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Ekologie střevlíkovitých brouků (Coleoptera: Carabidae) v prostředí lužního lesa

Ecology of carabid beetles (Coleoptera: Carabidae) in floodplain forest conditions

Diplomová práce
v oboru
Ochrana a tvorba životního prostředí

Vedoucí práce: Mgr. et Mgr. Ivan H. Tuf, Ph.D.

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Poděkování

Na tomto místě bych chtěl poděkovat především Mgr. et Mgr. Ivanu H. Tufovi Ph.D., za všestrannou pomoc, cenné rady a v neposlední řadě i trpělivost při vedení mé diplomové práce. Dále bych chtěl poděkovat také RNDr. Milanu Veselému Ph.D. za pomoc při determinaci a také všem studentům a kolegům, kteří pomáhali při náročné terénní fázi výzkumu.

Prohlášení

Prohlašuji, že jsem se na jednotlivých studiích podílel následujícím způsobem:

Kap. 02 a 03 – terénní práce, determinace materiálu, spoluautor textu;

Kap. 04 – autorská práce.

Za hlavní autory a spoluautory stvrzuje:

Ivan H. Tuf

V Kroměříži 8. září 2006

Abstrakt

Předkládaná diplomová práce sestává ze tří samostatných manuskriptů, v nichž jsme se věnovali různým tématům, týkajícím se střevlíkovitých brouků (Coleoptera: Carabidae). Lokalita, na níž výzkumy probíhaly, se nachází v CHKO Litovelské Pomoraví nedaleko obce Horka nad Moravou.

První manuskript je věnován problematice obnovy společenstev půdní fauny po katastrofické povodni v roce 1997. Společenstvo bylo studováno metodou formalínových zemních pastí po dobu sedmi let po povodni. Vzorky z jednotlivých let byly srovnávány s referenčním společenstvem, představujícím předpovodňový stav. Již po dvou letech bylo společenstvo zkoumané lokality podobnější tomu předpovodňovému, než společenstvu z předešlého roku.

Ve druhém příspěvku jsme se zabývali vlivem mýcení na společenstva edafonu lužního lesa. I v tomto případě jsme používali k získávání vzorků metodu formalínových zemních pastí rozmístěných ve starém lesním porostu a na smýcené ploše. Výzkum probíhal od dubna 2003 do června 2004. Mýcení mělo na společenstvo střevlíků signifikantně pozitivní vliv (vyšší diverzita i abundance na mýtině ve srovnání s lesním porostem). Mýtina byla rychle kolonizována novými druhy především z řad letuschopných druhů otevřených stanovišť. Důležitým faktorem pro rychlost kolonizace byla i blízkost zdrojových lokalit (pole a břehové biotopy).

Poslední část diplomové práce je věnována vlivu faktorů sezonality, lokality a teploty povrchu půdy na diurnální aktivitu střevlíků. Výzkum probíhal na jaře a na podzim 2004. Použili jsme metodu padacích pastí bez fixáže, které byly vybírány každé 3 hodiny. U většiny druhů, jejichž aktivita závisela na faktoru denní doby jsme nalezli i signifikantní závislost na teplotě povrchu půdy, přičemž tento faktor hrál významnější roli na mýtině a v podzimní sezoně.

Klíčová slova: Carabidae, lužní les, povodně, mýcení, diurnální aktivita, Litovelské Pomoraví

Abstract

The submitted thesis is composed of three individual manuscripts, each devoted to various topics related to carabid beetles (Coleoptera: Carabidae). The locality where the research on the beetles was conducted was in the Litovelské Pomoraví Protected Landscape Area near the town of Horka nad Moravou.

The first manuscript is devoted to the problem of restoring populations of ground fauna following the catastrophic floods in 1997. The population was studied by means of formaldehyde pitfall traps over a period of seven years following the floods. Samples from individual years were compared with a reference population represented by the pre-flood condition. After two years the population at the research site was already more similar to the pre-flood population than it had been just one year earlier.

In the second work we were concerned with the influence of clear-cutting on the edaphone populations in riparian woodlands. In this case we also collected specimens using formaldehyde pitfall traps placed in old forest growths, as well as in clear-cutts. The research was conducted from April 2003 to June 2004. Clear-cutting had a significantly positive influence on carabid beetle populations (greater diversity and abundance in the clear-cutts in comparison to the forest growth). The clear-cutts was quickly colonized by new species, especially flying field species. Another important factor in the speed of colonization was the proximity of a source locality (field and riparian biotopes).

The final part of the thesis is devoted to the influence of factors such as season, locality, and temperature of the surface of the soil on the diurnal activity of carabid beetles. The research was conducted in the spring and autumn of 2004. We employed the method of pitfall traps without fixation, and these were collected every three hours. With the majority of species whose activity is dependent on the time of day we found an additional significant dependence on the temperature of the surface of the soil; this factor played a more significant role in clear-cutts as well as in the autumn.

Key words: Carabidae, floodplain forest, flood, clear-cutting, diurnal activity, Litovelské Pomoraví Protected Landscape Area

Obsah

01. Úvod

Předkládaná práce je souborem tří manuskriptů, sepsaných na různá témata týkající se střevlíkovitých brouků. První z nich se věnuje obnově společenstev půdních bezobratlých po katastrofické letní povodni, která postihla území Moravy v roce 1997. Druhý příspěvek je věnován vlivu mýcení lesa na společenstva edafonu. Třetí je pak zaměřen na poznání diurnální aktivity střevlíkovitých brouků.

Z území ČR je známo cca. 570 druhů střevlíků (Buchar et al. 1995), v celosvětovém měřítku je to pak zhruba 35 000 druhů, tato čeleď se tak řadí mezi nejpočetnější čeledi brouků u nás i na světě. Druhová diverzita se odráží také v rozmanitosti obývaných stanovišť (od pouští až po mokřady a břehové porosty). Většina druhů střevlíků jsou nespecializovaní predátoři, vyhledávající živou kořist i uhynulé živočichy. Existují však i specializovaní dravci (*Calosoma, Cychrus*) a také druhy býložravé (*Ophonus, Zabrus*) či všežravé (*Amara, Harpalus*).

Střevlíci jsou často využíváni jako modelová skupina pro různé ekologické studie (Dufrêne & Baguette 1990). Důvodů je celá řada: střevlíci tvoří důležitou složku epigeonu různých biocenóz, jde o poměrně dobře prozkoumanou skupinu s často vyhraněnými (a známými) ekologickými nároky a důležitá je také skutečnost, že pomocí jednoduchých metod lze získat početný materiál (Maelfait & Desender 1990).

Společenstva střevlíků zaplavovaných území

Aluviální ekosystémy, existenčně závislé na pravidelných záplavách, hostí ve středoevropských podmínkách bohatá společenstva půdní fauny, jejichž významnou součástí jsou i střevlíkovití brouci (Coleoptera: Carabidae). Povodně jsou pak přirozeným faktorem, formujícím tato společenstva a antropogenní zásahy do přirozené dynamiky vodních toků (např. ve formě jejich regulací a výstavby přehrad) představují bezprostřední ohrožení těchto unikátních ekosystémů a společenstev na ně vázaných.

V rámci střední Evropy můžeme rozlišit dva typy záplav – 1) pravidelné (jarní, podzimní) a nepravidelné. Výskyt pravidelných povodní v čase i jejich intenzitu lze predikovat a půdní bezobratlí si v průběhu evoluce vytvořili řadu adaptací, jež jim umožňují tyto disturbance přežít (Adis & Junk 2002). Daleko fatálnější důsledky mají nepravidelné povodně, na něž nemají společenstva půdní fauny možnost se adaptovat.

Problematice vlivu povodní na půdní faunu byla věnována zvýšená pozornost až v posledních letech a informace jsou zatím jen kusé. Většina prací se věnovala strategiím přežívání povodní u terestrických bezobratlých (Zulka 1994, Zerm & Adis 2003a, 2003b, Tufová & Tuf 2005). Jen málo studií se dosud zabývalo důsledky změn přirozeného režimu řek na společenstva střevlíků (Bonn et al. 2002, Günther & Assman 2005) nebo rychlostí obnovy společenstev po povodni (Hering et al. 2004, naše studie).

Ucelenější prací, věnující se strategiím přežívání povodní, je studie Adise & Junka (2002) , ve které srovnávají různé způsoby adaptací na záplavy u terestrických bezobratlých ve střední Amazonii a střední Evropě. Stabilní a dobře predikovatelné podmínky v oblasti Amazonie daly vzniknout pestré škále adaptací, zatímco v hůře predikovatelných středoevropských podmínkách je nejčastější jednoduchá strategie „riskování“ spojená s vysokým reprodukčním potenciálem, dobrou schopností disperze a rychlou reimigrací postižených oblastí po odeznění povodní. Strategie přežívání povodní u střevlíků je do značné míry závislá na charakteru biotopu – zatímco v lesních porostech dominují brachypterní druhy a jejich strategie se opírá především o vertikální migraci po kmenech stromů, na otevřených stanovištích pak převládají druhy schopné letu, pro něž únik před vodou nepředstavuje problém (Zulka 1994, Klimeš 2002).

Mnoho druhů střevlíků je známo svým křídelním polymorfismem. Na zaplavovaných stanovištích je podíl makropterních jedinců vyšší (Klimeš 2002) a rovněž při porovnání lokalit, lišících se dynamikou povodní, je zastoupení letuschopných jedinců vyšší na nepravidelně zaplavovaných stanovištích (Adis & Junk 2002).

V laboratorních experimentech zkoumajících schopnost střevlíků snášet dlouhodobější ponoření se ukázalo, že některé druhy jsou schopné vydržet pod vodní hladinou od několika týdnů až po řádově měsíce (Palmén & Suomalainen 1945, Palmén 1949, Heydemann 1967). Rozhodujícím faktorem, ovlivňujícím délku přežití, se ukázala být teplota vody (čím nižší, tím delší přežívací čas), se kterou souvisí nejen aerace vody, ale i úroveň metabolismu střevlíků. Z tohoto pohledu jsou letní povodně pro přežívání střevlíků méně příznivé, protože teplota vody je při nich relativně vysoká. Významné rozdíly v přežívání se projevily i mezi vývojovými fázemi životního cyklu střevlíků – u některých druhů vykazovaly larvy mnohem delší čas přežití pod vodní hladinou než dospělci (Heydemann 1967).

Pro rychlost obnovy společenstev po povodni je rozhodující blízkost potenciálního zdrojového stanoviště, z něhož by mohly být oslabené populace dotovány (Klimeš 2002). Naše studie (kap. 02) se zaměřila na rychlost obnovy společenstva po katastrofické povodni z roku 1997. Zjistili jsme, společenstvo se vrátilo do stavu blízkého předpovodňovému již po dvou letech.

Vliv mýcení na společenstva střevlíků

Mýcení představuje po povodních druhou nejvýznamnější disturbanci v prostředí středoevropských lužních lesů a této problematice je věnována druhá část předložené diplomové práce. V posledních letech je vliv deforestace na společenstva půdních bezobratlých častým předmětem studia, pozornost je však věnována především boreálním lesům ve skandinávských zemích, lužní lesy byly v tomto ohledu dosud opomíjeny.

Ve většině studií se po vykácení části porostu na mýtinách projevilo zvýšení druhového bohatství (Ings & Hartley 1999, Werner & Raffa 2000, Koivula 2002, Magura 2002, du Bus de Warnaffe & Lebrun 2003), pouze některé práce uvádí jako druhově bohatší lesní porosty (Fahy & Gormally 1998, Poole & Gormally 2003). Vyšší počet druhů v lese bývá dáván do souvislosti s přítomností hluboké vrstvy opadu, která přispívá k rozrůznění vertikální distribuce střevlíků a k omezení vnitrodruhové kompetice (Magura 2002). Naopak, vyšší druhové bohatství střevlíků na mýtinách bývá vysvětlováno jako důsledek příznivějších mikroklimatických podmínek pro druhy otevřených stanovišť a stanovištní generalisty (Werner & Raffa 2000, Koivula 2002) a vyšším druhovým bohatstvím vegetace na mýtinách, které ovlivňuje společenstva střevlíků jak přímo (více potravy pro herbivorní druhy), tak nepřímo (víc herbivorních bezobratlých jako potravy pro střevlíky). Více rostlin zároveň poskytuje úkryt před predátory a více využitelného prostoru ve vertikálním směru (Koivula 2002).

Obecně na mýtinách roste podíl druhů preferujících otevřená stanoviště. Jde většinou o druhy makropterní a schopné kolonizovat nové mýtiny již krátce po jejich vzniku (Koivula 2002). Rovněž množství habitatových generalistů na mýtinách roste. Naopak, lesní specialisté výrazně ubývají, nebo zcela mizí (Koivula 2002, Werner & Raffa 2000, Dunger & Wanner 2000).

Postupná přeměna mýtiny v uzavřený porost ovlivňuje druhové složení zpočátku jen mírně. K dramatičtějším změnám dochází až několik desetiletí po osazení (Koivula

2002). S rostoucí velikostí stromů se však zásadním způsobem mění stanovištní podmínky (zejména zastínění a vlhkost), což vede k homogenizaci mikroklimatu a omezení druhového bohatství (Ings & Hartley 1999). Nicméně, lesní druhy jsou většinou brachypterní a jsou poměrně špatnými kolonizátory a pokud jednou z krajiny zmizí, nemusí se do ní již nikdy vrátit (du Bus de Warnaffe & Lebrun 2003).

V naší studii (kap. 03) se projevilo očekávané zvýšení druhového bohatství na mýtině (ve srovnání s lesním porostem), přibyly zde druhy typické pro otevřená stanoviště. Ke změnám došlo také v dominancích druhů. Jako klíčová se zde projevila blízkost zdrojového stanoviště (pole a břehové biotopy), jež urychlila kolonizaci mýtiny novými druhy.

Diurnální aktivita střevlíků

Diurnální aktivita je charakterizována jako specifický vzorec aktivity v rámci 24-hodinových cyklů. Primárně je diurnální aktivita řízena endogenními fyziologickými faktory (tzv. časovači), délka trvání jednotlivých fází (aktivita, klid) je však do různé míry ovlivňována podmínkami prostředí. Nejdůležitějším exogenním faktorem ovlivňujícím diurnální aktivitu střevlíků je světlo (Thiele 1977), ovšem důležitou roli může hrát v závislosti na typu habitatu také teplota (Kegel 1990) a vlhkost (Novák 1980, Thiele 1977).

Studium diurnální aktivity nám může mimo jiné osvětlit příčiny koexistence často velkého počtu druhů střevlíků na různých lokalitách. Specifický vzorec aktivity může být jedním z aspektů, na základě nichž může dojít k diferenciaci nik a tím i k umožnění soužití většího množství druhů na jedné lokalitě, aniž by došlo ke kompetičnímu vyloučení. V této souvislosti se zabýval distribucí diurnální aktivity během dne Park (1941), který formuloval hypotézu, podle níž se aktivita s postupným vývojem společenstva stává stále symetričtější, což umožňuje lepší využívání zdrojů.

Poslední část diplomové práce (kap. 04) se zabývá vlivem exogenních faktorů na diurnální aktivitu. Jako nejvýznamnější prediktor aktivity se projevila denní doba (resp. množství světla), ale u většiny druhů, jejichž aktivita se řídila denní dobou, se projevila i závislost na teplotě povrchu půdy.

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02. Length of recovery of soil macrofauna communities (Coleoptera: Carabidae, Isopoda: Oniscidea) after irregular summer flood

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Abstract

A large part of central Europe was affected by disastrous summer flood in 1997. This flood had a negative impact on soil macrofauna, too. Recovery of communities of ground beetles and terrestrial isopods was studied during next seven years in hardwood floodplain forest near Morava River (Moravia, Czech Republic). Communities were sampled by pitfall traps and by extractions of soil samples. Assemblages of individual years were compared with the reference community representing pre-flood state. The community of carabids returned near to this state after two years, epigeic part of terrestrial isopod communities after six years and the edaphic part of isopod communities after four years. The assemblage response is related to dispersal ability, intraspecific competition and unique history of individual sites.

Keywords: floodplain forest, pitfall traps, restoration, Litovelské Pomoraví PLA

Introduction

Terrestrial invertebrates of floodplains are relatively well known. Many authors studied communities of terrestrial invertebrates from different sites (Gulička 1957, Obrtel 1971, Zulka 1991, 1994, Zerm 1997, 1999, Farkas et al. 1999, Van Looy et al. 2005), some papers about the influence of water regime on community or population structure (Gulička 1960, Krumpál 1973, Tajovský 1999, Farkas 1998, Bonn et al. 2002) or directly about impact of flood to communities (Haferkorn 1996, Pižl & Tajovský 1998, Hering et al. 2004) can be found. Few papers were published on the ability to survive flooding of terrestrial isopods and carabids (Tufová & Tuf 2005, Zulka 1994, Zerm & Adis 2003a, 2003b). Floods are significant factor in shaping the soil fauna assemblages in alluvial areas. Terrestrial invertebrates occupying such habitats possess various life strategies of how to survive temporary periods of high water level connected with low oxygen availability (Adis & Junk 2002).

In Europe, there can be distinguished two basic types of floods with strong effects on terrestrial ecosystems: (1) *Regular* floods at spring or autumn that are rather short and (2) *irregular* floods that often have disastrous consequences. As mentioned above, in the long-term selection process, terrestrial invertebrates have developed different strategies to survive flood. However, organisms are adapted to the *regular* floods that are generally predictable in time and intensity. Therefore, there is no surprise that irregular and less predictable floods of above-average intensity can have several impacts on demography even in well-adapted organisms. After an irregular flood there is a decrease in the density of isopods (Haferkorn 1996) or carabids (Hering et al. 2004), e. g., during the irregular flood caused by storm rainfall more than half of *Periscyphis granai* Arcangeli, 1929 population drowned (Warburg 1993).

The Litovelské Pomoraví Protected Landscape Area, located in central Moravia, Czech Republic, is included in the list of registered wetlands by the Ramsar Convention. In July 1997 a disastrous flood event occurred in the Litovelské Pomoraví PLA. Floodwater remained standing in the forests for several weeks. The direct negative impact of this summer flood on soil macrofauna immediately after the flood was documented by Pižl & Tajovský (1998): The leaf-litter and fermentation layer with inhabiting animals were washed away, the soil was twice inundated by relatively warm water for three weeks, and the humus and mineral layers were covered by mud and subsequently desiccated. The development of ground beetles (Coleoptera: Carabidae) and woodlice (Isopoda: Oniscidea) communities during the following seven years is described in this paper.

Material and Methods

Carabids and terrestrial isopods were studied in the hardwood floodplain forest (*Querco-Ulmetum*) in the Litovelské Pomoraví PLA near Olomouc city (49°65′N, 17°20´E, altitude 210 m a.s.l.). The herbal layer was composed of *Anemone nemorosa, Polygonatum* spp., *Lathyrus vernus* and *Maianthenum bifolium*, the dominant moss was *Eurhynchium hians*. In November 1998, litter biomass (dry weight) was 622 g/m^2. Alluvial soil was loamy-sandy to loamy at the locality, with pH 4.8–5. The mean annual precipitation was around 520 mm, mean annual temperature was 9.1 °C.

An array of six pitfall traps at 8 m intervals was exposed at locality to catch the epigeic part of the soil macrofauna assemblage. Traps (plastic containers with a diameter of 7 cm and height of 10 cm, filled with 4% water solution of formaldehyde with detergent, metal covers) were inspected and changed fortnightly (in winter at 28-days intervals) from February 1998 to February 2005. The endogeic part of the isopod community was heat-extracted from soil samples using a modified Tullgren apparatus (60 W bulb about 10 cm above soil ample, 10-14 days of extraction, Tuf & Tvardík 2005). Five soil samples (circular metal corer with sample area 1/16 m^2, depth 10 cm) were taken monthly at locality from March 1998 to February 2005.

To analyze the direction of the development of the isopod community, it was compared with the pre-flood state using the assemblage described by Karel Tajovský (Pižl & Tajovský 1998) from similar floodplain forest at site Záseky (*Ficario-Ulmetum*), in the Litovelské Pomoraví PLA (cca 9 km from our study site). Isopod assemblage was studied by pitfall trapping (five traps) and heat extracting of soil samples (five samples of 1/16 m^2) during May-July in 1997. Similarly, the community of ground beetles described by Blahoušek (1997) in his master thesis was used for comparison with our community. In 1995, Blahoušek caught carabids with 18 formaldehyde pitfall traps in the floodplain forest in Litovelské Pomoraví (*Querco-Ulmetum,* cca 6 km to our locality) from April to October (catch from six traps was used as reference community). Assemblages from individual years were compared using cluster analysis (by Ward’s method) by JMP statistical software (SAS Institute Inc., 1995). In the analysis, dominances of species were used. Scientific names of carabids and terrestrial isopods were used in accordance with Fauna Europaea (Boxshall 2004, Vigna Taglianti 2004).

Results

Altogether, 2,068 individuals of carabid beetles and 2,312 individuals of terrestrial isopods were trapped and 1,789 individuals of terrestrial isopods were extracted from soil samples. This represents 22 species of ground beetles and nine species of isopods.

The assemblage structure in individual years compared to the reference assemblage showed, that some species, which were presented at the undisturbed site and absent in the first year after flood, reappeared during the next years (*H. luteicornis*, *P. cupreus*, *P. rufipes*, *P. oblongopunctatus*, Table 1). On the other hand, several species, which inhabited the study site during the first years after flood, abandoned this community in the subsequent years (*A. carinatus*, *A. familiaris*, *H. latus*, *P. versicolor*, *S. pumicatus*, *T. quadristriatus*, *T. octomaculatus*). The similar pattern was observed in terrestrial isopods community. In the pitfall traps, *L. hypnorum* was subsequently replaced by *T. rathkii* (Table 2, $r = -0.829$, $p \leq 0.05$), and in the soil samples, *H. riparius* was step by step outnumbered by *T. pusillus* (Table 3, $r = -0.867$, $p \leq 0.05$). Both these changes were pointed at the pre-flood state.

Analysis of dissimilarity of carabid communities from individual years showed, that the first two years after flood were different from other years, i.e. that the community from the third year (2000) was more similar to the pre-flood state and the next years than to the previous year (Figure 1). The situation in the epigeic part of the terrestrial isopod community (trapped animals), was different; an assemblage more similar to pre-flood state than to the assemblage in previous year was trapped in 2004, the 7th year after the summer flood. However, the edaphic part of the isopod community (extracted from soil samples) was compared, too. Five years after summer flood, the assemblage was more similar to the undisturbed assemblage (from 1997) than to the assemblages from the years 1998 to 2001 (Figure 3).

Discussion

A direct impact of irregular summer flood 1997 to communities of soil fauna was described for centipedes, millipedes, earthworms and terrestrial isopods (Pižl & Tajovský 1998), unfortunately we have not data about direct impact of this flood to carabid beetles. After flood, communities of terrestrial isopods (in autumn 1997) impoverished in both qualitative and quantitative parameters (number of animals, number of species, dominance structure). In the pitfall traps, there the species number remained unchanged although epigeic activity decreased by five times. Yet more evident was the negative impact of the flood to the edaphic part of isopod community (extracted from soil samples). Only two species out of five were recorded in autumn

1997 and abundances decreased by 60 times (Pižl & Tajovský 1998). Impact of 100-year flood (May 1999) on ground beetles was studied in Germany (Hering et al. 2004). In riparian forests they recorded a strong decline in density of ground beetles but this decline was overcompensated in following months due to low level of competition in low density.

Although we did not study effect of flood under the best research-design (Underwood 1994), we believe that our reference communities are useful for our evaluation in spite of different position. All forests (Blahoušek 1997, Pižl & Tajovský 1998, our locality) are similar in main characteristics as mesoclimatic conditions, dominant tree species, amount of litter, and light-intensity at soil surface. To study communities of soil invertebrates at original sites was not possible from technical reason (availability).

Ground beetles

The number of species of carabids caught in individual year was relatively low (11 to 15), but adequate to used method (only six pitfall formaldehyde traps).

We recorded lower density of Carabidae in the first year after flood but it increased in next year. Those big changes in carabid beetles density are well known (Guillemain et al. 1997, Östman 2005), they are caused by many factors, e.g. competition for prey (Lenski 1982). It is in accordance with results of Hering et al. (2004), which described return to high abundances in several months after abnormal flood. Nevetheless, their dominant species were from genus *Bembidion*, with good ability to fly and good chance to survive flood and recolonize locality later, too.

In the first year after flood some species missed in the community (*H. luteicornis*, *P. cupreus*, *P. rufipes*, *P. oblongopunctatus*) which returned to the site in the next years. These species are prefer fields and meadows (Hůrka 1996), their position in community is not important probably (only *P. oblongopunctatus* is forest species). Those species, which colonized the locality in the first years after flood and disappeared in next years are mostly indifferent to biotope type (eurytopic species *A. familiaris*, *H. latus*, *P. versicolor*, *S. pumicatus*, *T. quadristriatus*, *T. octomaculatus*) (Hůrka 1996). However, these species are not main members of forest Carabidae community. Recovery of this community is based on changes in density of dominant species since competition is significant mainly in dominant species (Loreau 1990), although no significant competition is apparent from our data. From the comparison it is evident that the recovery of carabid community look two years – the third year (2000) was more similar to the pre-flood situation than to previous year (1999). This recovery rate is quick (in comparison with isopods), similarly as recovery of carabid community after 100-years flood in 1999 (Hering et al. 2004).

Terrestrial isopods

The communities of terrestrial isopods inhabiting *Fraxino-Ulmetum* forests near the confluence of the Dyje and Morava rivers were influenced and formed by duration of inundation: in non-flooded forest there were four species, in regular brief flooded forest there were five species, whereas long-term flooded forest was inhabited by two species only (Tajovský 1999). The highest density was in forest with short floods (Tajovský 1998). The same impact to isopod communities had extraordinary spring flood in floodplain forests in central Germany (Haferkorn 1996). A similar pattern was described from non-forested sites in the Morava valley in Austria. The length of over-flooding is negatively correlated with the number of species and the community density (Zulka 1991). From these reasons a community consisting of five to seven terrestrial isopod species is typical for hardwood forests with relatively regular, but short floods.

Although the number of species is typical, lower densities were recorded during post-flood succession. For this there could be by two reasons. First, our densities represent averages calculated from densities of the whole year (March to February) and during winter, densities are lower due to vertical migration to deeper layers of soil (Tuf 2002). A high density at reference site (Záseky) was recorded in one month, May 1997, only (Pižl & Tajovský 1998). Second, this high density was caused by one species, *T. pusillus*, with more than 1000 ind./m^2. Similar densities were noted for this species in a grassland ecosystem by Sutton (1972). At this locality, the highest abundances of *T. pusillus* were about 150 ind./m^2. Nevertheless, in according with pre-flood state, dominance of *T. pusillus* is still increasing at the expense of *H. riparius*. Thus, the changes in the community structure are probably due to interspecific competitive interactions (negative correlations) for food sources (Hassall & Dangerfiel 1989) and distinct predation pressures on individual group size, and on individual species, respectively. Changes in density of smaller species *T. pusillus* were negatively correlated with changes in density of centipede *Lithobius mutabilis* L. Koch, 1862 at this locality (Tuf 2003).

In the epigeic part of isopod community, *T. rathkii* is a typical dominant species in central European alluvial forests (Tajovský 1998, Farkas 1998), whereas *L. hypnorum* is a hygrophilous isopod, which is not a characteristic member of hardwood floodplain forest communities. In Litovelské Pomoraví it was more abundant in non-forest habitats (Tuf 1997). Similarly, *L. hypnorum* was not recorded in the hardwood floodplain forest in the southern Moravia (Tajovský 1999), but it was dominant in several open-canopy alder groves and softwood floodplain forests (Farkas et al. 1999, Gulička 1960, Krumpál 1973). Situation between decreasing population of *L. hypnorum* and increasing population of *T. rathkii* is the next example of interspecific competitive suppression probably. *L. hypnorum* probably did not inhabit forests not for preferences for non-forested sites, but it prefers sites without others isopods with a similar niche.

Return to almost pre-flood state in agreement with our analysis took six years in the epigeic part of the communities, what seems to be a relatively long time with comparison of life span of isopods (1-2 years). But there are two sources of difficulties. Firstly, in the Tajovský's community sampled in 1997, there were animals trapped before flood and *at start* of flood together. Although the same species inhabited this locality were trapped during flood, they showed a different pattern of epigeic activity. For example, the endogeic species *T. pusillus* showed very high activity. It is evident, that *T. pusillus* escaped from the flooded soil by epigeic activity and by climbing to non-flooded objects (Tuf, *pers. observ.* 2006). Unfortunately, we do not have a better referential community. Furthermore, the presence of *P. politus* after flood is surprising. This species is a typical inhabitant of other types of forests, for example mountain forests (Farkas et al. 1999). Its massive colonization of this locality in 2003 is probably caused by import connected with forest planting near to study site (re-planted clear-cut in spring 2003, approximately 100 m from trap-line). The similar situation is for millipedes on this locality too (Tufová, *pers. comm.* 2005).

The recovery of the edaphic part of isopod community was quicker (4 years). Almost all species inhabited the locality in the first year and changes in dominance structure took place only. This could be caused by a higher fecundity (parthenogenesis and potential to two broods) of dominant species *T. pusillus* (Sutton 1972).

Conclusion

Communities of soil macrofauna disturbed by irregular summer flood return to a state near to pre-flood situation step by step, although some alternative communities can develop. The recovery of disturbed communities of soil macrofauna is a long process not only for long-lived species, but for species with short live cycles too. The speed of recovery depends of the dispersal abilities of species. Carabids are quick runners and most of them can fly; the recovery of community of terrestrial isopods, as non-flying animals, takes a longer time.

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Table 1: Structure (dominance of individual species, %) and size (catch per year, ind./6 traps) of community of ground beetles before (1995) and during 7 years after summer flood. Community from 1995 was sampled by Blahoušek (1997).

Carabidae - pitfall traps	**1995**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**
Abax carinatus (Duftschmid, 1812)	-	2.7	2.5	-	-	-	-	-
Abax parallelepipedus (Piller & Mitterp., 1783)	24.8	15.2	6.4	10.6	13.8	14.1	34.3	26.1
Abax parallelus (Duftschmid, 1812)	12.8	2.7	1.6	7.5	10.2	13.0	10.7	12.7
Amara familiaris (Duftschmid, 1812)	-	0.4	-	-	-	-	-	-
Carabus coriaceus Linnaeus, 1758	9.7	14.8	9.2	10.6	6.2	0.8	4.1	7.3
Carabus granulatus Linnaeus, 1758	2.2	1.6	2.0	0.4	0.6	0.4	-	-
Carabus scheidleri Panzer, 1799	3.0	11.7	36.6	22.0	31.1	8.0	19.4	7.9
Carabus ullrichii Germar, 1824	4.9	6.2	17.1	29.9	16.9	1.9	2.9	32.7
Harpalus latus (Linnaeus, 1758)	-	-	0.2	-	-	-	-	-
Harpalus luteicornis (Duftschmid, 1812)	0.2	-	-	-	0.3	-	-	-
Limodromus assimilis (Paykull, 1790)	1.5	3.1	4.1	3.5	1.5	-	-	1.2
Molops piceus (Panzer, 1793)	1.8	-	-	-	-	-	-	-
Poecilus cupreus (Linnaeus, 1758)	0.3	-	-	0.4	-	0.8	1.7	-
Poecilus versicolor (Sturm, 1824)	-	-	0.2	-	-	-	-	-
Pseudoophonus rufipes (De Geer, 1774)	0.4	-	-	-	0.3	0.4	1.2	0.6
Pterostichus melanarius (Illiger, 1798)	28.0	19.5	11.4	12.2	6.2	14.1	19.0	6.1
Pterostichus niger (Schaller, 1783)	0.7	21.0	6.7	2.0	12.3	46.2	5.0	0.6
Pterostichus oblongopunctatus (Fabricius, 1787)	8.5	-	0.9	0.8	0.6	-	1.2	2.4
Pterostichus ovoideus (Sturm, 1824)	1.2	0.4	0.9	-	-	0.4	0.4	1.8
Pterostichus strenuus (Panzer, 1797)	-	-	-	-	-	-	-	0.6
Stomis pumicatus (Panzer, 1796)	-	-	0.4	-	-	-	-	-
Trechus quadristriatus (Schrank, 1781)	-	0.4	-	-	-	-	-	-
Trepanes octomaculatus (Goeze, 1777)	-	0.4	-	-	-	-	-	-
number of species	**15**	**14**	**15**	**11**	**12**	**13**	**11**	**12**
year catch (ind./6 traps)	**416**	**257**	**563**	**254**	**325**	**262**	**242**	**165**

Table 2: Structure (dominance of individual species, %) and size (mean catch, ind./6 traps/month) of epigeic part of community of terrestrial isopods before (1997) and during 7 years after summer flood. Pre-flood community was sampled by Tajovský in May-July 1997 (Pižl & Tajovský 1998).

Oniscidea - pitfall traps	**1997**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**
Ligidium hypnorum (Cuvier, 1792)	13.1	70.5	75.8	77.1	86.3	80.8	46.8	14.3
Trachelipus rathkii (Brandt, 1833)	45.9	6.9	15.1	16.6	9.8	5.1	13.7	31.8
Protracheoniscus politus (C.L. Koch, 1841)	-	-	0.5	1.9	-	1.0	30.6	38.6
Porcellium conspersum (C.L. Koch, 1841)	5.5	0.2	0.5	1.2	-	0.3	4.0	7.6
Porcellium collicola (Verhoeff, 1907)	-	-	-	-	-	-	-	3.4
Trichoniscus pusillus Brandt, 1833	32.3	19.0	5.5	1.1	2.9	12.1	1.6	3.0
Hyloniscus riparius (C.L. Koch, 1838)	3.2	3.4	2.7	2.1	1.0	0.7	3.2	1.3
number of species	**5**	**5**	**6**	**6**	**4**	**6**	**6**	**7**
mean catch (ind./6 traps/month)	**183.4**	**49.1**	**35.1**	**32.8**	**17.0**	**24.8**	**10.3**	**23.6**

Table 3: Structure (dominance of individual species, %) and size (mean density, ind./m^2) of endogeic part of community of terrestrial isopods before (1997) and during 7 years after summer flood. Pre-flood community was sampled by Tajovský in May 1997 (Pižl & Tajovský 1998).

Oniscidea - soil samples	**1997**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**
Ligidium hypnorum (Cuvier, 1792)	-	11.4	8.3	30.9	12.0	11.8	6.5	7.7
Trachelipus rathkii (Brandt, 1833)	1.0	2.2	1.1	2.4	2.9	7.2	4.4	3.3
Protracheoniscus politus (C.L. Koch, 1841)	-	-	0.2	-	0.5	2.6	2.4	3.3
Porcellium conspersum (C.L. Koch, 1841)	0.7	-	0.7	0.4	0.5	-	1.0	2.2
Trichoniscus pusillus Brandt, 1833	80.6	26.8	34.5	28.5	51.2	45.8	66.3	66.1
Hyloniscus riparius (C.L. Koch, 1838)	0.3	53.1	51.5	32.5	32.1	32.7	17.3	14.2
Androniscus roseus (C.L. Koch, 1838)	-	-	0.7	3.6	1.0	-	-	2.7
Haplophthalmus mengei (Zaddach, 1844)	17.4	6.6	3.0	1.6	-	-	2.0	0.5
number of species	**5**	**5**	**8**	**7**	**7**	**5**	**7**	**8**
mean density (ind./m^2)	**1286.4**	**60.8**	**116.0**	**66.4**	**55.7**	**40.8**	**56.0**	**81.3**

Figure 1: Dissimilarity of assemblages of carabid beetles from individual years after the summer flood 1997 and reference community sampled before flood (in the year 1995). Analysis was done from data about dominance of species.

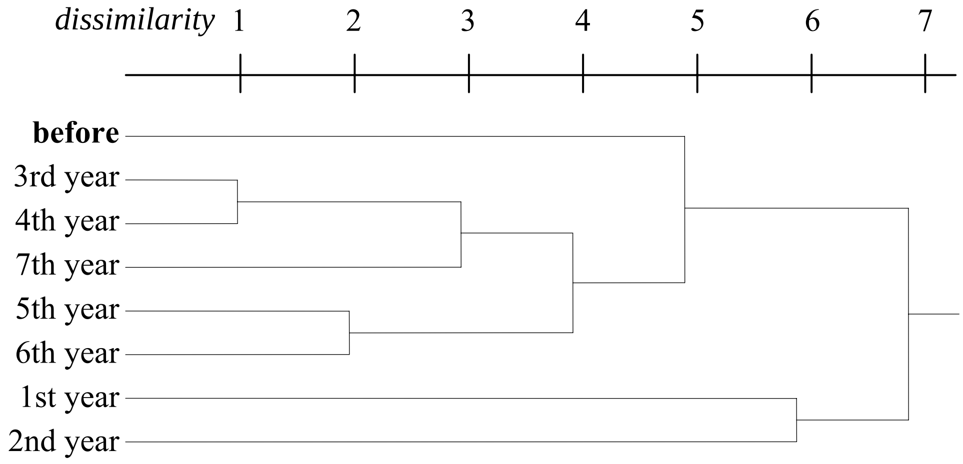


Figure 2: Dissimilarity of epigeic part of terrestrial isopod assemblages from individual years after the summer flood 1997 and of reference community sampled before flood (in the May-July 1997). Analysis was done from data about dominance of species.

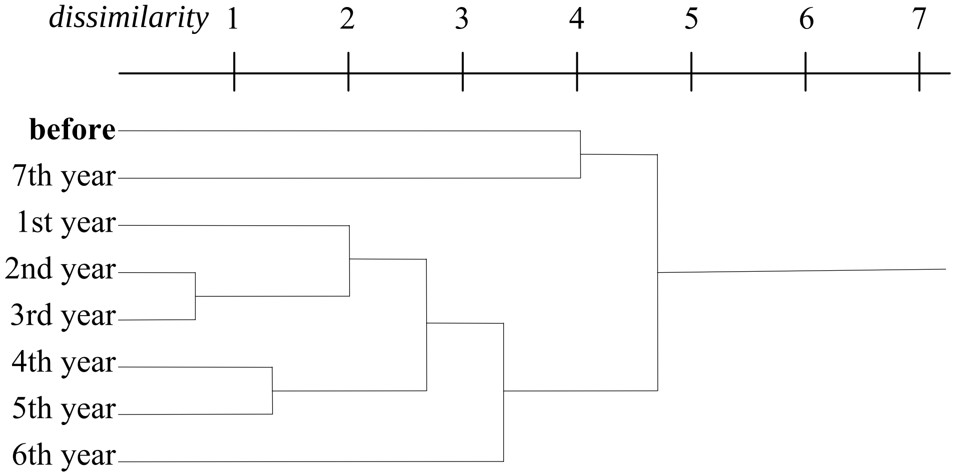
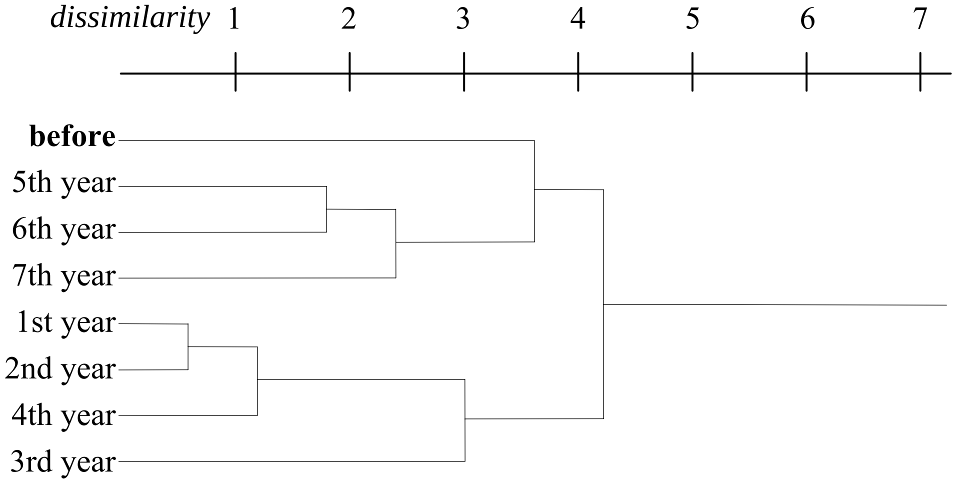


Figure 3: Dissimilarity of edaphic part of terrestrial isopod assemblages from individual years after the summer flood 1997 and of reference community sampled before flood (May 1997). Analysis was done from data about dominance of species.



03. Response of soil fauna to clear-cutting – different sampling methods, different results?

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Abstract

The effect of clear-cutting on soil macrofauna was studied in floodplain forest of Litovelské Pomoraví Protected Landscape Area from April 2003 to June 2004. Two methods of sampling were used: pitfall trapping and extraction of soil samples. Impact of clear-cutting management on epigeic subcommunities was minor for centipedes, millipedes and isopods, and significantly positive for carabid beetles (higher diversity and activity abundance in cutover than in forest), while effect on soil fauna inhabiting soil profile (such as small isopods, geophilomorph centipedes and millipedes juveniles) was significantly negative as their abundances rapidly decreased. It was caused by higher soil compaction on cutover after using heavy forestry machines for timber carrying and replanting.

Soil invertebrates / Oniscidea / Chilopoda / Diplopoda / Carabidae / clear-cutting / floodplain forest

Introduction

Floodplain forests are distributed in bottomlands of larger rivers. Recently, they are limited to small fragments in Central Europe. Rich and specific assemblages of invertebrates, including soil fauna, occupy floodplain forests, therefore major part of them belongs to protected areas. In Central European conditions one of richest communities of soil invertebrates, e.g. centipedes or else millipedes occur in such habitat [21]. Floodplain forests and their inhabitants are threat by human management of flooding regime [19, 20] and by forestry as well. Clear-cutting is regularly associated with changes of diversity and abundance of soil invertebrates. Decrease of both, diversity and abundance, may degrade soils and soil functioning [2]. Impact of clear-cutting to soil fauna is frequently studied in boreal forests [4, 15, 13, 7, 9, 18, 17, 16, 25], mainly because of high importance of forestry in these areas [12, 2]. The most popular group of soil insect frequently used in environmental assessing studies as good indicators of the habitat conditions are carabid beetles [14, 3, 5, 7, 9, 10].

Higher species number of ground beetles in cutover is repeatedly reported by many authors [e.g. 13, 9]. Small cutovers in forests attracts also typical open areas species which are usually able to fly and colonized such habitats very quickly. Typical forest fauna is still occurring in these sites (at least temporarily) and thus the species number in such places is higher than in unaffected forests. In fact this interpretation might be misleading as the real impact of clearing on soil fauna could be unfavourable.

Unfortunatelly, most of studies on comparing forest and cutover communities of soil fauna are based on just one method for collecting of soil animals, most often pitfall trapping [7, 4, 5, 25] vs extraction of soil samples [17, 24, 11]. This could work for such typical model group of soil invertebrates carabid beetles or nematods, but some groups of soil macrofauna are collected by combination of both methods. From these reason our research was aimed to changes in epigeic and edaphic subcommunities of centipedes (Chilopoda), millipedes (Diplopoda) and terrestrial isopods (Isopoda: Oniscidea) in floodplain forest after clear-cutting. For better comparison of our results with other papers we included also carabid beetles (Coleoptera: Carabidae).

Materials and methods

Study was conducted in the Litovelské Pomoraví Protected Landscape Area (central Moravia, eastern part of Czech Republic) in old floodplain forest and surrouding cutover (49°65´N, 17°20´E, altitude 210 m a.s.l., mean year precipitation 520 mm, mean year temperature 9.1 °C, *table I*, *figure 1*). Forest site belongs to plant association *Querco-Ulmetum* and its part was clear-cutted in November 2002. This cutover (size cca 50 × 100 m) was replanted in March 2003 by oak, elm and lime tree (ratio 8 : 1 : 1) using heavy forest machines. Before that, remaining wood residue was chipped and scattered throughout whole area.

Epigeic subcommunities of terrestrial isopods, centipedes, millipedes and ground beetles were studied using pitfall traps. Row of six traps (spacing 10 m, Ø of mouth 7 cm, 4% formaldehyde solution, metal hood) was installed in middle of cutover in April 2003. Another row on pitfall traps was installed in forest, about 60 m from the edge. Traps were inspected in 2-4 weeks period till June 2004.

Edaphic subcommunities of terrestrial isopods, centipedes and millipedes were studied using heat extraction of soil samples. Seven soil samples (area 1/16 m^2, depth 10 cm, including litter) were taken monthly from both sites. Soil samples were heat-extracted in modified Tullgren apparatus [23] for 10-14 days. From abiotic parameters, soil compaction, air humidity and temperature were compared. Soil compaction was measured by hand penetrometer (Eijkelkamp, model P1.50). Temperature and air humidity were measured by dataloggers Minikin TH (Environmental Measuring Systems, Brno) from April to June 2003. Dataloggers were located in soil with sensors in depth less than 1 cm.

Results

Soil on the cutover was significantly more compact (figure 2), than in forest ($t = -5.888$, $P < 0.01$). In the research period soils on both sites were comparably moist having air humidity about 100 %. Soil temperatures were significantly higher on the cutover ($t = -9.6397$, $P < 0.01$).

Epigeic subcommunities

Using pitfall traps we recorded 6 species of terrestrial isopods, 10 centipede species, 10 millipede species and 21 species of ground beetles. A large difference in number of species was recorded between forest site and cutover for carabids only (13 vs 20, *table II*). The same situation is for mean catch (*figure 3*), significant difference was proved for carabids only (*table III*).

In dominance, there are some species more dominant in forest such isopod *Protracheoniscus politus*, geophilomorph centipedes genus *Strigamia* and some recedent *Lithobius* species (*Lithobius agilis*, *Lithobius nodulipes* and *Lithobius erythrocephalus*), millipedes genus *Unciger* and carabid *Abax parallelipipedus*. Some other species are more dominant on cutover: isopod *Hyloniscus riparius*, centipedes genus *Geophilus*, millipedes *Glomeris connexa* and *Leptoiulus proximus* and small sized ground beetles from genus *Poecilus.* Some other species of carabids were recorded from cutover only, usually that which are typical for open habitats (*Amara aenea, Bembidion lampros, Bradycellus caucasicus, Clivina fossor, Harpalus progrediens, Notiophilus palustris* and *Poecilus versicolor*).

Edaphic subcommunities

From soil sampes were heat extracted 7 species of terrestrial isopods, 10 centipede species and 8 millipede species (*table IV*), numbers of species in forest and cutover were similar. There were great differences in abundance, all groups of soil macrofauna were more abundant in forest than in cutover (*figure 4*) and these differences were significant (*table V*).

Differences in dominance were notable for some species (*table IV*). In the forest were more dominant isopod *Trichoniscus pusillus*, centipede *Strigamia acuminata*, and millipede *Melogona voigti*. Isopods *Trachelipus rathkii, Hyloniscus riparius*, centipede *Lithobius mutabilis* (and its juveniles, group *Lithobius* spp.) and millipede *G. connexa* were more dominant at cutover.

Discussion

Forest management highly affects assemblages of soil invertebrates. For example, Werner and Raffa [25] described more species of ground-habitat beetles affected by management type than by dominant tree or canopy structure. Clear-cutting has strong impact on microclimate conditions, mainly light, temperature and humidity. These changes of conditions are accompanied with increasing presence of open habitat species [13, 7, 9, this work]. Surrounding field and riparian stands were source of ground beetles of genus *Poecilus, Notiophilus palustris, Clivina fossor* or *Bradycellus caucasicus*, species, which prefer higher temperature on cutover. On the opposite, these changes in conditions caused decrease of number of forest species as e.g. millipede *Melogona voigti*, major part of centipede species genus *Lithobius*, isopod

Protracheoniscus politus or carabids genus *Abax*. Even more, cutting can also change availability and quality of food sources for detritophagous groups [17]. Similar or even higher (Carabidae) species spectrum and epigeic activity of studied groups of soil fauna could indicate minimal (or positive) impact of clear-cutting to soil macrofauna. Comparing species spectrum of edaphic subcommunities of all groups we can conclude the same. However, indexes mentioned above doesn't show dramatically decrease of density following such manipulation [24, 6].

Forest management with minor impact on soil organic layer has little influence on soil invertebrates [15]. As mentioned above, harvest at cutover was in our case carried out by heavy forest machines and therefore the soil is significantly more compact and less favourable for soil fauna inhabiting upper layer of soils now. Unsuitable conditions in soil probably force animals to move at the soil surface and caused higher epigeic activity of non-epigeic species. For example small isopod *Trichoniscus pusillus* or centipedes *Geophilus electricus* and *Geophilus alpinus* were much more abundant in forest than in cutover, but in research period they had appeared in pittfall traps in cutover only. In addition, higher activity of some generalist species such as *Lithobius mutabilis* on the cutover can be caused by local higher temperatures. *L. mutabilis* development includes six early stages with endogeic way of life and subsequent six or seven stages with higher epigeic activity. Faster individual development and accompanying longer period of epigeic activity were described for this centipede by Tuf [22]. Pronounced differences between forest and cutover in soil abiotic factors can persist for a long time and are known to inhibite re-establishing of soil fauna community and its density as well [1].

Conclusion

From our results is evident, that forest management has some accompanying effects on forest inhabitants. Single small area clear-cutting (0.5 ha) can cause increase of species number and density of ground beetles and relatively small changes in number of species of some other groups of soil invertebrates (terrestrial isopods, centipedes, millipedes). Nevertheless accompanying effects, such as soil compaction by heavy forestry machines makes soil environment unfavourable for fauna occupying upper soil layers, therefore abundance of these groups strongly decrease.

Acknowledgement

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Table I: Soil parameters measured in forest site in 1998 [8].

Table II: Comparison of epigeic subcommunity structure (dominance %) of soil macrofauna of floodplain forest and surrouding cutover. Material collected from April 2003 till June 2004.

Table III: Comparison of forest and cutover for size of epigeic subcommunity of group of soil macrofauna (two-paired t-test).

Table IV: Comparison of edaphic subcommunity structure (dominance %) of soil macrofauna of floodplain forest and surrouding cutover. Material collected from April 2003 till June 2004.

Table V: Comparison of forest and cutover for size of edaphic subcommunity of group of soil macrofauna (two-paired t-test).

Figure 1. Situation on the locality, floodplain forest and cutover and their surroudings.

Figure 2: Comparison of epigeic activity (ind./6 traps/10 days) of soil macrofauna in floodplain forest and surrouding cutover from April 2003 to June 2003 (mean + S.D.).

Figure 3: Comparison of abundance (ind.*m^{-2}) of soil macrofauna in floodplain forest and surrouding cutover from April 2003 to June 2003 (mean + S.D.).

Table I

C_{org}	2.5 %
humus	4.4 %
N_{org}	3.6 mg * kg^{-1}
P	76.9 mg P_2O_5 * kg^{-1}
pH	5.0
Amount of litter	622.0 g *m^{-2}

Table III

	t stat	P
Oniscidea	0.699875	0.247028
Chilopoda	-1.55278	0.070015
Diplopoda	-0.36934	0.358358
Carabidae	-2.37709	0.015133

TableV

	t stat	P
Oniscidea	4.188431	0.000757
Chilopoda	5.009972	0.000198
Diplopoda	3.436271	0.002781

Table II

	forest	cutover
Isopoda: Oniscidea		
Ligidium hypnorum (Cuvier, 1792)	31.8	45.0
Trachelipus rathkii (Brandt, 1833)	28.0	43.3
Porcellium conspersum (C.L. Koch, 1841)	7.0	4.2
Protracheoniscus politus (C.L. Koch, 1841)	32.5	0.8
Hyloniscus riparius C.L. Koch, 1838	-	5.0
Trichoniscus pusillus Brandt, 1833	0.6	1.7
Chilopoda		
Lithobius agilis C.L. Koch, 1847	2.7	-
Lithobius erythrocephalus C.L. Koch, 1847	0.5	-
Lithobius forficatus (Linnaeus, 1758)	11.8	11.9
Lithobius mutabilis L. Koch, 1862	68.8	84.8
Lithobius nodulipes Latzel, 1880	0.5	-
Geophilus alpinus Meinert, 1870	-	0.4
Geophilus electricus (Linnaeus, 1758)	-	0.4
Strigamia acuminata (Leach, 1814)	7.0	0.4
Strigamia transsilvanica (Verhoeff, 1928)	6.5	1.5
Schendyla nemorensis (C.L. Koch, 1836)	2.2	0.7
Diplopoda		
Glomeris connexa C.L. Koch, 1847	16.7	54.0
Polydesmus complanatus (Linneaus, 1761)	1.2	-
Polydesmus denticulatus C.L. Koch, 1847	2.4	2.3
Polydesmus spp.	-	1.1
Melogona voigti (Verhoeff, 1899)	8.3	-
Haplogona oculodistincta (Verhoeff, 1893)	2.4	1.1
Leptoiulus proximus (Němec, 1896)	3.6	6.9
Megaphyllum projectum (Verhoeff, 1894)	1.2	-
Unciger foetidus (C.L. Koch, 1838)	32.1	19.5
Unciger transsilvanicus (Verhoeff, 1899)	32.1	13.8
Polyzonium germanicum Brandt, 1831	-	1.1
Coleoptera: Carabidae		
Abax parallelepipedus (Piller,Mitterpacher, 1783)	31.0	3.1
Abax parallelus (Duftschmidt, 1812)	9.5	5.6
Amara aenea (De Geer,1774)	-	0.2
Bembidion lampros (Herbst, 1784)	-	0.2
Bradycellus caucasicus (Chaudoir, 1846)	-	0.2
Carabus coriaceus Linnaeus, 1758	3.7	5.0
Carabus granulatus Linnaeus, 1758	-	1.7
Carabus scheidleri Panzer, 1799	14.9	19.0
Carabus ullrichi Germar, 1824	17.2	29.5
Clivina fossor (Linnaeus, 1758)	-	0.2
Harpalus progrediens Schauberger, 1922	-	0.6
Notiophilus palustris (Duftschmid, 1812)	-	0.8
Platynus assimilis (Paykull, 1790)	0.6	-
Poecilus cupreus (Linnaeus, 1758)	1.1	7.8
Poecilus versicolor (Sturm, 1824)	-	1.4
Pseudoophonus rufipes (De Geer, 1774)	1.1	3.9
Pterostichus melanarius (Illiger, 1798)	14.4	15.1
Pterostichus niger (Schaller, 1783)	3.4	4.7
Pterostichus oblongopunctatus (Fabricius, 1787)	2.0	0.4
Pterostichus ovoideus (Sturm, 1824)	0.6	0.6
Pterostichus strenuus (Panzer, 1797)	0.3	0.2

Table IV

	forest	clearcut
Isopoda: Oniscidea		
Ligidium hypnorum (Cuvier, 1792)	6.4	3.9
Trachelipus rathkii (Brandt, 1833)	4.3	19.4
Porcellium conspersum (C.L. Koch, 1841)	0.9	1.0
Protracheoniscus politus (C.L. Koch, 1841)	2.5	3.9
Haplophthalmus mengei (Zaddach, 1844)	2.7	9.7
Hyloniscus riparius C.L. Koch, 1838	12.8	45.6
Trichoniscus pusillus Brandt, 1833	70.3	16.5
Chilopoda		
Lithobius agilis C.L. Koch, 1847	0.3	0.3
Lithobius mutabilis L. Koch, 1862	4.3	13.1
Lithobius microps Meinert, 1868	0.4	-
Lithobius curtipes C.L. Koch, 1847	0.3	1.2
Lithobius spp.	6.4	12.8
Geophilus alpinus Meinert, 1870	0.1	0.9
Geophilus electricus (Linnaeus, 1758)	0.9	-
Geophilus flavus (DeGeer, 1778)	26.5	25.5
Strigamia acuminata (Leach, 1814)	14.6	1.2
Strigamia transsilvanica (Verhoeff, 1928)	0.3	1.6
Schendyla nemorensis (C.L. Koch, 1836)	46.1	43.3
Diplopoda		
Glomeris connexa C.L. Koch, 1847	26.3	44.4
Brachydesmus superus Latzel, 1884	-	2.2
Blaniulinae genn.sp.	-	2.2
Melogona voigti (Verhoeff, 1899)	55.7	22.2
Haplogona oculodistincta (Verhoeff, 1893)	7.3	8.9
Leptoiulus proximus (Němec, 1896)	0.8	-
Unciger foetidus (C.L. Koch, 1838)	6.1	8.9
Unciger transsilvanicus (Verhoeff, 1899)	1.1	6.7
Unciger spp.	2.7	4.4

Figure 1

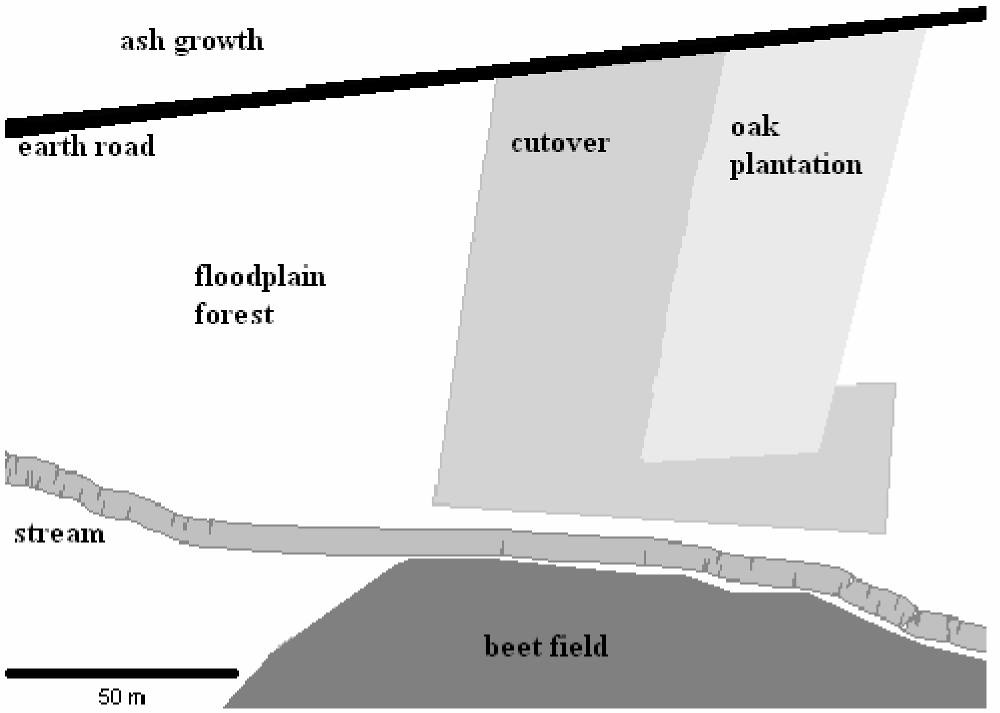


Figure 2

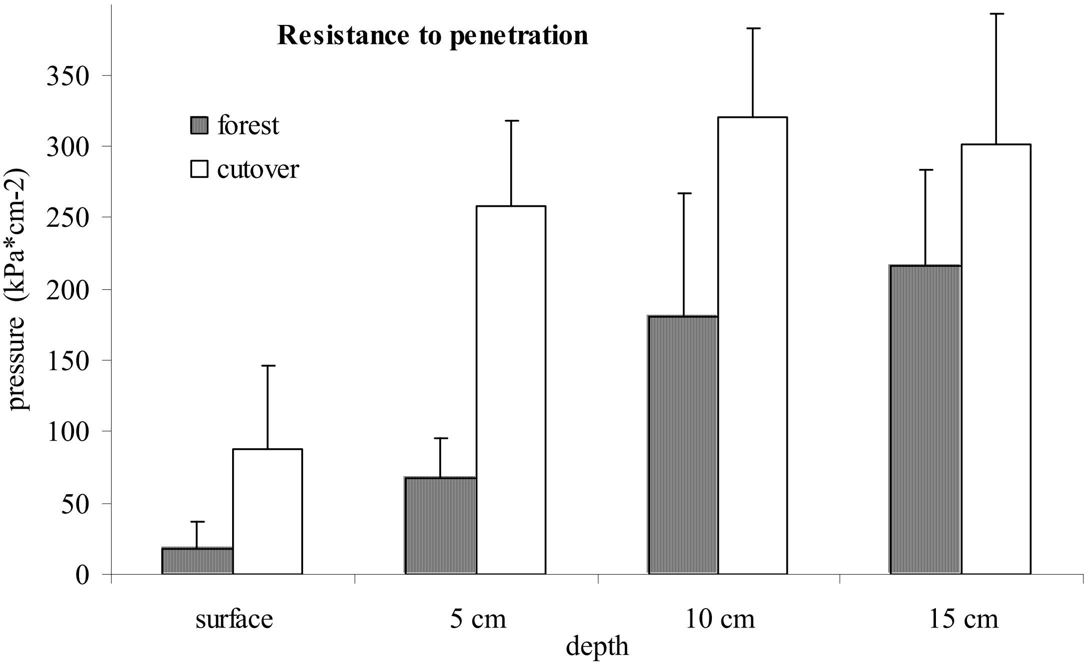


Figure 3

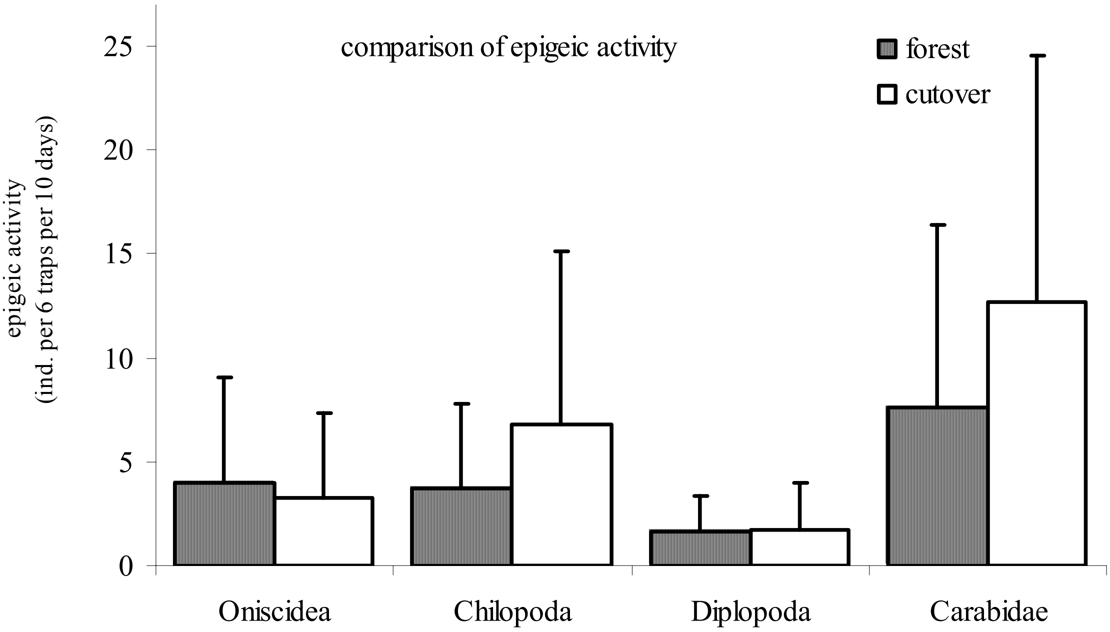
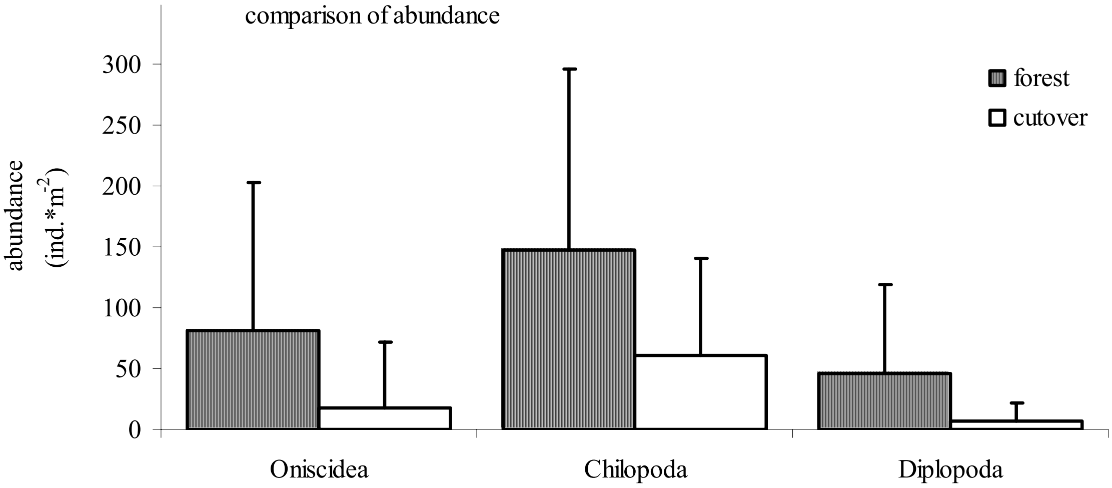


Figure 4



04. Diurnal activity pattern of carabid beetles in dependence to season, temperature and biotope

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Abstract

Diurnal epigeic activity of ground beetles (Coleoptera: Carabidae) in floodplain forest and neighbouring clear-cut was studies in late spring and early in autumn of 2005 by pitfall trapping. 100 traps were checked every three hours. In total, 35 species of ground beetles were trapped. The significant influence of day-time factor to epigeic activity was recorded in 16 species; epigeic activity of 13 species was affected by temperature of the soil surface too. Activity of some species differed between seasons or localities.

Key-words: Carabidae, ground beetles, epigeic activity, diurnal activity, diel activity, seasonality, temperature, soil fauna, floodplain forest, cutting, Litovelské Pomoraví

Introduction

Diurnal activity represents a specific pattern of activity during the course of a 24-hour cycle. We can divide carabid beetles into three basic categories on the basis of their activity in the course of the day - species that are strictly diurnal, species with nocturnal activity, and flexible species whose activity to a great extent is modified by microclimatic and geographic conditions (Thiele 1977, Novák 1977). However, differences in activity appear not only among species and populations of the same species, but even within a single population (Thiele & Weber 1968). Species can also show various preferences to light intensity in various phases of ontogenetic development (differing periods of development of larva and imago – *Carabus problematicus* Herbst) or changes in periodicity in the reproduction period (*Carabus cancellatus* Illiger). Annual rhythms are also closely connected to circadian rhythms; Thiele & Weber (1968) state that 90% of species that reproduce in the autumn are active at night, while with species that reproduce in the spring the proportion of nocturnal activity is substantially lower (33%).

Diurnal activity is primarily regulated by endogenous physiological factors, so-called timers, but the length of their duration is to various extents modified by environmental conditions. Light is presented as the most important factor influencing carabid beetle activity (Thiele 1977), but temperature (Kegel 1990) and moisture levels (Thiele 1977, Novák 1980) can also play an important role in connection with the type of habitat.

A study dealing with diurnal activity can be conducted under natural or laboratory conditions. In laboratory studies of the diurnal activity of groups of carabid beetles (homo- and heterotopic) direct observation or instruments recording activity on the basis of weight (Park 1935) can be employed, but most often actographs are used to record activity on the basis of electric impulses, infra-red light, or sound; Novák (1978) designed a special trap with automatic sampling for his laboratory research.

Two basic methods are most commonly used in natural conditions: 1) simple pitfall traps in various modifications (Williams 1958, Loreau 1986) or 2) automatic traps that separate catch in individual periods (Novák 1979, 1980).

Material and Methods

Study area was located in Litovelské Pomoraví Protected Landscape Area, natural landscape around meandered Morava River (Central Moravia, Czech Republic) with floodplain forests and meadows. Compared localities were old floodplain forest (*Querco-Ulmetum*) and neighbouring clear-cut (49°65´N, 17°20´E, altitude 210 m a.s.l.).

Herbal layer of floodplain forest was created by *Anemone nemorosa, Polygonatum* spp., *Lathyrus vernus* and *Maianthenum bifolium*, dominant moss was *Eurhynchium hians*. In November 1998, litter biomass (dry weight) was 622 g/m2. Alluvial soil was loamy-sandy to loamy at the locality, with pH 4.8-5. Annual precipitation was around 520 mm; mean annual temperature was 9.1 °C. Part of this forest was cut in November 2002 and replanted in March 2003 by oak, elm and lime tree (ratio 8 : 1 : 1) using heavy forest machines. Before that, remaining wood residue was chipped and scattered throughout whole area. Epigeic invertebrates were catching

by pitfall traps (plastic pots) without fixative solution. 60 traps were arranged in forest and 40 traps in clear-cut in line with spacing three meters.
Experiment carried out in late spring (May 20th – June 7th, 18 days) and early autumn (September 23rd – November 18th, 25 days) of 2004. Traps were checked every three hours during these seasons (i.e. at 3, 6, 9, 12, 15, 18, 21, and 24 o'clock).

Presented results were modified at individual caught by 60 traps during 18 days. Division of the species by their preferences to biotope (forest *vs* open-habitat species) and by reproduction biology (spring *vs* autumn breeders) was realized according to Thiele (1977), Novák (1979, 1980), Larsson (1939) and Lindroth (1949). Temperatures of soil surface were measured in checking times at both localities by using of data-loggers Minikin TH (Environmental Measuring Systems Brno, www.emsbrno.cz). Canonical Correspondence Analysis and Generalised Additive Models for evaluating of results were created in programme CANOCO for Windows 4.5© (ter Braak & Šmilauer 1998), graphs were created in CanoDraw for Windows 4.0 and Microsoft Excel.

Results

Summary of material

Over the entire course of the research a total of 924 individual carabid beetles were captured, representing 35 species (Table 1). The clear-cut was more abundant in species (32) and the overall number of beetle (598, 65%); 326 specimens representing 25 species of carabid beetles were collected in the forest. Of significance was the quantitative dominance of specimens collected in the spring – a total of 791 specimens (85%) of thirty species, while only 133 specimens from 21 species were collected in the autumn.

The most numerous species were *Abax parallelus* and *Bembidion lampros,* the first of these dominated in the forest growth (70%), while the second occurred nearly exclusively in the clear-cut. Together these two species formed nearly 40% of the overall number of collected specimens.

The similarities between the forest and clearing populations were not great - the Jaccard index was 51%. The low similarity of populations is caused by a significant representation of characteristically forest species in the woodlands (11 species, 44%) and species typical for the open habitats (15 species, 47%).

Epigeic activity in the forest environment was concentrated mainly in the evening and night-time hours, with a peak in the period between 21:00 and 0:00; in the clear-cut activity had a distinctive daytime character, with peaks in the afternoon hours.

In the spring epigeic activity was more or less evenly spaced throughout the entire day, with a decline in the late night and early morning hours. On the other hand, the autumn season was characterized by significant afternoon peaks of activity in a relatively narrow span between 12:00 and 15:00 and gradual declines during the evening hours (Figure 1).

If we take into consideration all representatives of the order *Coleoptera,* activity in the forest growth was spread evenly throughout the entire day (Figure 2), while the clear-cut maintained a distinct diurnal character. An observed decrease in carabid beetle activity in the autumn season can be applied to the whole order of beetles. Species in the clear-cut had the same pattern of activity in both seasons with afternoon peaks, in the autumn with a much narrower distribution – 50% of all specimens were collected in the period between 12:00 and 15:00 (Figure 3).

The second comparison was done after their reproduction biology. So called spring breeders activated at twilight in forest and during daylight in clear-cut respectively. Autumn breeders, in comparison to spring breeders, exhibited an elevated proportion of nocturnal activity; in the forest environment nocturnal activity clearly dominated, while in the clear-cut a second peak appeared – in addition to the afternoon maximum there was also increased activity in the early night-time hours (Figure 4).

Analysis of the influence of exogenous factors on epigeic activity

From the total number of recorded species we included in the analysis only the dominant species with significant responses to at least one of the factors. A total of 8 species responded significantly to the *day-time*, while 9 species responded to the factor of *temperature* (Table 2).

RDA analysis was performed (Figure 5) - the majority of species were positively influenced by the spring season and the clear-cut environment. A bond to the forest environment was shown by the species *A. parallelipipedus*, *A. parallelus*, *Calosoma inquisitor,* and *P. oblongopunctatus*, which were also the only species with a more significant representation in the autumn.

The influence of *day-time* and *temperature* abiotic factors on the epigeic activity of the dominant species was expressed using GAM, generalized additive models

(Figures 6a, 6b). Both representatives of the *Abax* genus and *P. rufipes* exhibited significant nocturnal activity. On the other hand, *A. similata*, *P. versicolor*, *P. cupreus*, and *B. lampros* appear as diurnal species, and the single representative of forest species among these diurnal species is *P. oblongopunctatus*.

An increasing amount of activity with rising temperatures of the soil surface was shown with both representatives of the *Poecilus* family, and other representatives of open clearing species, *B. lampros*, *A. similata* and *P. melanarius* had a positive connection to higher temperatures. On the other hand, the forest species *A. parallelus*, *A. parallelipipedus* and *P. oblongopunctatus* preferred lower temperatures.

In a comparison of material from individual localities and during individual seasons the influence of *temperature* and the *day-time* were tested on all species. Activity of 16 species was significantly affected by *day-time*, while 13 species were active in relation to *temperature* (Tab. 3).

Comparison of diurnal activity in connection to the season

A separate analysis of material collected in the spring and in the autumn showed that the factor of *locality* had a greater significance in the spring. On the other hand, the factors of the *day-time* and *temperature* of the ground surface played a more significant role in the autumn (Fig. 7).

In a comparison of epigeic activity in the spring and the autumn only *P. cupreus* provided a significant response to *day-time* for both periods; they were only active during the day in both seasons, although this activity ended earlier in the autumn. Four species exhibited a significant connection between epigeic activity and *temperature* in both seasons: *A. parallelipipedus*, *P. melanarius*, *P. versicolor,* and *P. cupreus* (Figures 8a and 8b). The species *P. melanarius* and *A. parallelipipedus* preferred higher temperatures in the autumn in comparison to the spring season. *P. cupreus* was more active in the autumn than in the spring under lower temperatures. *P. versicolor* exhibited this same pattern of behaviour.

Comparison of diurnal activity in connection to locality

Samples collected in the forest growth were significantly influenced by *season*, while the influence of *temperature* was significantly greater in the clear-cut. Both localities differed with regard to the temperature regime, with temperatures more significantly fluctuating in the clear-cut than in the forest. While spring temperatures in the clear-cut fluctuated between 7-21 °C, in the forest temperatures only ranged from 7 to 15 °C. In the autumn temperatures fluctuated between 1 and 21 °C in the clear-cut, in the forest in a much lower range, from 5 to 13 °C. *Day-time*, and even the amount of light influenced epigeic activity at both localities approximately the same (Figure 9).

The species *A. parallelipipedus*, *A. parallelus* and *A. similata* responded significantly to the *day-time* factor at both localities (Figures 10a and 10b). Both species of the *Abax* family exhibited more pronounced nocturnal activity in the forest and in the clear-cut; *A. similata* had one significant peak in the forest at 15:00 and was active there in a relatively narrow range of conditions, while this peak in the clear-cut came already around noon, and the range of activity there was broader. The *temperature* factor was significant for *A. parallelipipedus*, *A. parallelus* and *P. melanarius* at both localities. *A. parallelipipedus* exhibited a peak of activities under similar temperatures at both localities. *A. parallelus* was active in the clear-cut under lower temperatures than in the forest; on the other hand *P. melanarius* was active at the clear-cut under higher temperatures than in the forest environment (Figures 11a and 11b).

Discussion

Park (1941) formulated a hypothesis according to which populations have a tendency in the course of their development to converge toward symmetry of activity in the framework of a 24-hour cycle. Population at a two-year old clear-cut represented the primitive stage in our study, while the forest growth represented the developed (climax) stage. According to Park's hypothesis it is therefore possible to predict that the activity at the open habitats will probably be asymmetric while the activity in the forest will approach symmetry. If we were to include in the analysis all collected representatives of the order *Coleoptera* (besides carabid beetles this mainly concerned representatives of the families *Staphylinidae* and *Geotrupidae*), activity in the forest growth would truly have approached symmetry (Figure 2). On the other hand, in the case of carabid beetles at the clear-cut there was significant asymmetry in favour of diurnal activity, and in the forest environment the assumed symmetrical activity was not confirmed – activity there had a significant nocturnal character. Consequently, our results do not correspond to the research by Williams (1959b), which was able to confirm the validity of Park's hypothesis for carabid beetles. Our results more closely correspond to those reached by

Loreau (1986), who in a beech forest found predominately nocturnal activity among all dominant species of carabid beetles.

It was shown in our research that clear-cuts in general have greater species diversity than woodlands. A number of other researchers dealing with the influence of forest clearing on carabid beetle populations reached this same conclusion (Koivula 2002, Magura 2002, Ings & Hartley 1999).

Carabid beetles showed substantially greater activity in the spring (85% of specimens), which is in agreement with the results presented by Dondale et al. (1972), whose specimens collected in the spring (*Carabidae* and *Staphylinidae*) composed 85% of their collections for the year. Novák (1980) also recorded quantitatively richer takes in the spring and summer in comparison to the autumn season.

With the species *P. melanarius* and *A. parallelipipedus* we recorded a preference for higher temperatures in the autumn than in the spring. This fact seems surprising with respect to the annual course of temperatures (when the autumn season was substantially cooler). A preference toward higher temperatures in the autumn period is apparently related to the biology of their reproduction – both are representatives of autumn breeders, i.e. their sexual glands mature in the autumn and the influence of higher temperatures is known, for example, in the relationship to the size of eggs with the species *Notiophilus biguttatus* (Fabricius) (Ernsting & Isaaks, 1997) or the speed of development in the families *Amara* (Saska & Honek, 2003a) and *Brachynus* (Saska & Honek, 2003b). It is therefore possible to anticipate the influence of higher temperatures on the accelerated maturation of sexual glands – this could provide an answer to the question as to why the activity of these otherwise nocturnal species shifts to the light phase of daytime in the autumn. They were evidently actively searching for a locality with higher temperatures.

The significant influence of locality in the spring in comparison to the autumn season was given by the fundamental differences in character of vegetative cover in the open habitats between both seasons. In the spring the vegetative cover at the clear-cut was thin and spotty, often with completely exposed areas of soil. In the autumn the locality was covered with *Impatiens glandulifera.* Areas overgrown with dense vegetation show a higher moisture level and therefore the populations in them significantly differ (Haysom et al. 2003). The activity of forest species reached a peak in the spring in the evening and early night-time hours; in the autumn activity peaked in the afternoon. Ilosavy (1982), who conducted his research in June and July, describes a significant peak of activity in the night-time hours (22:00-4:00). Thiele (1977) likewise shows that with forest species there is a characteristic prevalence of activity at night. The peaks of activity that we determined in the afternoon hours during autumn monitoring is evidently related to extremely low temperatures in the night-time and early morning hours, which shifted the activity of forest species toward the afternoon.

Species in the clear-cut showed a peak of activity in the afternoon in both periods, though the carabid beetles in the autumn were active in a much narrower time range. We recorded a significant decline in activity in the autumn night-time and early morning hours, similar to that found by Dondale et al. (1972), who recorded the lowest number of collected specimens in the field in the period between 4:00 and 6:00.In theses periods the temperature of the soil surface is the lowest and according to Thiele (1977) it is temperature, along with light, that has the greatest influence on activity of these species living in the open habitats. Preiszner & Karsai (1990), who conducted their research on sandy grasslands, reached this same conclusion. In our study an absolute majority of species (66%) showing a significant response to temperature are species living in the open habitats.

Spring breeders in the forest environment were the most active at dusk and in the early night-time hours, while at the clear-cut their activity had a significant diurnal character. With spring breeders Novák (1980) recorded a predominance of activity in the daylight phase both in the forest and in the open habitats; at the same time he adds that the behaviour of the spring breeders is markedly variable in connection with the microclimate. The evening and night-time peak of activity in the forest is mainly given by the presence of the species *A. parallelus*, which is among the species with a predilection toward moisture (Thiele 1964), and is therefore connected mostly with nocturnal activity. In the study by Kegel (1990), which involved the activity of carabid beetles in agro-cenosis conditions, spring breeders also display predominantly diurnal activity – which is in agreement with our results from the clear-cut.

Autumn breeders showed a significant increase of activity in the night-time hours in comparison with spring breeders. In the forest environment nocturnal activity clearly predominated; in the clear-cut this was supplemented by more significant activity in the afternoon hours. Kegel (1990) also recorded a predominance of nocturnal activity in autumn breeders, and these results were likewise confirmed by Novák (1979, 1980), who recorded a peak of activity in the first two night-time hours; our results likewise show the highest activity of autumn breeders in the forest environment at the beginning of the dusk phase.

Discussion on selected species

Thiele (1977) describes *A. parallelipipedus* as a eurytopic forest species without a pronounced relationship to temperature, but naturally preferring lower light intensities. Novák (1980) also describes the peak of activity of this species in early night-time hours. In agreement with this the activity of *A. parallelipipedus* was limited mainly by the daytime period (50% of specimens were collected in the interval of 21:00 to 0:00), while in the autumn extremely low night-time temperatures showed a marked influence and limited activities to afternoon hours.

The activity of the species *Abax parallelus* had the same pattern as *A. parallelipipedus*. Though Thiele (1977) describes *Abax parallelus* as a stenotopic forest specie, in our study it was rather abundantly represented in the material collected from the clear-cut; in the autumn the number of specimens of this species were even balanced at both localities.

Both species from the *Poecilus* genus can be considered as typical representative species of the open habitats, as these show a positive connection to higher temperatures of the soil surface, and in relationship to light Thiele (1977) classifies them among euryphotic species. *P. cupreus* also showed noticeable diurnal activity in the study by Novák (1979, 1980), both in the forest and in the open habitats. It follows from the GAM that this species preferred lower temperatures in the autumn than in the spring – this was given by the fact that temperatures in the autumn period didn't reach the spring temperatures, and that *P. cupreus* in fact preferred the highest temperatures reached in both periods.

The species *Pseudoophonus rufipes* is classified among thermophile and xerophile field species with nocturnal activity (Thiele 1977). According to Kegel (1990) this species in the field also showed significantly higher activity during warm nights. While nocturnal activity dominated in our study, the number of specimens collected in the light phase was also significant. GAM analysis demonstrated a significant dependence of epigeic activity on the period of the day, while a dependence on temperature was not confirmed, despite the fact that its activity was divided more or less evenly throughout the entire day, with a peak in the evening and early night-time hours.

Thiele (1977) describes *P. melanarius* as a eurytopic field species preferring low light intensity; with respect to temperature he categorizes this species as eurythermal. On the contrary, in our research its activity was significantly dependent on the temperature of the soil surface and was active during periods with the highest temperatures. Alderweireldt & Desender (1990) likewise show activity in the field during the day, however with a substantial peak in the evening hours and in the early night-time hours they surmise that declining light intensity increases its activity. This pattern would correspond to our results from the forest, while in the clear-cut the activity of this species is substantially diurnal. However, Novák (1979, 1980) recorded an opposite pattern of activity for this species – in the forest diurnal activity and in the open habitats nocturnal.

The species *Bembidion lampros*, characteristic of open habitats, is known for prevalence toward diurnal activity in both this environment (Alderweireldt & Desender 1990, Novák 1979) and in a forest environment (Novák 1980). In our research this species was also significantly active during the afternoon, and this relationship is related to the temperature.

Thiele (1977) evaluates the species as eurytopic forest with a strong ecological bond to temperature and light. The work of both Thiele (1977) and Novák (1980) confirms the predominantly diurnal activity of this specie, even though Loreau (1986) labels it as substantially nocturnal. This species dominated in the autumn season and in the forest environment, where its activity was significantly diurnal (15:00 – 21:00) and also influenced by temperature.

Conclusion

1. A total of 924 specimens representing 35 species of carabid beetles were collected. The carabid beetles were significantly more active in the clear-cut and in the spring season.
2. In the forest growth nocturnal activity dominated, while in the clear-cut activity had a significant diurnal character. This is contrary to Park's hypothesis regarding the development of populations toward symmetry of activity - this would predict symmetric activity in the forest environment, which represents the climax stage in the study. The time distribution of the epigeic activity of the entire beetle population better corresponded to Park's hypothesis.

3. In the spring the activity was divided mostly evenly during the course of the entire day, while in the autumn we recorded a significant afternoon peak of activity caused by low temperatures in the night-time and early morning hours.
4. The day-time had a significant influence on 16 of the total 35 species and temperatures of the soil surface significantly influenced the activity of 13 species.
5. CCA analysis showed in the autumn season a substantial increase in the explanatory potential of factors of the day-time and temperature for the activity of carabid beetles in comparison to the spring season. CCA analysis also showed the substantial influence of the temperature of the surface of the soil on the activity of carabid beetles in the clear-cut.
6. The activity of the forest species during the course of the year shifted from the evening and night-time hours in the spring to the afternoon hours in the autumn season, especially in the last weeks of the research when temperatures in the night-time and early morning hours dropped all the way to freezing in the clear-cut. The activity of the species in the clear-cut maintained the same pattern during the course of the year – i.e. significantly diurnal.
7. Activity of the spring breeders in the forest environment reached a peak at dusk, while their activity in the clear-cut was clearly diurnal. Autumn breeders in both environments showed an increased share of activity at night.

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Figure 1: Influence of daytime temperatures on the level of epigeic activity of carabid beetles in individual seasons and at individual locality.

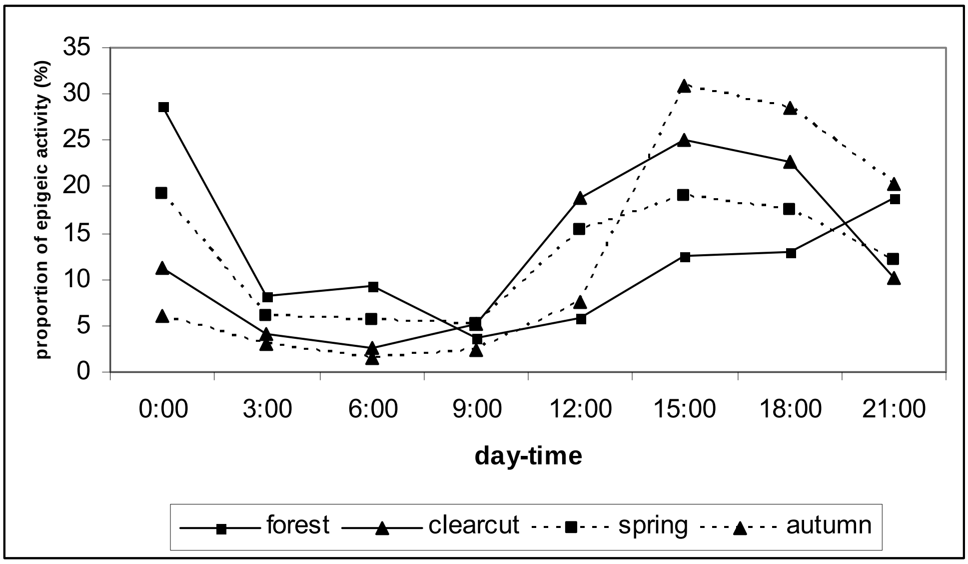


Figure 2: Comparison of diurnal activity of carabid beetles in dependence to locality.

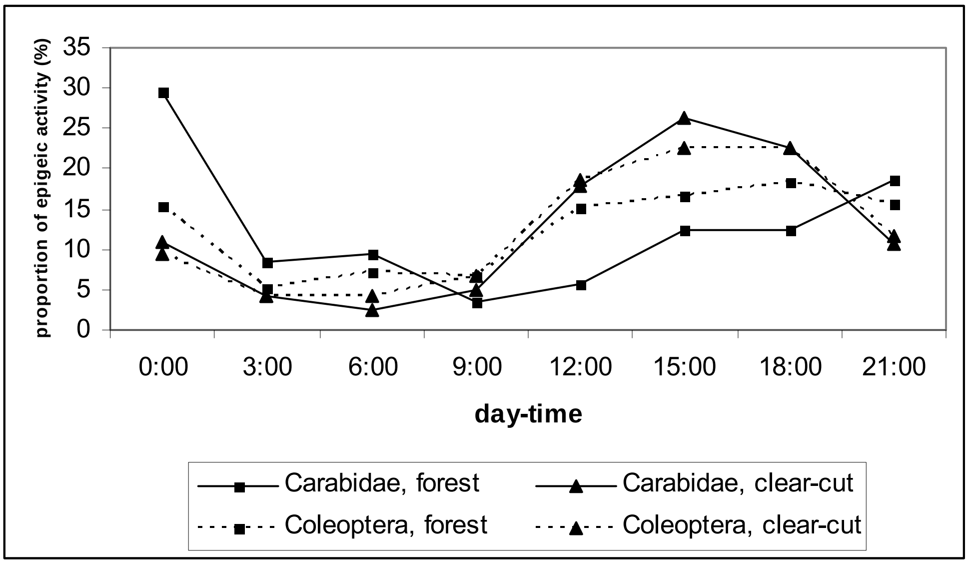


Fig. 3: Comparison of epigeic activity of forest species and open-habitat species of carabid beetles in dependence to season.

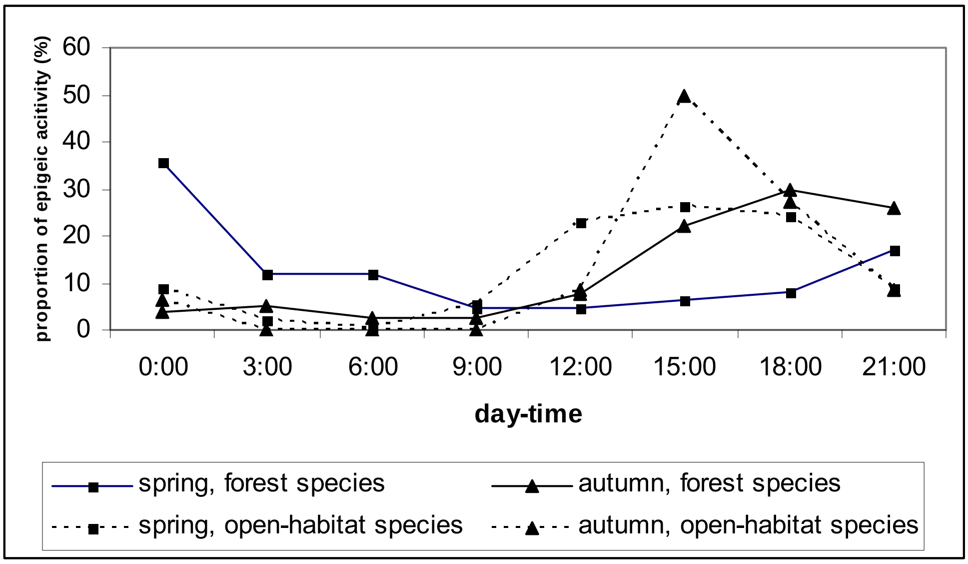


Fig. 4: Comparison of epigeic activity spring breeders and autumn breeders in dependence to locality.

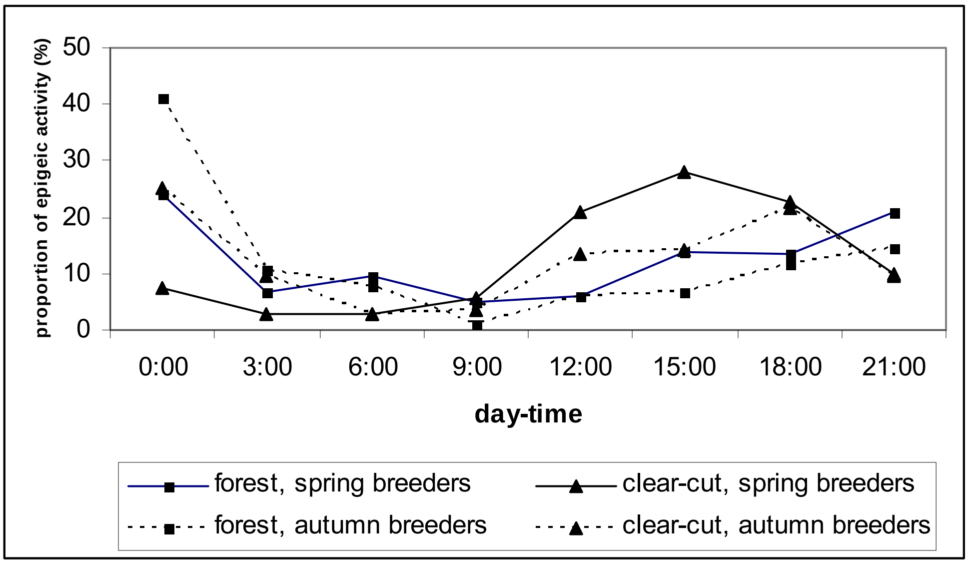


Fig. 5: RDA ordination illustrating distribution of the most numeral carabid species (dominancy more than 1.5 %) in relation to environmental factors. Significancy of factors: spring – F 40,85, forest – F 21,42, temperat – F 12,70, time – F 7,35, p for all factors lower than 0,01.

Summary of explained variability of the main canonical axes of the RDA model:

Axes	**1**	**2**	**3**	**4**
Eigenvalues:	0.066	0.037	0.006	0.002
Species-environment correlations:	0.479	0.336	0.340	0.169
Cumulative percentage variance				
of species data:	6.6	10.3	10.9	11.1
of species-environment relation:	59.6	92.9	97.8	100.0

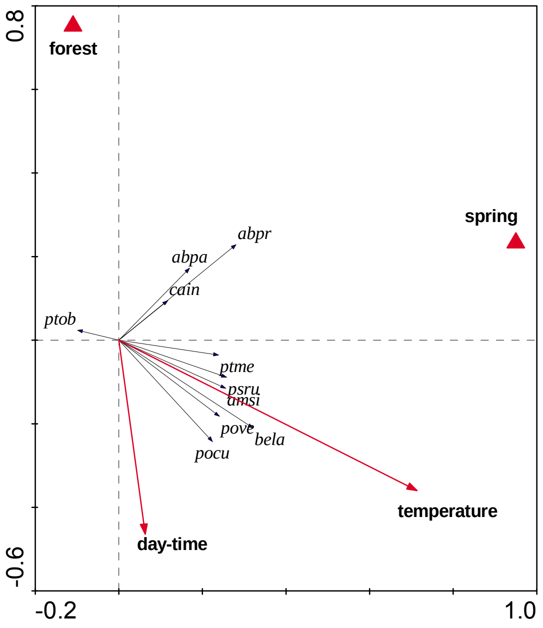
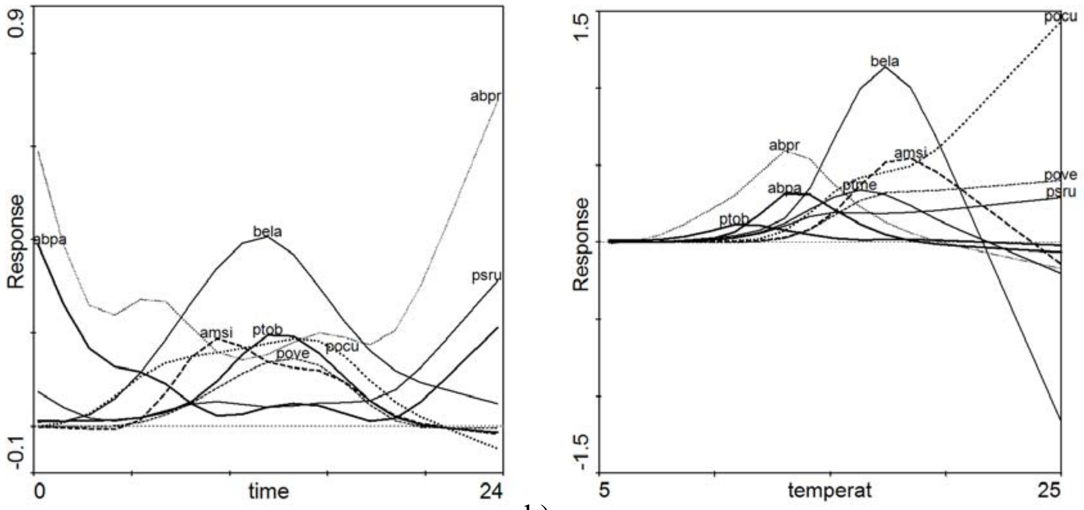
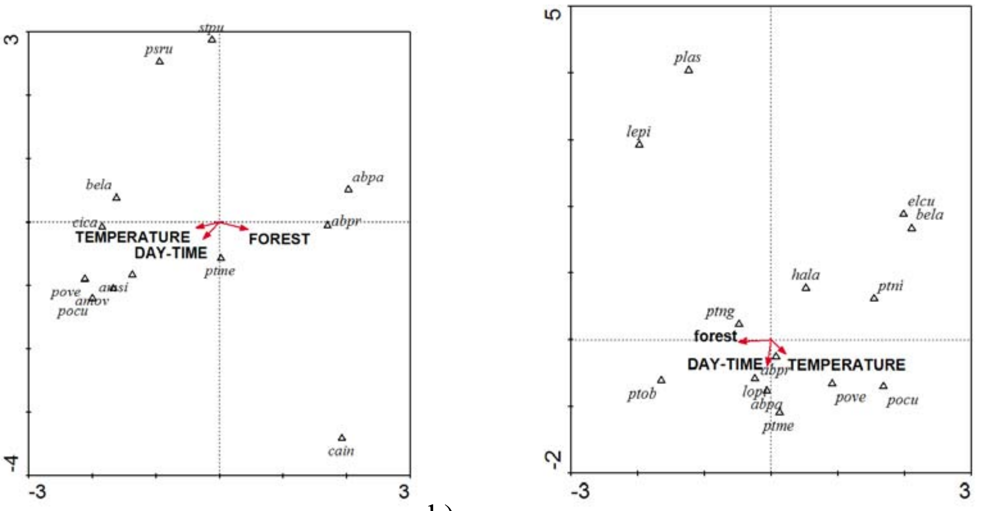


Fig. 6: Respone of epigeic activity of carabid species to (a) *time* and (b) *temperature*. For significancy of response see Tab. 2.



a) b)

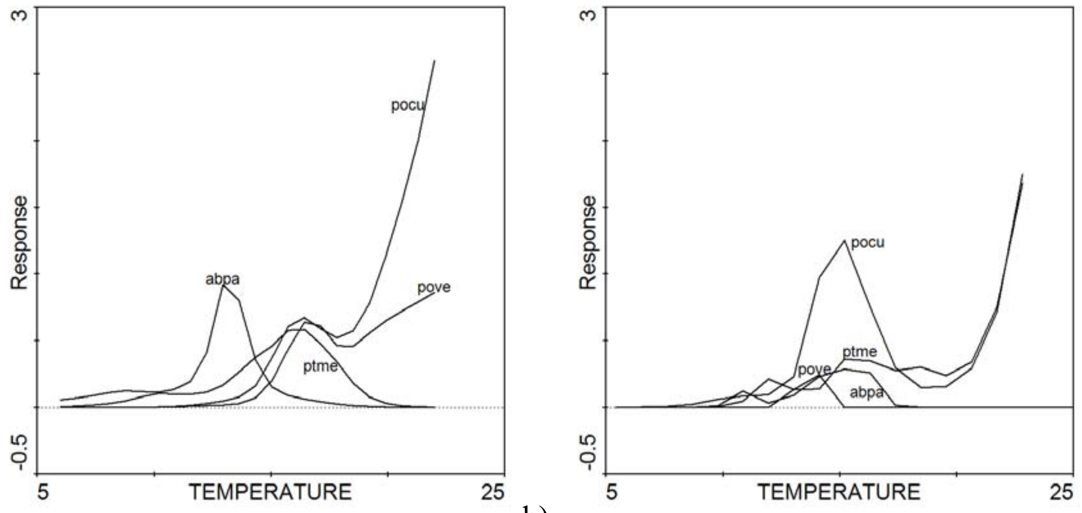
Fig. 7: CCA analysis for spring (a) and autumn season (b).



a) b)

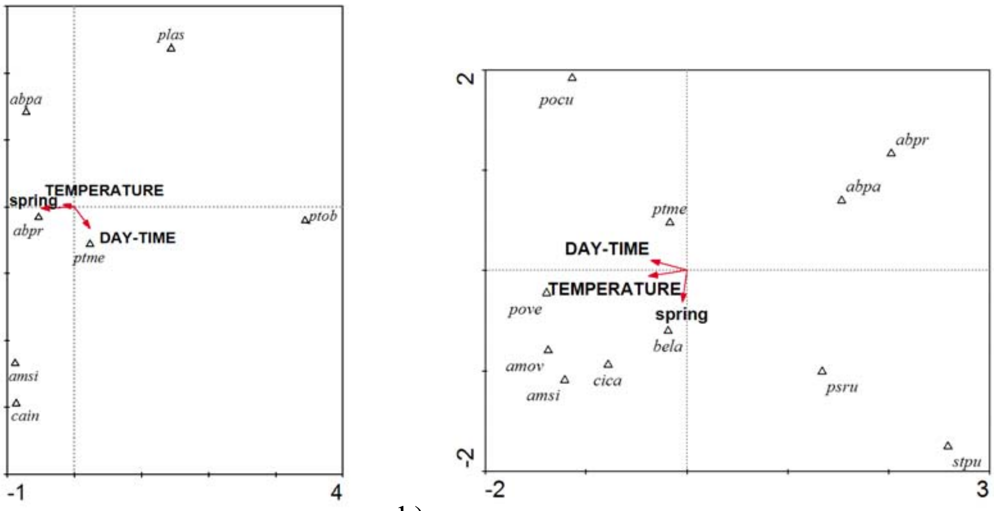
spring	CCA	86.80%	autumn	CCA	89.90%
	F	%		F	%
forest	29.739	57.1	forest	4.201	40.4
time	9.599	17.7	time	2.987	28.1
temp	6.728	12.0	temp	2.312	21.4

Fig. 8: Respone of epigeic activity of carabid species to *temperature* at (a) spring and (b) autumn. For significancy of response see Tab. 3.



a) b)

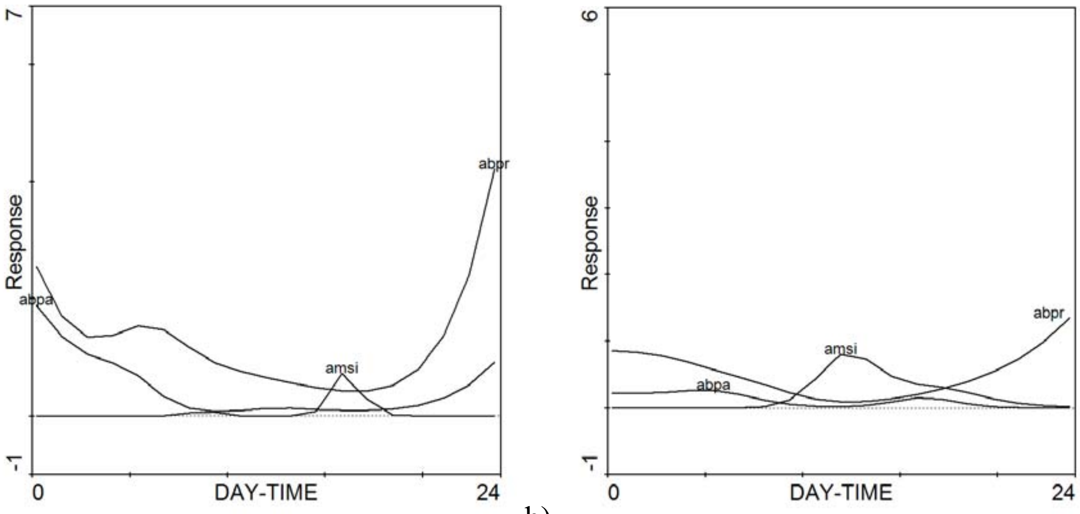
Fig. 9: CCA analysis for forest (a) and clear-cut (b).



a) b)

forest	**CCA**	**65.50%**	**clear-cut**	**CCA**	**49%**
	F	%		F	%
spring	18.248	44.2	spring	4.47	8.2
time	6.841	15.9	time	5.712	14.8
temp	2.371	5.4	temp	8.565	26.0

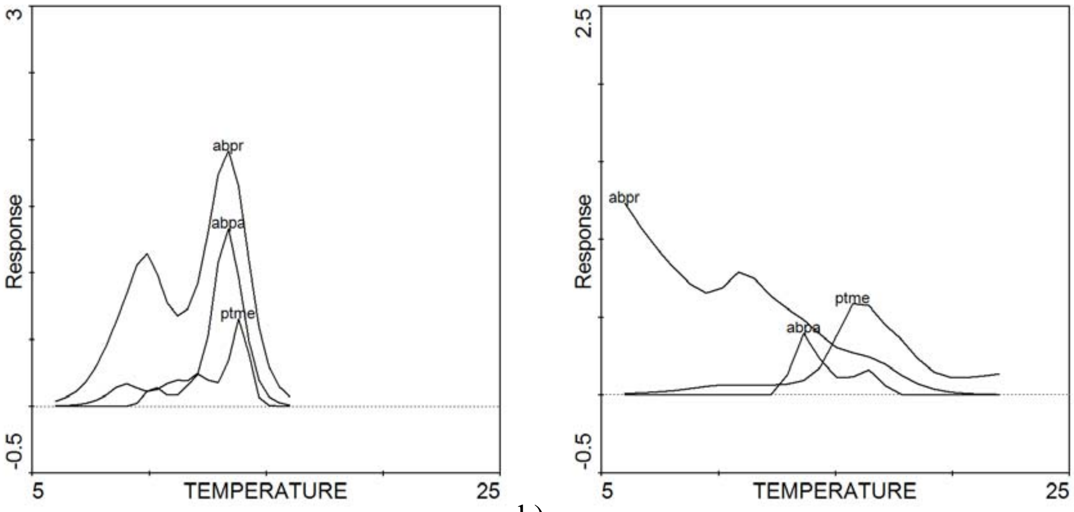
Fig. 10: Respone of epigeic activity of carabid species to *day-time* (a) in forest and (b) at clear-cut. For significancy of response see Tab. 3.



a)

b)

Fig. 11: Respone of epigeic activity of carabid species to *temperature* (a) in forest and (b) at clear-cut. For significancy of response see Tab. 3.



a)

b)

Table 1: Review of trapped material of carabids during spring and autumn period at forest and clear-cut sites (number of animals trapped in individual day-time period in 18 days by 60 traps). Abbreviations: type of preference/biology: O – open-habitat species, F – forest species, E – eurytopic species, S – spring breeders, A – autumn breeders, ? – unknown preference or biology. Time periods: 3, 6, 9, 12, 15, 18, 21 and 0; 3 means period from 0:00 to 3:00.

		SPRING																**AUTUMN**															
		FOREST								**CLEARCUT**								**FOREST**								**CLEARCUT**							
	type	**3**	**6**	**9**	**12**	**15**	**18**	**21**	**0**	**3**	**6**	**9**	**12**	**15**	**18**	**21**	**0**	**3**	**6**	**9**	**12**	**15**	**18**	**21**	**0**	**3**	**6**	**9**	**12**	**15**	**18**	**21**	**0**
Abax parallelipipedus (Piller et Mitterpacher)	F/A	10	7	-	2	1	-	6	34	2	2	1	-	-	2	-	3	-	-	-	-	1	2	1	-	-	-	-	-	3	-	-	-
Abax parallelus (Duftschmid)	F/S	12	19	7	7	9	6	25	47	7	4	4	-	1	3	8	11		1	1	1	1	3	6	-	-	-	-	2	2	6	2	1
Amara aulica (Panzer)	O/A	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Amara eurynota (Panzer)	O/S	-	-	-	-	1	2	-	-	-	-	-	2	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Amara ovata (Fabricius)	E/?	-	-	-	-	-	1	-	-	-	-	-	-	7	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Amara similata (Gyllenhal)	O/S	-	-	1	-	5	1	-	-	-	-	1	17	10	6	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Badister bullatus (Schrank)	?/?	-	-	-	-	2	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Badister lacertosus Sturm	?/?	-	-	-	-	2	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bembidion lampros Herbst	O/S	-	-	-	-	-	-	1	-	1	1	11	26	36	22	11	6	-	-	-	-	-	-	-	-	-	-	-	1	1	1	-	1
Carabus coriaceus Linnaeus	F/A	-	1	-	1	-	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-
Carabus granulatus Linnaeus	O/S	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Calosoma inquisitor (Linnaeus)	F/S	1	-	-	1	4	3	6	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Carabus scheidleri Panzer	F/A	-	-	-	-	1	-	2	-	-	-	-	1	2	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Carabus ullrichi Germar	E/S	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cicindela campestris Linnaeus	O/?	-	-	-	-	-	-	-	-	-	-	1	4	2	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Clivina fossor (Linnaeus)	O/S	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Elaphrus cupreus Duftschmid	?/?	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	2	2
Epaphius secalis (Paykull)	E/?	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Harpalus latus (Linnaeus)	O/A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	-	-	-	-	-	1	1	2	1
Harpalus luteicornis (Duftschmid)	O/S	-	-	-	-	1	-	-	-	-	-	-	2	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Leistus ferrugineus (Linnaeus)	O/A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Leistus piceus Froelich	F/?	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	2	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Loricera pilicornis (Fabricius)	F/S	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	1	-	-	-	-	-	-	2	-	-
Notiophilus palustris (Duftschmid)	O/S	-	-	-	-	-	-	-	-	-	-	1	2	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Platynus assimilis (Paykull)	F/S	-	1	-	1	-	-	-	2	-	-	-	-	-	-	-	1	1	-	-	-	-	-	1	2	1	-	-	-	-	-	-	-
Poecilus cupreus (Linnaeus)	O/S	-	-	-	-	2	-	-	-	-	-	1	6	14	14	5	-	-	-	-	-	2	1	-	-	-	-	-	2	10	5	-	-
Poecilus versicolor (Sturm)	O/S	-	-	-	-	-	-	-	-	-	-	-	4	12	11	1	-	-	-	-	-	1	-	-	-	-	-	-	-	1	1	-	-
Pseudoophonus rufipes (De Geer)	O/A	1	-	-	-	-	-	-	1	6	-	-	5	3	5	5	16	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-
Pterostichus anthracinus (Illiger)	E/S	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pterostichus melanarius (Illiger)	O/A	-	-	1	2	1	6	3	7	-	1	3	7	1	9	2	2	-	-	-	-	2	3	1	-	-	-	-	1	4	-	-	-
Pterostichus niger (Schaller)	F/A	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	2	-	-	-	1	1	-	-	-	-	-	-	-	1	-	-	-
Pterostichus nigrita (Paykull)	F/S	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	2	-	2	1
Pterostichus oblongopunctatus (Fabricius)	F/S	-	-	1	1	-	2	-	1	-	-	-	-	-	-	-	-	-	-	1	1	6	17	10	-	-	-	-	-	1	-	1	-
Pterostichus vernalis (Panzer)	E/S	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Stomis pumicatus (Panzer)	E/S	1	-	-	-	-	-	1	-	1	2	1	-	-	1	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Tab. 2: Table 2: Epigeic activity of the dominant species of carabid beetles in dependence to predictor (*day-time, temperature*) (n.s. – non significant, * p lower than 0.05, ** p lower than 0.01).

predictor	**epigeic activity of**	**F**	**AIC**
day-time	*A. parallelipipedus*	4,21**	299,59
	A. parallelus	4,33**	473,996
	A. similata	4,55**	95,63
	B. lampros	4,01**	376,997
	P. cupreus	3,6**	121,119
	P. versicolor	4,92**	50,49
	P. rufipes	2,81*	72,907
	P. melanarius	n.s.	-
	P. oblongopunctatus	6,07**	65,352
temperature	*A. parallelipipedus*	5,44**	296,552
	A. parallelus	8,6**	457,631
	A. similata	19,64**	84,925
	B. lampros	25,03**	320,46
	P. cupreus	21,8**	105,02
	P. versicolor	16,83**	45,937
	P. rufipes	6,23**	70,855
	P. melanarius	11,82**	73,52
	P. oblongopunctatus	2,51*	67,334

Tab. 3: Epigeic activity of carabid species in connection to predictor (*day-time, temperature*) and locality/season.

			specimens collected in/at							
			forest		**clear-cut**		**spring**		**autumn**	
predictor	**epigeic activity of**		**F**	**AIC**	**F**	**AIC**	**F**	**AIC**	**F**	**AIC**
day-time	*A. parallelipipedus*		7,3**	179,511	2,27*	62,21	7,97**	227,726	n.s.	-
	A. parallelus		7,87**	169,547	4,99**	106,717	10,59**	250,292	n.s.	-
	A. ovata	n.t.	n.s.	-	9,42**	42,835	13,49**	49,072	n.s.	-
	A. similata		7,84**	32,76	6,37**	122,923	12,66**	139,169	n.s.	-
	B. lampros		n.s.	-	3,02**	226,128	5,65**	297,746	n.s.	-
	C. campestris	n.t.	n.s.	-	n.s.	-	5,67**	59,038	n.s.	-
	E. cupreus	n.t.	n.s.	-	n.s.	-	n.s.	-	2,77*	36,511
	L. piceus	n.t.	n.s.	-	n.s.	-	n.s.	-	14,4**	13,57
	P. asimilis	n.t.	3,37**	40,831	n.s.	-	n.s.	-	14,21**	15,391
	P. cupreus		n.s.	-	11,26**	122,376	10,87**	138,181	5,77**	66,547
	P. versicolor		n.s.	-	11,34**	86,896	16,73**	96,558	n.s.	-
	P. rufipes		n.s.	-	7,4**	99,582	6,1**	138,378	n.s.	-
	P. melanarius		2,59*	96,865	n.s.	-	4,45**	147,678	n.s.	-
	P. niger	n.t.	n.s.	-	n.s.	-	n.s.	-	7,17**	16,199
	P. oblongopunctatus		6,27**	98,995	n.s.	-	n.s.	-	3,72**	84,971
	S. pumicatus	n.t.	n.s.	-	4,45**	37,702	2,29*	59,353	n.s.	-
temperature	*A. parallelipipedus*		3,08**	224,221	4,08**	54,438	4,86**	254,939	2,4*	37,685
	A. parallelus		2,53*	207,705	4,23**	110,417	7,96**	260,467	n.s.	-
	A. ovata	n.t.	n.s.	-	3,64**	50,834	6,29**	54,33	n.s.	-
	A. similata		n.s.	-	7,88**	110,372	9,05**	138,706	n.s.	-
	B. lampros		n.s.	-	4,31**	214,284	11,29**	250,303	n.s.	-
	C. campestris	n.t.	n.s.	-	5,79**	47,712	7,11**	51,594	n.s.	-
	E. cupreus	n.t.	n.s.	-	n.s.	-	n.s.	-	2,93**	34,2
	H. latus	n.t.	n.s.	-	n.s.	-	n.s.	-	3,35**	34,448
	P. cupreus		n.s.	-	4,26**	147,948	14,01**	115,124	6,81**	58,334
	P. versicolor		n.s.	-	3,99**	104,834	10,57**	91,354	5,12**	12,685
	P. melanarius		3,09**	93,782	3,89**	94,869	3,78**	152,011	3,31**	44,296
	P. niger	n.t.	n.s.	-	n.s.	-	n.s.	-	2,3*	35,285
	P. oblongopunctatus		n.s.	-	n.s.	-	n.s.	-	2,52*	90,062

* p less than 0.05

** p less than 0.01

n.s. - non significant

n.t. - non tested in whole material for low dominancy (≤ 2,0 %)

05. Souhrn

Tato práce je příspěvkem k poznání ekologie střevlíkovitých brouků v prostředí lužního lesa. Tvoří ji tři manuskripty zaměřené na odlišná témata.

První manuskript se věnuje **obnově společenstva střevlíků lužního lesa po katastrofické povodni z roku 1997** (přijat do tisku v časopise *Peckiana*, ISSN 1618-1735). Společenstvo jsme studovali pomocí formalínových zemních pastí po dobu sedmi let (únor 1998 – únor 2005). Vzorky z jednotlivých let jsme pak porovnávali s referenčním společenstvem, představujícím předpovodňový stav.

V průběhu sedmi let po povodni docházelo ve struktuře společenstva střevlíků k zásadním změnám ve druhovém složení a dominancích jednotlivých druhů. Některé druhy, přítomné v referenčním společenstvu a chybějící v prvních letech po povodni, se na lokalitu postupně vracely (*Harpalus luteicornis, Poecilus cupreus, Pseudoophonus rufipes, Pterostichus oblongopunctatus*), zatímco jiné druhy, přítomné ve již krátce po povodni, společenstvo postupně opouštěly (*Abax carinatus, Amara familiaris, Harpalus latus, Poecilus versicolor, Stomis pumicatus, Trechus quadristriatus, Trepanes octomaculatus*). Obnova společenstva střevlíků i po tak významné disturbanci, jakou byla letní povodeň roku 1997, probíhala poměrně rychle – společenstvo se již po dvou letech podobalo více předpovodňovému stavu než společenstvům těsně po povodni.

Ve druhém příspěvku jsme se zabývali **vlivem mýcení na společenstvo střevlíků lužního lesa.** Vzorky jsme opět odebírali metodou formalínových zemních pastí, rozmístěných ve starém lesním porostu a na nově vzniklé mýtině. Výzkum probíhal od dubna 2003 do června 2004.

Mýcení mělo na společenstvo střevlíků spíše pozitivní vliv, což se projevilo vyšším druhovým bohatstvím na mýtině (20 druhů) ve srovnání s lužním lesem (13 druhů) a rovněž abundance mnoha druhů byly na mýtině vyšší. Pouze *A. parallelipipedus* významněji preferoval lesní prostředí a jeho dominance na mýtině byla zanedbatelná. U ostatních druhů, přítomných na obou lokalitách, se jejich abundance na mýtině zvyšovaly nebo zůstávaly podobné jako v lese.

Mýtina byla krátce po svém vzniku kolonizovány řadou nových druhů, charakteristických pro otevřená stanoviště (*Amara aenea, Bembidion lampros, Bradycellus*

caucasicus, Clivina fossor, Harpalus progrediens, Notiophilus palustris, Poecilus versicolor). Důležitým faktorem, ovlivňujícím rychlost kolonizace, se ukázala být blízkost zdrojových habitatů, jako byla obdělávaná pole a břehové biotopy.

V poslední části diplomové práce jsme studovali **vliv teploty, sezonality a lokality na diurnální aktivitu střevlíků**. Výzkum probíhal ve dvou etapách (jarní a podzimní) a byla použita metoda jednoduchých padacích pastí bez fixáže, rozmístěných v lesním porostu a na přilehlé mýtině. Celkem jsme instalovali 100 pastí, které byly vybírány ve tříhodinových intervalech.

Celkem jsme zaznamenali 35 druhů střevlíků (924 jedinců). U 16 z nich se projevil signifikantní vzorec aktivity v závislosti na denní době, přičemž aktivita většiny z nich byla zároveň ovlivňována i teplotou povrchu půdy. Faktor teploty ovlivňoval epigeickou aktivitu střevlíků ve větší míře na mýtině a v podzimní sezoně.

Zajímavým zjištěním je rovněž fakt, že druhy *Abax parallelipipedus* a *Pterostichus melanarius* preferovaly na podzim vyšší teploty než v jarní sezoně. Tato skutečnost zřejmě souvisí s biologií jejich rozmnožování – jedná se o podzimní druhy a aktivní vyhledávání míst s vyšší teplotou zřejmě napomáhá dozrávání jejich gonád.