Regeneration	Soil moisture	Litter moisture	Herb cover	Grass cover
Canopy closure	1						
Moss cover		-.601**					
Regeneration		-0.092	1				
Soil moisture		-0.078	-.027	1			
Litter moisture		-0.102	.212*	0.061	1		
Herb cover		-.569**	.236*	0.085	0.304**	1	
Grass cover		-0.188	-.263**	0.002	-0.013	-0.002	1
			-0.131	0.002	-0.171	0.086	.440**

Sign. corr. \*p < 0.05; \*\*p < 0.01.

<sup>a</sup> Age class.

<sup>b</sup> Microhabitat.

Table 6  
Environmental parameters of microhabitats for spring and summer and relations of habitat parameters (i.e. spearman rank correlations of all 96 pitfall trap data)

The vegetation cover, especially the herb and grass vegetation, had a strong impact on the species distribution throughout the season with differing effects on species. The influence of plant vegetation increases with the advanced season and we found a high degree of constancy in structure and composition of many species in similar vegetation plots on a very small scale at the trap level. This matches the findings of Thiele (1977) who derived close correlations between vegetation structure of forest habitats and carabid assemblages. Several species showed additional or enhanced adhesions to grass, moss and summer developing herb vegetation later in the season.

Structural heterogeneity due to vegetation parameters may also influence carabid communities indirectly by its positive effect on prey densities. For instance, herbivorous invertebrates reach higher densities in structurally more diverse habitats because they benefit from the greater variety of food resources themselves (Harmon et al. 2000; Siira-Pietikainen et al. 2003). The development of a diverse vegetation structure might, besides giving rise to beneficial environmental conditions, increase the niche differentiation (Greenstone 1984; Dennis et al. 1998; Ings and Hartley 1999).

## 4.6 Conclusions

Being able to describe the influence of microhabitat conditions on carabid species and assemblages is the first step to understand and predict the species distribution and therefore the impact of forestry management activities.

Our results document that in production forests the composition of ground beetle assemblages varies not only between but also within the stand types and within a forest ecosystem due to a small scaled mosaic of environmental parameters shifting with the seasons as has been recognized for spider assemblages (Ziesche and Roth 2008).

Confirming our expectations, the most important environmental parameters affecting the small-scale distribution of ground beetle species along with the seasons comprised intrinsic factors of the covering tree species (like

characteristics of the litter and deciduous or coniferous tree type) and factors not strictly attributed to the tree species itself (like canopy closure, vegetation, temperature, humidity, litter depth and pH of the soil). The results confirm the influence of forestry practice on the composition of the soil-dwelling ground beetle community – beside the selection of the tree species. Thus we conclude that forest management, resulting in a shift of environmental key factors such as light, soil moisture and air humidity, temperature aspects, and the formation of ground vegetation cause substantial changes in surface dwelling ground beetle assemblages. In production forests, these changes are generated by alterations of the degree of canopy closure by thinning or variation of the tree species spectrum. As a consequence, identical stand types most likely differ in the composition and distribution pattern of carabid assemblages, when environmental key factors care for varied microhabitat conditions. On the other hand, different stand types may correspond in their ground beetle community if they comprise the same microhabitat pattern.

Further investigations have to show if impacts on the functionality of carabids on the level of the forest ecosystem are likely to occur as a consequence of altered microspatial environmental gradients. Improving knowledge about causal mechanisms of relationships between habitat complexity and beetles are critical for the development of general principles linking habitat, functional roles and diversity (Rosenzweig and Abramsky 1993; Waide et al. 1999).

Nevertheless, the investigation on small-scale carabid distribution enhances the understanding of species requirements to habitat factors since the ecology of several carabid species in forests is still not well understood. Moreover, our results on ground beetles are likely to assume that the composition of further functional guilds and indicator taxa may show correlations to small-scale environmental conditions of a forest stand (e.g., Weaver 1995; Taylor and Doran 2001; Lindenmayer et al. 2000) and react with community alterations on human-induced habitat changes (see Charnley et al. 2007; Pohl et al. 2007). We could already show for spiders different reactions on some micro-environmental factors compared to ground beetles suggesting taxa specific reactions on management

impact (Ziesche and Roth 2008). Spiders are more related to the litter type and the canopy closure in spring while showing a lower correlation to the soil and litter layer characteristics like pH or litter depth.

Considering conservation aspects, given heterogeneity in forests due to small spatial scale gradients of environmental parameters along with the seasons will promote species diversity. This applies also for taxa like the ground beetles that are not strictly bound to the tree species like many herbivorous insects. Thus, sustainable forestry practice plays an important role for maintaining biodiversity.

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## 5 Is the age of forest habitats affecting the reproductive rate of generalist predatory ground beetle species?

### 5.1 Abstract

The study aimed at the effects of habitat age on the reproductive rate of three ground beetle species that are common and widely distributed in forest ecosystems of Europe (*Abax parallelepipedus* (Pill. & Mitt.), *Pterostichus oblongopunctatus* (F.), *Pterostichus burmeisteri* (Heer.)). The study sites comprised comparable age classes, i.e. young stands, mature stands, and mature forests with upcoming and established natural regeneration of four different forest types, namely pure stands of spruce and Douglas fir, and mixed stands of beech-spruce and oak-beech. As an indicator for the reproductive rate of female beetles, the number of ripe eggs in the ovaries and the duration of the reproduction period were investigated from captures of pitfall trapping (n = 8 per site). The dissection of a total of 1236 females uncovered 1704 eggs. A broad spectrum of environmental factors including microclimate (temperature, humidity, precipitation), soil parameters (moisture, pH, thickness and coverage of litter layer) and vegetation characteristics (coverage of moss, herb, grass, shrub and natural regeneration, degree of canopy closure) was assessed to reveal the relevant factors influencing the reproductive success.

Within the forest types the egg-load of the ground beetle species showed statistically significant relations to the age of the stand type. For *A. parallelepipedus* a quite uniform reaction pattern was evident with significantly higher egg-loads in the mature forests compared to the young stands. This was accompanied by a longer duration of the reproduction period. A stronger influence of the forest type was obvious for the egg-load of *Pt. oblongopunctatus* and *Pt. burmeisteri*. The reproductive rate was generally increasing with temperature aspects in forest sites and was significantly influenced by moisture parameters. The mean maximum temperature of the habitat cared for most of the variation in

*A. parallelepipedus* (61.4 %), while the mean minimum temperature explained 60.7% of the reproductive potential in *Pt. oblongopunctatus*. The variation of *Pt. burmeisteri* was best explained by the humidity of the air (49.4 %). Thus the results of our study emphasize the role of abiotic parameters on the reproductive rate of ground beetles.

**Keywords:** Carabidae, *Abax parallelepipedus*, *Pterostichus oblongopunctatus*, *Pterostichus burmeisteri*, forest succession

## 5.2 Introduction

The age of forest habitats with all its successional alterations is likely to influence the fitness of individual arthropods and the composition of communities including the soil-dwelling predacious taxa (Brown and Southwood 1987; Hurd and Fagan 1992; Heyborne et al. 2003). As forests in Europe are mostly human-induced environments that change continuously with the successional dynamics (Fagan 1992; Paquin and Coderre 1997; Dajoz 2000), the age of forest habitats and the resulting changes in environmental conditions are often reflected in significant effects on the relative abundance of ground beetles (Southwood et al. 1979; Niemelä et al. 1996; Butterfield 1997; Ziesche et al. 2004; Magura et al. 2003, 2006). Thus, soil dwelling carabid beetles have proved to be a useful arthropod group for monitoring and detecting changes in the environment (Eyre and Luff 1990; Rainio and Niemelä 2003) and many species are non-randomly distributed with respect to distinct environmental requirements. While the carabid species distribution pattern in forests of different tree composition is a well investigated field (Loreau 1986; Butterfield et al. 1995; Ings and Hartley 1999), the reproductive potential as a measure of habitat aptitude along the successional development of forests is still a matter of research. As a study of Van Dijk (1983) showed, the egg-load of females is considered to be a good indicator of habitat quality in this context.

As habitat age is the result of the specification of a broad variety of environmental factors, the question raises if there are specific habitat parameters that affect the reproductive potential of carabid species in forest habitats. Barone and Frank (2003) documented that increasing habitat age promoted the reproductive potential of *Poecilus cupreus* in early successional stages of wildflower meadows. This was also an effect of better nutritional condition of individuals with increasing vegetation cover (Bommarco 1998; Denys and Tschardtke 2002).

Van Dijk (1982, 1986b) found direct and sharp reactions in carabid fecundity upon experimental changes in quantities and the kind of food under constant

temperature. Quantity as well as quality and composition of available food is known to affect fitness and the egg production rate of carabid beetles in experimental studies (Mols 1979; Van Dijk 1979; Heessen 1980; Lenski 1982; Van Dijk 1983; Grüm 1984; Sota 1985; Juliano 1986; Wallin et al. 1992). Szyszko et al. (1996) suggested that changes in food availability for the larvae and adults of *Pt. oblongopunctatus* arose in the course of successional changes in forests. But on the other hand the respiration rate of adult beetles as an indicator of consumption rate decreased in this study with increasing age of forests. Food limitation during the developmental cycle of polyphagous carabids is likely to appear frequently in the course of the season (Van Dijk 1986b; Bilde and Toft 1998; Bommarco 1999) and the food availability is an intrinsic feature of the habitat (Schneider 1997), but is still less well studied (Pearson and Knisley 1985; Van Dijk 1986a).

Beside the nutritional influence on the number of eggs laid there is strong indication that microclimatic conditions during the reproductive period directly influence the reproduction rate (Van Dijk 1994). By the time only few studies considered the impact of detailed environmental conditions on carabid reproduction in the course of forest succession. As for example the egg production has found to be highly temperature dependent under constant feeding conditions in laboratory studies (Van Dijk 1979, 1982, 1983; Ernsting and Huyer 1984). Usually it is a complex of factors, like food availability, temperature and humidity, that determines the egg production in the field (Thiele 1975, 1977; Van Dijk 1986a; Begon et al. 1992).

The aim of this study was to test the thesis that the reproductive rate of various ground beetle species is affected by the age of forest habitats. Moreover, it is assumed that the relation between habitat age and reproductive rate is due to the performance of environmental parameters varying with the characteristic features of the successional stages. Thus, the reproductive rate of three common silvicolous ground beetle species (*A. parallelepipedus*, *Pt. oblongopunctatus*, *Pt. burmeisteri*) was examined in four forest types of different age classes.



### 5.3 Methods and materials

#### Study sites

The investigation was carried out in the cultural landscape around Augsburg (48°19′/11°06′, Central Bavaria, South Germany), with a high share of forested area. The study area belongs to the tertiary hill country of the government district Swabia. It is predominantly characterized by a subatlantic climate with annual mean temperatures of 7.5 to 8.0 °C. The average of annual precipitation ranges between 700–900 mm. The soils developed on these sites are fertile brown and parabrown earths. They originate from sediments of the Upper Miocene, overlaid by a fine, more or less mighty loam layer which is derived from loess loam.

The study sites (n = 12) comprised forest ecosystems of four different tree species compositions (stand type), which are representative for the cultural landscapes of South Germany: pure stands of spruce (*Picea abies*) and Douglas fir (*Pseudotsuga menziesii*), mixed stands of beech and spruce (*Fagus sylvatica*, *Picea abies*), as well as mixed stands of oak and beech (*Quercus robur*, *Fagus sylvatica*). The following age classes (successional stages) were included in the study design, as far as they were part of the silvicultural practice of the stand type and present in the study area: young stand (YS), mature stand (MS), mature stand with upcoming (MR) and established regeneration (eMR; Table 1). The age classes referred to silvicultural thinning measures representative for regional forestry practice (YS: age class of young stands which passed through the first thinning measure after planting of trees; MS: age class of mature stands before thinning measures to promote natural regeneration; MR: age class of mature stands after thinning measures to promote natural regeneration).

The study sites corresponded in terms of altitude, soil and macroclimatic conditions, namely mean annual rainfall and mesoclimatic temperature.

In the center of each study site (1ha) a core investigation area of 50 x 50m was established for the sampling of ground beetles and the assessment of

environmental parameters. The core area of each study site was surrounded by a belt of at least 25 m of forest of the same tree composition representing a buffer zone (Molnár et al. 2001) and beyond that by further forest ecosystems up to a distance of several kilometres, to exclude side effects from adjacent forests.

**Table 1**

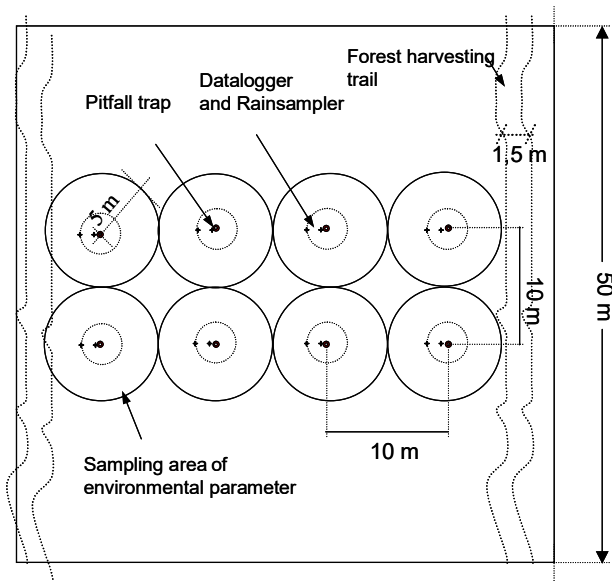
Characteristics of the study sites (1 ha) – Age class: YS (young stand), MS (mature stand), MR (mature stand with upcoming natural regeneration), eMR (mature stand with established regeneration) – \* The degree of canopy closure refers to the summer aspect under complete foliation, the same applies to relative air humidity and soil moisture

Stand structure	Pure stand						Mixed stand					
	spruce (YS)	spruce (MS)	spruce (MR)	Douglas fir (YS)	Douglas fir (MR)	beech - spruce (YS)	beech - spruce (MS)	beech - spruce (MR)	beech - spruce (eMR)	oak - beech (YS)	oak - beech (MS)	oak - beech (eMR)
Stand composition	<i>Picea abies</i>			<i>Pseudotsuga menziesii</i>		<i>Picea abies / Fagus sylvatica</i>				<i>Quercus robur / Fagus sylvatica</i>		
Stand age [years]	30	62	89	15	80	38	73	89	105	28	75	112
Vegetation cover average [%]	4.4	10.6	34.4	20.5	86.9	0.64	10	31.3	16.3	34.4	23.8	11.9
Canopy closure [%] in summer	69-79	50-53	38-50	42-46	38-43	67-82	45-72	49-69	18-46	45-68	54-83	48-70
T d - season [C°]	10.57	11.25	11.50	10.79	11.62	10.48	11.25	11.58	11.32	10.97	11.23	11.54
T min [C°] in summer	12.34	13.07	13.32	12.73	13.73	12.35	13.31	13.35	12.93	12.97	13.32	13.75
Humidity air [%] in summer	79.63	92.74	89.19	69.49	91.29	75.0	52.5	88.1	89.53	49.69	74.27	56.04
Soil moisture [%] in summer	50.19	46.32	43.79	40.13	32.58	44.32	34.25	47.49	48.54	32.33	33.40	32.31
Upper soil pH <sup>H<sub>2</sub>O</sup>	3.5-4.1	3.4-3.8	3.3-3.8	4.48-4.96	3.98-4.26	3.58-4.16	3.73-4.06	3.55-4.05	3.49-4.03	4.54-4.86	3.98-4.91	4.06-4.18

**Sampling of carabid beetles and assessment of the reproductive rate**

Carabid beetles were sampled by pitfall trapping (8 replicates per study site, volume: 370 ml,  $\varnothing = 7.5$  cm, fixing agent: solution of saturated benzoic acid and detergent). The traps were arranged in the center of a core area (50 x 50 m) of the study site in two linear transects with 4 traps each. The distance of the traps between and within the transects covered 10 m (Fig. 1). The study period started on March 12<sup>th</sup> and lasted until October 22<sup>th</sup> of 2002. The pitfall traps were emptied every 4 weeks.

To assess the reproductive rate of the ground beetle species the number of ripe eggs in the ovaries and oviducts of the females was analysed (Van Dijk 1983). The females, preserved in pure alcohol, were dissected according to Renner (1999). To complete the picture about the reproduction pattern, the duration of the reproduction period was calculated from sampling intervals with females carrying developed eggs. The proportion of females carrying eggs was calculated likewise from the total catch-results of females in pitfall traps of each study site.



**Fig. 1** Design of data sampling in the core investigation area (50 x 50 m) within each study site (1 ha)

### Assessment of environmental variables

During the study period twenty five environmental parameters were recorded for statistical analyses regarding the influence of habitat factors of forest successional stages on the number of eggs in the ovaries. Soil temperature was measured continuously during the investigation period every 45 minutes at each trap ( $n = 8$  per study site ( $\Sigma = 96$ ) in a depth of 1 cm in the litter layer) by data loggers (Tinytalk II, TK – 0023, Spectra Computersysteme, Leinfelden-Echterdingen), air temperature and humidity every 90 minutes twice in a trap line ( $n = 2$  per study site ( $\Sigma = 24$ ) 80 cm above the ground) by Tinytags Ultra (TG 1500, Spectra Computersysteme Leinfelden-Echterdingen). From the recordings were calculated daily, monthly and seasonal (spring: March 8<sup>th</sup> to June 5<sup>th</sup>, summer: June 6<sup>th</sup> to August 28<sup>th</sup>, fall: August 29<sup>th</sup> to October 23) values of mean temperature and air humidity, mean minimum and maximum temperature, the temperature variation between  $t_{\min}$  and  $t_{\max}$ , the number of days with a mean temperature above 8 °C.

The temperature aspects were also applied to the time span of reproduction for each species (i.e., *A. parallelepipedus*: 08.03.–27.08., *Pt. oblongopunctatus*: 12.03.–30.07., *Pt. burmeisteri*: 10.04.–27.08.). The precipitation was measured at each pitfall trap by rain samplers (funnel diameter: 7.6 cm) gathering the precipitation of four week intervals, which corresponded with the sampling periods of ground beetles. Also every 4 weeks the composition and thickness of the litter layer was recorded in a radius of 1 m around each trap, the cover value of litter in a radius of 5 m around each trap. At the same time intervals structural parameters of the vegetation were assessed within a radius of 5 m around each pitfall trap including an estimation of the degree (%) of canopy closure and - according to Braun-Blanquet (Mühlenberg 1989) - the coverage (%) and standing height (cm) of moss, herbs, grass and natural regeneration. Species composition of the vegetation (moss, herb, grass, shrub layer) as well as soil and litter samples for the determination of moisture (% water content; Scheffer and Schachtschnabel 1989) and  $\text{pH}_{(\text{H}_2\text{O})}$  were taken in spring (April 9<sup>th</sup>), summer (July 30<sup>th</sup>) and fall (September 24<sup>th</sup>) of 2002.

### **Statistical analyses**

Statistical analyses were based on the software SPSS 11.5. To test the impact of the successional stage of each forest type on the number of eggs in the ovaries of species one-way ANOVA was applied on trap level followed by Tukey's honestly significant difference test (HSD).

To acquire the correlation between mean egg-loads and mean environmental parameters of the study sites ( $n = 12$ , on site level) a stepwise multiple linear regression analysis was performed for each species. The data of each pitfall trap of sites ( $n = 8$ ) were averaged over time for the analyses. Subsequently a regression model with the significant habitat factors explaining the gradient in the egg-load of ground beetle species was run. To analyse the influence of habitat age on egg-load the regression analysis was performed for all stand types classified in age classes ( $n = 4$ , YS, MS, MR, eMR).

A stepwise multiple linear regression analysis was performed to elucidate the effects of specific environmental habitat parameters on the number of eggs produced per female in each species based on the results of single pitfall traps ( $n = 96$ , on microhabitat level). Spearman rank correlations of mean egg numbers per female were applied to reveal correlations between the egg-load and the environmental conditions for each trap and species (significance level:  $P^{**} < 0.01$ ,  $P^* < 0.05$ ).

## 5.4 Results

The species *Abax parallelepipedus*, *Pterostichus oblongopunctatus* and *Pterostichus burmeisteri* counted for 3218 specimen and made up 74.7% of the total catch of ground beetles. *A. parallelepipedus* and *Pt. oblongopunctatus* are known as eurytopic generalists and were caught at each study site in almost every pitfall trap. *Pt. burmeisteri* was nearly missing at two study sites (beech-spruce: eMR; Douglas fir. MR) and additionally missing in single pitfall traps of other study sites (Table 2). Consequently, on these sites the sample size of *Pt. burmeisteri* was too low to judge potential effects of habitat age on the reproductive rate.

In total, 1174 eggs were detected in *Pt. oblongopunctatus*, 217 eggs in *A. parallelepipedus* and 313 eggs in *Pt. burmeisteri*. The variance in egg size lined 0.8–0.85 mm in *Pt. oblongopunctatus*, 2.4 – 2.52 mm in *Pt. burmeisteri* and 3.12 – 3.24 mm in *A. parallelepipedus*. The number of eggs in the ovaries of individual females varied within each species between 1–15 in *A. parallelepipedus*, 1–14 in *Pt. oblongopunctatus* and 1–23 in *Pt. burmeisteri*.

**Egg-load of ground beetle species at forest stands differing in tree species composition and age class**

In all forest types – except the pure stands of Douglas fir – the egg-load of the ground beetle species showed statistically significant relations to the age of the stand type (Table 3). However, the effects of habitat age on the egg-load varied between the ground beetle species and the forest types (Table 3).

A clear and uniform relation between habitat age and egg-load of the ovaries was obvious for *A. parallelepipedus* (Table 3). The females of *A. parallelepipedus* carried significantly more ripe eggs at the older (MS, MR, eMR) than at the young stands of spruce, beech-spruce and oak-beech (Table 3). Between the age classes of mature forests (MS, MR and eMR) the egg-load did not differ significantly. Although, at spruce and beech-spruce there was a tendency of decreasing egg-load of the females at stands with upcoming (MR) or established regeneration (eMR), respectively.

**Table 2**

Number of adult beetles (males, females) of *A. parallelepipedus*, *Pt. oblongopunctatus* and *Pt. burmeisteri* in forests of different tree species composition and age class - according to pitfall catches during the vegetation period of 2002

Stand structure	Pure stand					Mixed stand						
Stand composition	spruce (YS)	spruce (MS)	spruce (MR)	Douglas fir (YS)	Douglas fir (MR)	beech- spruce (YS)	beech- spruce (MS)	beech- spruce (MR)	beech- spruce (eMR)	oak- beech (YS)	oak- beech (MS)	oak- beech (eMR)
	<i>Picea abies</i>			<i>Pseudotsuga menziesii</i>		<i>Picea abies</i> / <i>Fagus sylvatica</i>				<i>Quercus robur</i> / <i>Fagus sylvatica</i>		
Stand age (years)	30	62	89	15	80	38	73	89	105	28	75	112
<i>A. parallelepipedus</i>	33	47	31	103	182	32	137	89	93	36	96	98
male:	17	23	15	74	99	25	89	55	55	20	57	71
female:	16	24	16	29	83	7	48	34	38	16	39	27
(fem. with eggs):	(26%)	(43%)	(71%)	(15%)	(12%)	(40%)	(28%)	(38%)	(27%)	(8%)	(11%)	(27%)
<i>Pt. oblongopunctatus</i>	21	129	220	82	58	53	179	313	55	86	28	202
male:	11	68	132	52	36	34	112	186	32	43	15	113
female:	10	61	88	30	22	19	67	127	23	43	13	89
(fem. with eggs):	(30%)	(53%)	(57%)	(63%)	(65%)	(50%)	(83%)	(69%)	(58%)	(73%)	(50%)	(66%)
<i>Pt. burmeisteri</i>	11	31	80	17	2	53	101	201	2	130	142	45
male:	8	21	58	14	2	41	83	148	1	66	79	27
female:	3	10	22	3	0	12	18	53	1	64	63	18
(fem. with eggs):	(33%)	(30%)	(14%)	(0%)	(0%)	(8.3%)	(23.5%)	(11.5%)	(100%)	(23%)	(6.4%)	(22%)

A stronger impact of the specific stand type on the number of ripe eggs was evident for *Pt. oblongopunctatus* and *Pt. burmeisteri* (Table 3). In the pure spruce stand series the egg-load pattern of *Pt. oblongopunctatus* and *Pt. burmeisteri* corresponded with that of *A. parallelepipedus*, showing the significantly lowest reproductive rate in the young stand (YS), the highest in the mature stand (MS). The differences between YS and MR were significant for all species, the differences between MR and MS only for *Pt. burmeisteri* (Table 3). At the beech-spruce stands females of *Pt. oblongopunctatus* carried a high load of ripe eggs in all age classes, except the mature stand with established regeneration (eMR). Considering beech-spruce, *Pt. burmeisteri* carried the lowest number of ripe eggs



in the young stand and the mature stand with established regeneration. In the oak-beech series the egg-load of females decreased with increasing age of the forest habitat (Table 3).

In the oak-beech stands the egg-load of *Pt. oblongopunctatus* was high in the young stand, decreased to the lowest level in the mature stand and reached its (statistically significant) maximum in the mature stand with established regeneration.

**Table 3**

Number of ripe eggs (mean±SD) per female in *A. parallelepipedus*, *Pt. oblongopunctatus*, *Pt. burmeisteri*, in forests of different tree species composition and age class, according to the catch results of pitfall traps during the vegetation period 2002. Egg-loads marked with the letter “a” differed significantly from egg-loads marked with the letter “b” according to one-way ANOVA, Tukey-HSD-test ( $P < 0.05$ )

*A. parallelepipedus*

	YS	MS	MR	eMR	df	F	P
Spruce	0.63 ± 1.41 a	2.02 ± 2.03 b	1.69 ± 2.15 b		2.21	14.621	<0.001
Beech-pruce	0.63 ± 1.77 a	1.53 ± 1.64 b	1.56 ± 1.59 b	1.13 ± 1.46 b	3.28	3.209	<0.038
Oak-beech	0.01 ± 0.04 a	1.13 ± 1.89 b		1.25 ± 2.44 b	2.21	15.974	<0.001
Douglas fir	1.00 ± 1.41 a		1.21 ± 1.19 a		2.21	10.369	<0.001

*Pt. oblongopunctatus*

	YS	MS	MR	eMR	df	F	P
Spruce	0.81 ± 1.51 a	3.87 ± 1.02 b	2.90 ± 1.21 b		2.21	12.19	<0.001
Beech-spruce	3.19 ± 2.59 a	3.89 ± 1.82 a	4.15 ± 1.00 a	1.46 ± 2.02 b	3.28	13.771	<0.001
Oak-beech	2.82 ± 1.66 a	1.63 ± 2.26 a		4.19 ± 0.95 b	2.21	18.708	<0.001
Douglas fir	3.46 ± 2.04 a		2.36 ± 2.73 a		2.21	2.286	<0.201

*Pt. burmeisteri*

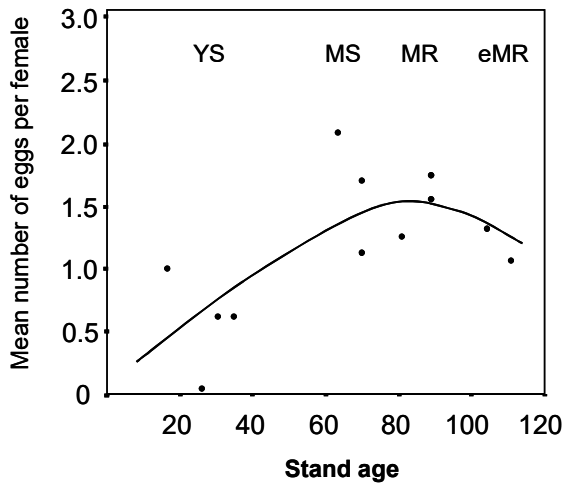
	YS	MS	MR	eMR	df	F	P
Spruce	0.01 ± 0.03 a	1.92 ± 4.05 b	0.13 ± 0.35 a		2.21	29.729	<0.001
Beech-Spruce	0.01 ± 0.02 a	4.13 ± 5.05 b	1.46 ± 2.74 b	0.01 ± 0.02 a	3.28	182.997	<0.001
Oak-beech	4.94 ± 4.39 a	2.00 ± 5.66 b		1.75 ± 4.95 b	2.21	44.634	<0.001
Douglas fir	0 ± 0		0 ± 0		2.21	0.0	<0.001

## Effect of environmental parameters on the egg-load of carabid species

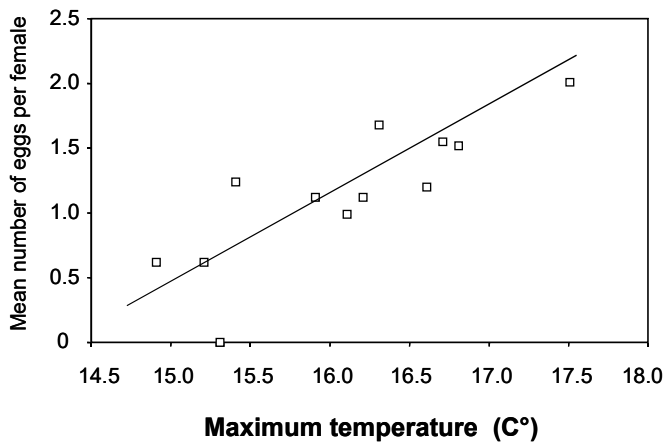
### On site level

The stepwise multiple linear regression analysis for each species revealed different habitat factors explaining the gradient in site specific egg-load. As the linear regression analysis uncovered, the habitat age was no significant criterion for *Pt. burmeisteri* and *Pt. oblongopunctatus*. For *Abax parallelepipedus* it accounted for 33.3 % of the variation of egg-load ( $F_{1,10} = 5.024$ ,  $R^2 = 0.333$ ,  $P = 0.049$ ,  $n = 12$ ). The low degree of explanation of variance is shown to be attributed to the low eggload in mature forests with established regeneration (Fig. 2).

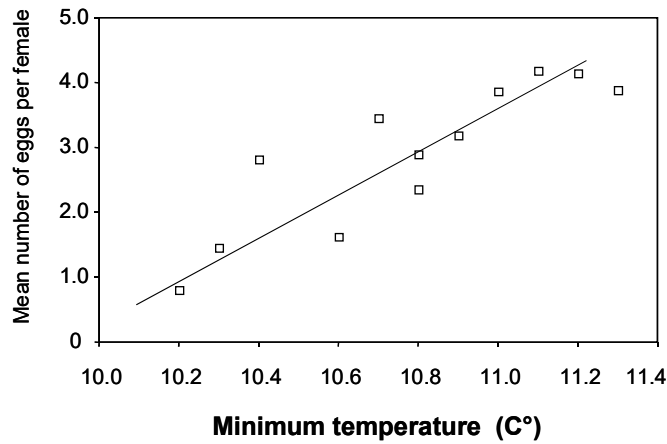
The result of a regression analysis of the relation of mean maximum soil surface temperature and the egg-load of *A. parallelepipedus* is displayed in Figure 3. This abiotic parameter explained 61.4 % of the variation in a regression model (multiple stepwise forward) (Fig. 3). Adding the thickness of the litter layer explained 79.8 % of the variation, adding additionally the litter moisture 83.9 % ( $F_{1,9} = 17.818$ ,  $R^2 = 0.839$ ,  $P = 0.001$ ,  $n = 12$ ). The variation in egg-load at site level for *Pt. burmeisteri* was best explained by the humidity of air (49.4 %, negative), the mean maximum soil surface temperature and the degree of canopy closure accounting for 91.5 % ( $F_{1,8} = 28.865$ ,  $R^2 = 0.915$ ,  $P = 0.0001$ ,  $n = 12$ ), while the egg production in *Pt. oblongopunctatus* was found to increase with the mean minimum soil surface temperature explaining 60.7 % of variation (Fig. 4). The vegetation parameters had no significant effect on the species egg-load.



**Fig. 2** Egg-load (mean±SD) per female of *A. parallelepipedus* in the different age classes of all forest types ( $F_{1,10} = 5.024$ ,  $R^2 = 0.333$ ,  $P = 0.049$ ,  $n = 12$ ).



**Fig. 3** Relationship between the number of eggs in the ovaries of *A. parallelepipedus* and the mean maximum soil surface temperature of the different age classes of the forests during the reproduction period (8<sup>th</sup> of March till 27<sup>th</sup> of August). according to the results of the regression analysis ( $F_{1,10} = 15.91$ ,  $R^2 = 0.614$ ,  $P = 0.003$ ,  $n = 12$ ).



**Fig. 4** Relationship between the average egg-load in the ovaries of *Pt. oblongopunctatus* and the minimum soil surface temperature of study sites within the reproduction period of March to August according to the results of the regression analysis ( $F_{1,11} = 15.447$ ,  $R^2 = 0.607$ ,  $P = 0.003$ ,  $n = 12$ ).

#### **On microhabitat level**

The spearman rank correlations and the multiple linear regression analyses revealed the environmental parameters relevant for the egg-load per female at each pitfall trap (Table 4). *A. parallelepipedus* showed highly significant enhanced egg-loads at microsites with lower pH of the litter layer, increased air humidity and soil temperature (spearman  $\rho$   $p < 0.01$ ).

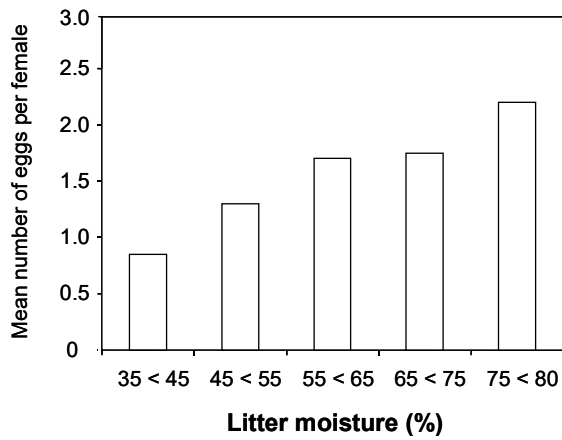
**Table 4**

Results of the Spearman rank correlations and regressions of environmental parameters and the egg-load of ground beetle species. Highly significant negative or positive correlations are underlined. The significant parameters according to the stepwise forward regression analyses are marked by (R). Spearman rho given for significant correlations (\*  $p < 0.05$ , \*\*  $p < 0.01$ )

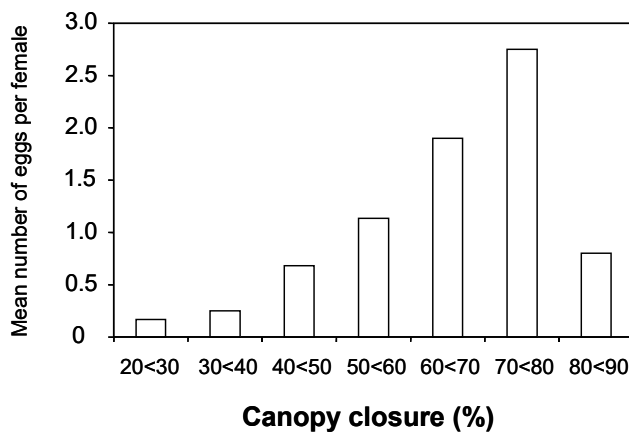
	<i>A. parallelepipedus</i>	<i>Pt. burmeisteri</i>	<i>Pt. oblongopunctatus</i>
habitat age (y)	.218(*)		
litter depth (cm)	.212(*)		
T max (C°)	<u>.236(**)</u>		
T min (C°)			.217(*)
canopy closure (%)		<u>.246(**)</u>	
moss cover (%)	.211(*) (R)	<u>-.243(**)</u>	
litter pH	<u>-.246(**)</u> (R)		
soil pH	-.170(*)		.187(*)
litter moisture (%)	.221(*)		(R)
soil moisture (%)		-.219(*)	
regeneration cover %		.202(*)	
grass cover (%)		.175(*)	
dead wood (%)			-.236(*) (R)
litter cover (%)			-.237(*) (R)
humidity air (%)	<u>.238(**)</u>	<u>-.388(**)</u> (R)	-.200(*) (R)

Significant at the level:  
 Spearman rank correlation \*\* P < 0.01  
 Spearman rank correlation \* P < 0.05

	<b>Ecological preference according to Thiele (1977)</b>		
temperature	eurythermic	cold preferent	eurythermic
humidity	xerophilic	xerophilic	hygro- & mesophilic
light	dark preferent	dark preferent	euryphotic



**Fig. 5** Relationship between the mean number of eggs found in the ovaries of *Pt. burmeisteri* and the degree of canopy closure based on the results of the stepwise regression analyses on microhabitat level (n = 96).



**Fig. 6** Relationship between the mean egg-load per female of *Pt. oblongopunctatus* and the water content of the litter layer in spring time based on the results of the stepwise regression analyses on microhabitat level (n = 96).

In addition, significant ( $P < 0.05$ ) effects were obvious for litter moisture, habitat age, litter thickness, the share of soil surface covered with moss, and the soil pH (Table 4). For *Pt. burmeisteri* the spearman rank correlation analysis identified significantly increased egg-loads per female at microsites with dry air conditions (this was confirmed by multiple linear regression analysis), with a high degree of canopy closure (Fig. 5), and low moss cover (Table 4). Additionally, a higher level of egg-load was found in patches of decreased soil moisture, as well as in patches covered with natural regeneration or grass (Table 4). Higher egg-loads of *Pt. oblongopunctatus* were positively correlated with minimum soil surface temperatures and the pH of the soil (Table 4). Extended litter cover and air humidity were leading to a significantly lower number of eggs in the ovaries of this ground beetle species. In addition, the linear regression analysis revealed the litter moisture as a strong impact factor for the egg-load (Fig. 6). The age of the study sites had no significant effect on the species egg-load on the basis of single trap data in the latter two species.

#### **Time span of females carrying eggs**

Referring to *A. parallelepipedus* the time span of pitfall trapped females carrying eggs lasted longer in the mature forests (MS, MR) compared to the young stands and the oldest sites (eMR) (Table 5). Only with the Douglas fir forests the reproduction period did not depend on the age class of the stands.

The deviating pattern of *Pt. burmeisteri* and *Pt. oblongopunctatus* in the oak-beech age class series was obvious: The egg carrying period of these ground beetle species in the young stand (YS) reached or exceeded that of the oldest site (eMR). The females in the mature site (MS) generated eggs for a decreased period of time, which corresponds with the egg-load pattern per female. The majority of females in *Pt. oblongopunctatus* carrying eggs were assessed in spring and early summer (10.04.–02.07.), while the female capture in *A. parallelepipedus* (07.05.–27.08.) and *Pt. burmeisteri* (07.05.–27.08. / 22.10.) prevailed between late spring and fall.



**Table 5**

Time span of females carrying eggs during the investigation period of 2002. The numbers representing the percentage of assessed females with eggs in the ovaries

Stand structure	Pure stands						Mixed stands					
	<i>spruce</i>			<i>Douglas fir</i>			<i>beech-spruce</i>			<i>oak-beech</i>		
Stand composition	(YS)	(MS)	(MR)	(YS)	(MR)	(YS)	(MS)	(MR)	(eMR)	(YS)	(MS)	(eMR)
<i>A. parallelepipedus</i>												
12.03.-10.04.												
11.04.-07.05.												
08.05.-04.06.	50	10		29	27		55	17	19		30	27
05.06.-02.07.		70	50	57	33		9	8		100	50	
03.07.-30.07.	50	10	43	14	40	100	27	42	75		20	64
08.07.-27.08.		10	7				9	33	6			
28.08.-24.09.												
25.09.-22.10.												9
<i>Pt. oblongopunctatus</i>	(YS)	(MS)	(MR)	(YS)	(MR)	(YS)	(MS)	(MR)	(eMR)	(YS)	(MS)	(eMR)
12.03.-10.04.		2	6		5		1	7		2		
11.04.-07.05.		14	32	29	42	22	33	29		20	60	7
08.05.-04.06.	75	82	36	47	53	44	34	44	97	65	20	70
05.06.-02.07.	25	2	26	18		33	28	18		11	20	19
03.07.-30.07.				6								4
08.07.-27.08.												
28.08.-24.09.								1				
25.09.-22.10.							5	1	3	2		
<i>Pt. burmeisteri</i>	(YS)	(MS)	(MR)	(YS)	(MR)	(YS)	(MS)	(MR)	(eMR)	(YS)	(MS)	(eMR)
12.03.-10.04.												
11.04.-07.05.												
08.05.-04.06.							25	18		13	20	25
05.06.-02.07.		20					75	27	100	10		
03.07.-30.07.	100		67			100		9		55	80	50
08.07.-27.08.		20						45		16		
28.08.-24.09.												
25.09.-22.10.		60	33							6		25

## 5.5 Discussion

With the capture and dissection of female ground beetles a moment survey of fecundity was assessed, since carabids lay eggs over a period of time during the reproductive season (Den Boer 1968; Thiele 1977). The amount of reproduction is a highly variable feature of individual females (Van Dijk 1979) and even age-dependent in ground beetles (Van Heerdt et al. 1976) (in *Calathus melanocephalus*, *Pterostichus coerulescens*). However, each female has a characteristic level of reproductive rate which varies only slightly with time under constant and optimal conditions (Van Dijk 1979). Van Dijk (1981, 1986a) showed for several species that there is generally a relationship between the weekly number of eggs in the ovaries and the weekly number of eggs laid. Thus, the egg-load of the ovaries seems to be a good indicator for the reproductive rate of ground beetle species in the field.

Confirming our hypothesis, we could clearly show in this investigation, that - except for Douglas fir stands - the age of forests is affecting the reproductive rate of ground beetle species. But the reaction pattern was species specific. A quite uniform reaction pattern was evident for *A. parallelepipedus*. For that species the reproductive rate increased with the age of forest stand. In *Pt. oblongopunctatus* and *Pt. burmeisteri* the reaction depended on the cover tree species.

As the egg-load is considered to be an indicator of the habitat quality (Van Dijk 1983), the results document strong alterations in the suitability of different age classes of forests for ground beetle species. This impression was confirmed by analysing the time span of females carrying eggs. Hence, longer periods of egg-production were documented at sites of increased egg-load per female. Those habitats also favour the duration of the reproduction period and likely the number of generations involved in egg production (Van Heerdt et al. 1976) and thus the fecundity. The increased egg production as well as the increased time period of reproduction might as a matter of fact promote the stability and growth of a population.

Moreover, the species specific relation between habitat age and reproductive rate indicate the influence of distinct environmental parameters on the reproduction level of a species. Van Dijk (1979, 1994) found that the reproduction level depends beside the availability of food on weather conditions.

The statistical analyses revealed the maximum temperature for *A. parallelepipedus* (61.4%) and the minimum temperature for *Pt. oblongopunctatus* (60.7%) to be an important impact factor influencing the egg-load of females in the forest habitats. The egg-laying period as well as the number of eggs laid per female were affected by temperature aspects in a beneficial way for all three species. Thiele (1977) stated that even forest species, living generally under lower temperature conditions than open land species, benefit from increased temperature. Apart from individual differences between females (Van Dijk 1979), the temperature will contribute considerably to the variation in numbers of eggs laid per female (Van Dijk 1983; Lenski 1984; Mols 1988, Van Dijk and Den Boer 1992). Also the number of eggs laid and temperature have shown to be highly correlated under constant feeding conditions (Ernsting and Huyer 1984). Thus, also *Pt. burmeisteri*, a cold and dark preferring species, carried increased egg-loads in the ovaries at sites of high maximum temperatures.

To reveal the effects of environmental parameters on the egg-load of ground beetle species on a microhabitat level we conducted analyses on single pitfall trap level, because a considerable variation of species distribution and environmental conditions on a small scale level has been measured. Similar small scale distribution patterns, which are maintained over periods of time (Baars 1979; Brunsting 1981, 1983), have been described in earlier investigations on forest carabids (Niemelä et. al 1996; Antvogel and Bonn 2001). There are also strong indications that females show distinct preferences for certain microhabitats within a forest to lay their eggs. Reise and Weidemann (1975) described the patchy distribution of adult and larval stages in *Pt. oblongopunctatus*. Thiele (1977) observed a difference in habitat affinity of male and female ground beetle species in forests, which he referred to certain egg-laying behaviour. Huk and Kühne (1999) described behavioural differences in *Carabus clathratus* females after

copulation, which indicates that oviposition site selection is an important factor in the life cycle of some carabid beetles.

Our investigation revealed significantly more eggs in the ovaries of females in places of ecologically preferred habitat conditions (Thiele 1975, 1977; Koch 1989) in the studied ground beetle species. Thus, the egg number per female analysed on single trap level increased significantly under moist litter conditions and was positively influenced by the temperature parameters in *A. parallelepipedus* and *Pt. oblongopunctatus*. Thiele (1977) observed in temperature gradient experiments that the females of *Pt. oblongopunctatus* seek for higher temperatures than the males and in doing so they choose a temperature that corresponds to the improved natural conditions of the larvae, laying their eggs in a site that is thermally suited to the needs of the hatching larvae. Van Dijk and Den Boer (1992) found, when taking the results of rearing carabid beetles into account, that abiotic factors, especially temperature and soil moisture, largely determine the survival of all three larval stages. The litter moisture may play an important role in protecting carabids from desiccation and may improve the density of prey. Huk and Kühne (1999) showed for the hygrophilous *Carabus clathratus* a significant substrat- and soil moisture selection in egg-laying behaviour regarding to the habitat preference of the adult beetles and it becomes reasonable that the favourable conditions for the development of the less mobile offspring stages are leaned towards the preferences of adult beetles and that reproductive success is strongly dependent on breeding site characteristics (Bernado 1996; Rudolf and Rödel 2005). Also, soil and litter moisture and humidity of the air of the study sites showed a strong impact on the reproduction of the species on the site level, as has been shown to promote carabid assemblages in a study of Magura et al. (2006).

In addition, females of *Pt. oblongopunctatus* are known to prefer for the egg deposition the well structured litter (Heessen 1980), perhaps making it more difficult for predators to prey on eggs and thus reduce the egg mortality, compared to low structured litter layers. However, extended litter cover was not leading to increased egg-loads as has been observed for the activity density of adults that

increased in plots of added leaf-litter in a study of Koivula et al. (1999) and Magura et al. (2004).

Thiele (1977) described *Pt. burmeisteri* as a cold preferent, xerophilic and dark preferent forest species, which was reflected in the reproduction value of female beetles. In our study, the reproduction of *Pt. burmeisteri* was increased in dry microhabitats under closed canopy. Besides, we found that microhabitats with natural regeneration and dense grass cover resulted in an increased egg-load. Also highly significant for *Pt. burmeisteri* was the decrease in egg-load at microsites covered only with moss. The regeneration and grass vegetation may as well serve as a shelter against predation and desiccation for this species (Sanderson et al. 1995). Barone and Frank (2003) found that fecundity and nutritional state of *P. cupreus* were promoted by increased vegetation cover in wildflower meadows.

## 5.6 Conclusion

Despite the study of only one age-class set of stand types due to logistic difficulties and the time intensity of the investigations, we found distinct habitat parameters influencing the egg-load in three forest carabid species of coniferous and deciduous woods. Especially temperature conditions significantly influenced the reproduction in a positive way in all species at study site level, as well as the litter moisture in *A. parallelepipedus* and *Pt. oblogonpunctatus* in a positive and humidity and soil moisture in *Pt. burmeisteri* in a negative way. While female choice of favourable microhabitat conditions for egg deposition enhances the chance for development of subadult and survival of adult stages (Paarmann 1966; Rudolf and Rödel 2005) we assume that presence and frequency of patches with species specific favourable environmental conditions in a forest ecosystem play an important role in carabid fecundity.

The results document, when discussing the factors limiting and improving the reproductive rate and the survival of subadult and adult beetles in nature it depends not only on the availability of food (White 1978; Van Dijk 1981; Dempster and Pollard 1981), but also on abiotic habitat parameters. Moreover, the

accessibility of food in the field is significantly influenced by the fact that the amounts and nutritional qualities of food together with the activities of the beetles will also be influenced by weather conditions (Van Dijk 1982), since prey species also react on abiotic factors (Van Dijk and Den Boer 1992). The impact of temperature on the reproduction of ectotherms (Huey and Berrigan 2001) has been described in laboratory studies, which not only affects the egg production (Ernsting and Isaak 2000), but also the egg size and thus the size of the first larval stage (Ernsting and Isaak 1997), the feeding rate of larvae and adults (Ernsting et al. 1992), the duration of development (Heessen et al. 1982) and mortality rate of subadult stages (Heessen and Brunsting 1981). Those factors also contribute to the size of single females and reproduction processes in a population (Wallin et al. 1992; Bommarco 1999). Consequently, the measured habitat parameters care to a great extent for the explanation in the variance of reproductive rate of ground beetles. Because these intrinsic habitat parameters often change with successional stages (Dajoz 2000), effects of forest age on the reproductive rate of carabid beetles are demonstrated

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## **6 General Discussion**

### **Spiders and carabids**

The stand type affects important environmental conditions that contribute to the formation of spider and carabid assemblages in temperate forests. There are different key factors for spiders and carabids (Chapter 2 and 4). Most effects are not bound to the tree species, but to the environmental modifications triggered by the covering tree species on a very small spatial scale (Chapter 3). In addition effects of key factors change with annual season and stand age (Chapter 2 and 4). So, population traits are influenced by stand age (Chapter 5), and can also be affected by management strategies.

I chose four stand types for the investigation of temperate forests representing pure (spruce, Douglas fir) and mixed forests (beech–spruce, oak–beech). The different stand types and age classes of the production forests generated a high variation of microhabitat conditions in the course of the studied seasons. The investigation revealed a species–rich spider and carabid fauna and many species proved to be non–randomly distributed at the forest floor. The broad spectrum of microhabitats allowed me to reveal specific responses of species to a variety of micro–environmental parameter gradients and furthermore a very sensitive segregation of species assemblages.

### **Environmental factors**

Composition of the spider and carabid assemblages was not strictly defined by the covering tree species or the age class of a forest, and single species were barely restricted to a single tree species or stand type during the whole season (Chapter 2 and 4). However, stand type characteristics became obvious for single

seasonal aspects and contributed to the composition of assemblages. The results display a considerable impact of environmental factors (Chapter 2 to 4).

Stand type characteristics became obvious. The species composition of microhabitats in spring suggests that there are intrinsic key parameters of the tree species, affecting the composition of spider and carabid assemblages. One of these characteristics was displayed by the degree of foliation separating evergreen from deciduous stands during spring season until the foliation of the deciduous trees was completed. Among the strongest environmental factors contributing to the explanation of spider species distribution was the litter type obviously correlated to the composition of tree species. Even if the litter was drifted by wind, similar litter types were characterized by similar species assemblages independent of the covering tree species during spring. Several species are bound to the coniferous or the deciduous litter type and several species were even strongly associated with a single litter type (Chapter 2). The litter type at each trap also revealed strong importance for carabid species, though not as significant as in spider assemblages during spring. However, intrinsic features of the tree species of all age classes were the litter type, while it is difficult to separate the preference on litter structure or habitat factors, which species favour in the litter, namely prey, protection from desiccation or extreme temperature.

Generally, analyses confirmed a distinct characteristic influence of the stand type on the species distribution of spiders and carabids in forest ecosystems. The pHs of the soil in spring, and temperature values or humidity in summer were detected as significant impact factors to reflect characteristic micro-environmental conditions of stand types. The pH of the soil and canopy closure represented significant discriminating variables of stand types in spring [litter type and the share of natural regeneration during all seasonal aspects]. In summer, the mean temperature and air humidity differed most between the stand types and soil moisture represented a stand characteristic during fall season.

However, the intrinsic factors of the tree species spectrum covering the ground are not the exclusive environmental variables, which explained the small-scale distribution pattern of spider and carabid assemblages. Among the key factors

affecting the distribution of species were strongly abiotic parameters such as irradiation, pH of the soil, temperature, air humidity, and water content of the litter.

Obviously, the conditions of several abiotic microhabitat parameters were affected by the degree of canopy closure. Canopy closure defined several important micro-environmental factors contributing to the explanation of species distribution. An increase in irradiation caused by a decrease of canopy closure was connected with a rise in temperature and air humidity. In spring the maximum temperature was a key habitat factor explaining the variance of species distribution of carabids and spiders.

The results also indicate that the composition and cover of ground vegetation, which are also affected by the degree of canopy closure were of major importance. The share of herbs, grasses and moss covering the ground contributed significantly to the explanation of variance in species composition, regardless of the covering tree species of the microhabitat groupings. There is considerable variation in the richness and abundance of understory plants among planted forest stands affected by the degree of canopy closure. Some of this variation can be attributed to the amount of light available to understory plants. Particular dense stands of spruce and Douglas fir can cast so much shade that they appear to literally shade out the understory vegetation (Humphrey et al. 2002).

The moss cover was influencing species distribution in a strong manner, especially during spring and summer. This niche occupation was often promoted by humid conditions within the moss layer or the litter layer below. Moreover, many spider species seem to adapt to the portion of natural regeneration, which offers possible protection from predation. Besides, there was a strong association of species to grass patches, even those remaining from the previous year in spring, or the shrub layer indicating a relationship between the species spectrum and the structure of plant communities. Thus, I found a high degree of constancy in species composition in similar vegetation plots on a very small scale at the trap level.

### **Microspatial distribution**

Environmental factors and thus species distribution changed within a stand on a fine temporal and spatial scale (Chapter 2 and 4). Many species preferred microsites with similar environmental conditions, while trees play a significant role in habitat heterogeneity (Chapter 3). These modify micro-environmental conditions leading to specific habitat preferences of species. The relevance of habitat parameters changed with the growing season (Chapter 2 and 4).

The broad spectrum of microhabitats allowed me to detect specific responses of species to a variety of micro-environmental parameter gradients and it revealed a very sensitive segregation of spider and carabid assemblages. Among the key habitat factors affecting the microhabitat distribution of spiders were abiotic parameters such as irradiation, temperature, air humidity, and water content of soil and litter, respectively. Those factors explained a great part of the species variation as determined by the discriminant, correlation and ordination (PCA, RDA) analyses. Strong gradients of these microspatial conditions became obvious during summer with the foliation of the deciduous trees and during fall with the fully developed ground vegetation.

Canopy closure has been regarded an important factor in forests, because it affects the microclimatic conditions of the lower forest strata in a diverse way (Lindh and Muir, 2004). The degree of canopy closure was shown to be one important factor during all seasons, resulting in alterations of species composition of spider and carabid assemblages. Here it was proven to have a profound influence on the small-scale regime of climatic conditions at the forest floor.

The results also indicate that the composition and cover of ground vegetation were of major importance. Species were characteristically affected by herbs, grasses and moss or even by natural regeneration. Structural heterogeneity is an aspect in spider distribution (Chapter 2), besides increasing the niche differentiation. Moreover, vegetation parameters may influence spider and carabid



communities indirectly by its positive effect on prey density also mediated by beneficial environmental conditions.

Distance to trees affects micro-environmental conditions at the forest floor. With the comparison of stem-close and stem-distant trap positions, I demonstrated an important small-scale spatial distribution pattern of a broad variety of spider species in forests. Many species were strongly associated with or even restricted to traps close or distant to the stem and species assemblages of different trap position were shown to be significantly different (Chapter 3). Trap position differed in a number of environmental parameters, such as the shading effect of the crown canopy, litter depth, or vegetation cover (i.e., grass, herb, moss, and natural regeneration). This effect might be also driven by differences of potential prey of spider species near the trunk.

However, the effect was not uniform among stand types attributed to tree species-specific heterogeneity at the forest floor. Thus, spider assemblages shifted significantly with the composition and structural diversity of the vegetation. Plant diversity and ground vegetation differed considerably in stands and microhabitats. This indicates that the plant species diversity has a significant impact on the invertebrate fauna at the forest floor. Especially the herb and grass vegetation had a strong impact on the species distribution throughout the season, the influence of plant vegetation increases with the advanced season. The stand type or tree species-specific differences in microhabitat conditions close and distant to the stems have to be regarded as drivers of community structure.

The relevance of habitat parameters changed with the growing season for spiders and carabids. I distinguished three time periods to assess the effects of seasonal habitat alterations on the spider and carabid community, mainly based on the development of the crown canopy and the ground vegetation. The impact of those microhabitat parameters, which were not strictly attributed to the tree species itself increased during the growing season while the covering tree species exerted its influence at all times. Several species showed additional or enhanced adhesions to grass, moss and herb vegetation later in the season. Higher

vegetational diversity was found to correlate with higher temperature parameters throughout the season.

While many spider species were correlated to litter type and canopy closure in spring, the influence of ground vegetation and humidity parameters prevailed during summer. In fall, the strength of correlations decreased besides ground vegetation and soil humidity. In contrast, many carabid species were affected by the vegetation cover overall and temperature aspects in spring, while the influence of soil and litter pH, litter moisture, and the canopy closure prevailed during summer. The litter type did not prove to be significant in the distribution of carabid species during spring as has been shown to be highly significant for spider species. However, the litter type at each trap revealed strong importance for some species for the summer aspect. A significant influence of leaf litter on carabid abundance and distribution can be attributed to abiotic factors controlling the micro-environmental conditions such as humidity, temperature, and acidity (pH) as well as biotic ones like the provision of niche structures and improved food supply (Koivula et al. 1999). Also the ground vegetation aspect expressed strong effects on the distribution of several carabid species at all times, but reflected a seasonal shifting key factor (Chapter 2 and 4).

An increase in irradiation caused by a decrease of canopy closure was connected with a rise in temperature and air humidity. In spring soil temperature was a key habitat factor explaining the site classification of spider species assemblages. The effect of the temperature decreased with the overall rising temperature from spring to summer. The temperature characteristics of the summer season reflected no significant influence on the assemblage classification of microhabitat groupings anymore. Accordingly, I assume that the temperature conditions during summer season reached a satisfactory level for a number of forest species. Temperature and humidity are known to influence the abundance and distribution of carabids and spiders across habitats. Significant relations of spider species to air humidity during summer were shown, while many species preferred dry microhabitats in spring, e.g. areas under deciduous trees.

Among the key habitat factors affecting the microhabitat distribution of carabids were strongly abiotic parameters such as irradiation, soil pH, temperature, air humidity, and water content of the litter. These factors explained a great part of the species variation. Strong gradients of these microspatial conditions became obvious during summer with the foliation of the deciduous trees and during fall with the fully developed ground vegetation. The impact of those microhabitat parameters that were not strictly attributed to the tree species itself increased during the growing season.

### **Stand age**

Within the forest habitats, the egg-load of three widespread ground beetle species showed significant relations to the age of a stand type (Chapter 5). Especially temperature conditions significantly influenced the reproduction in a positive way in all species.

The age of forest habitats with all its successional alterations is likely to influence the fitness of individual arthropods and thus forces in structuring communities including the soil-dwelling predacious taxa. Confirming my expectations, I could clearly show with the investigation of three ground beetle species, that the age of forests – except for Douglas fir stand – is affecting the reproductive rate of ground beetle species. However, the reaction pattern was species specific. For *A. parallelepipedus* a quite uniform reaction pattern was evident with significantly higher egg-loads in the mature forests compared to the young stands. This was accompanied by a longer duration of the reproduction period. A stronger influence of the forest type was obvious for the egg-load of *Pt. oblongopunctatus* and *Pt. burmeisteri*.

The reproductive rate was generally increasing with temperature aspects in forest sites and was significantly influenced by moisture parameters. The mean maximum temperature of the habitat cared for most of the variation in *A.*

*parallelepipedus* (61.4 %), while the mean minimum temperature explained 60.7 % of the reproductive potential in *Pt. oblongopunctatus*. The variation of *Pt. burmeisteri* was best explained by the humidity of the air (49.4 %).

Results document strong alterations in the suitability of different age classes of forests for ground beetle species. There is an interaction between the egg-load per female and the length of the period of egg-production. Thus, the increased egg production as well as the increased time period of reproduction may promote the stability and growth of a population in a given habitat. The species specific relation between habitat age and reproductive rate indicates the influence of distinct environmental parameters on the reproduction level of a species besides the availability of food. The egg-laying periods as well as the number of eggs laid per female were affected by temperature aspects in a beneficial way for all three species, obviously benefitting from increased temperatures although they generally live under lower temperature conditions than open land species. Thus, also *Pt. burmeisteri*, a cold and dark preferring species, carried increased egg-loads in the ovaries at sites of high maximum temperatures. Analyses on the trap level demonstrated that there is strong indication that females show distinct preferences for certain microhabitats within a forest to lay their eggs. Consequently, more eggs in ovaries of females were found in places of ecologically preferred habitat conditions. Thus, the reproductive rate increased significantly under moist litter conditions beside the positive influence of the temperature parameters. Litter moisture may play an important role in protecting carabid larvae from desiccation and may improve the density of prey. It becomes reasonable that the favourable conditions for the development of the less mobile offspring stages are leaned towards the preferences of adult beetles and that reproductive success is strongly dependent on breeding site characteristics. Also, soil and litter moisture and humidity of the air of the study sites were strongly correlated with the reproductive rate of the species. Microhabitats with natural regeneration and dense grass cover resulted in an increased egg-load for *Pt. burmeisteri*.

While female choice of favourable microhabitat conditions for egg deposition enhances the chance for development of subadult and survival of adult stages I assume that presence and frequency of patches with species specific favourable environmental conditions in a forest ecosystem play an important role in carabid fecundity. Thus, reproduction not only depends on the availability of food, but also on abiotic habitat parameters. Moreover, the accessibility of food in the field is significantly influenced by the fact that the amounts and nutritional qualities of food together with the activities of the beetles will also be influenced by weather conditions, since prey species also react on abiotic habitat parameters. Those factors also contribute to the size of single females and reproduction processes in a population. Consequently, the measured habitat parameters care to a great extent for the explanation in the variance of reproductive rate of ground beetles. Because these intrinsic habitat parameters often change with successional stages (Dajoz 2000), effects of forest age on the reproductive rate of carabid beetles are demonstrated.

### **6.1 Management effects**

Results confirm the influence of forestry practice on the composition of the soil-dwelling spider and carabid community – beside the selection of the tree species.

Forest management, resulting in a shift of environmental key factors such as light, moisture, temperature, and ground vegetation causes substantial changes in surface dwelling spider and carabid assemblages. In production forests, these changes are generated by alterations of the degree of canopy closure by thinning or variation of the tree species spectrum. The management practices incorporate selective felling, thinning operations or harvesting trails. These interventions affect the canopy closure of a stand and thus one key factor in community structuring. Canopy closure has been regarded an important factor in forests, because it affects the microclimatic conditions of the lower forest strata in a

diverse way (Lindh and Muir 2004). The canopy closure had a profound influence on the small-scale regime of climatic conditions at the forest floor and has been shown to be one important factor during all seasons.

Obviously, the conditions of several abiotic microhabitat parameters were affected by the degree of canopy closure, which is a result of the tree species specific crown architecture and silvicultural practice. Here I found that there is also considerable variation in the richness and abundance of understory plants among planted forest stands affected by the degree of canopy closure and thus by forestry management. Some of this variation can be attributed to the amount of light available to understory plants.

In conclusion, identical stand types differ in the composition of species assemblages and distribution pattern of single species, when environmental key factors care for varied microhabitat conditions. Those key factors are affected by management strategies. On the other hand, different stand types may correspond in their spider community if they comprise of the same microhabitat pattern.

## **6.2 Future prospects**

My results document that in production forests the composition of species assemblages varies not only between stand types but also within a forest ecosystem due to the small-scale mosaic of environmental parameters along with the seasons. Further investigations have to show if impacts on the functionality of spiders and carabids on the level of the forest ecosystem are likely to occur as a consequence of altered microspatial environmental gradients. Nevertheless, the investigation on small-scale spider and carabid distribution enhances the understanding of species requirements to habitat factors since the ecology of several species in forests is still not well understood. Moreover, the results on spiders and carabids are likely to assume that the composition of further functional guilds and indicator taxa may show correlations to small-scale

environmental conditions of a forest stand and react with community alterations on human-induced habitat changes.

Considering conservation aspects, given heterogeneity in forests due to small spatial scale gradients of environmental parameters along with the seasons will promote species diversity. This applies particularly for taxa like spiders and carabids that are not strictly bound to tree species like many herbivorous insects. Thus, sustainable forestry practice plays an important role for maintaining biodiversity. Waltz and Whitham (1997) demonstrated that alterations in the composition of common herbivores of upper tree canopies affected the abundance and diversity of arthropod communities below the crown during successional plant development. Consequently, the canopy and the floor area below are interrelated, affecting the abundance of species close to the stem, and thus, directly influencing the dominance structure of species assemblages. Further investigation is needed to determine how the stem distance-dependent distribution of spiders affects the role of spiders as regulators of detritivore food webs, as well as of natural enemies of invertebrate forest pests.

The reproductive potential as a measure of habitat aptitude of carabid species along the successional development of forests is still a matter of research. The egg-load of females can be considered to be a good indicator of habitat quality in forests. Besides the nutritional influence on the number of eggs laid, there is strong indication that microclimatic conditions during the reproductive period directly influence the reproductive rate (Van Dijk 1994). Until now, few studies considered the impact of detailed environmental conditions on reproduction in the course of forest succession.

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## Veröffentlichungen der Dissertation

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Ziesche TM (2005). Der Einfluß von Habitatumweltparametern auf die epigäische Arthropodengemeinschaft in repräsentativen Bestandstypen mittelschwäbischer Wirtschaftswälder.–Tagung der DGaaE in Dresden. Vortrag.

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## **Eidesstattliche Erklärung**

Ich erkläre hiermit an Eides statt, dass ich die vorliegende Dissertation selbständig und nur mit den angegebenen Hilfsmitteln angefertigt habe. Ich habe noch keinen Promotionsversuch unternommen.

Dresden, den 14.04.2015

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