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Does closure of traditionally managed open woodlands threaten epigeic invertebrates? Effects of coppicing and high deer densities

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ABSTRACT

The demise of traditional woodland management techniques, such as coppicing or woodland pasture, is causing a gradual closure of formerly sparse lowland woods across Central Europe. It is established that these processes threaten such organisms as butterflies and higher plants. Effects on other groups, such as epigeic invertebrates, are little known, hindering rational conservation decisions. We investigated the effects of stand openness on three epigeic groups, carabids (Carabidae), arachnids (Araneae + Opiliones) and myriapods-isopods (Chilopoda + Diplopoda + Oniscidea), in a lowland deciduous wood in the Czech Republic. Situating some of the traps in an intensive deer park allowed a simultaneous assessment of effects of high vs. low ungulate densities. Carabids reached the highest species richness in either sparse stands with low game or dense stands, high game. More arachnids occurred under low game and in sparse stands than under high game density and in dense stands. The highest richness of myriapods-isopods was in sparse stands with low game. Ordinations revealed that species of conservation concern ('relic species' according to C. European authors) tended to be associated with sparse stands and low game. A considerable proportion of epigeic woodland invertebrates, including many species of conservation concern, depends on preserving highly heterogeneous sparse canopy conditions. Restoring such conditions in selected areas will benefit these sensitive open woodland specialists while causing minimum harm to specialists of dense stands, that likely prosper in commercially managed high forests.

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1. Introduction

Deciduous woodlands of lowland temperate Europe have become increasingly dense and shady during the 20th century

due to replacement of millennia-old management techniques, such as woodland pasture, coppicing or litter harvest, by growing of even-aged high forests (Rackham, 1998; Warren and Key, 1991). Conservationists have long regarded

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the woodland closure as a beneficial process, returning the human-disturbed woodlands to a more natural state (Ellenberg, 1988; Vrska, 2006). More recently, it has been proposed that European temperate woodlands would be rather open even in the absence of human intervention as a result of activity of wild ungulates (Vera, 2000; Bakker et al., 2004) and natural disturbances (Reindl, 1997; Lindbladh et al., 2003; Bouget and Duelli, 2004). The ensuing debate has tremendous implications for conservation strategies. Had woodlands of lowland temperate Europe resembled an open savannah in a natural state, increasing shading of both commercially managed forests and minimum-intervention reserves would alter woodland biodiversity, even if the woods have retained a 'natural' tree species composition (cf. Decocq et al., 2004; Benes et al., 2006). The non-intervention strategy, often proposed for reserves, would be contradictory to conservation, because reserves would develop into brand-new habitats, not existing in temperate lowland Europe for millennia.

The deleterious impact of woodland closure is well documented for such conspicuous organisms as higher plants (Peterken and Francis, 1999; Strandberg et al., 2005), butterflies (Warren, 1991; Bergman and Kindvall, 2004; Freese et al., 2006), orthoptera (Theuerkauf and Rouys, 2006), saproxylic beetles (Ranius and Jansson, 2000; Lindhe et al., 2005), and birds (Fuller and Henderson, 1992; Hansson, 2001). Impacts on other groups of organisms are much less known, hindering rational debate about conservation strategies. Proposals for active management of woodland reserves established for specific open-canopy species are easily downgraded by arguing that the management may threaten other components of biodiversity, in particular the less conspicuous ones.

Another little studied aspect of the conservation management of European lowland woods is the increasing density of wild ungulates (Fuller and Gill, 2001; Cote et al., 2004). Pasture for domestic animals had represented an important woodland use until ca. one century ago (Vera, 2000; Konvicka et al., 2008) and it might be expected that high densities of deer and other wild ungulates should benefit specialised species of open forests. Many intensive game parks exist across Europe and some have retained a considerable proportion of open structures such as glades and coppiced panels that supply game animals with browsing and shelter. Presence of such structures increases the suitability of woodlands for wildlife (Stewart, 2001; Ewald et al., 2006), but too high game densities threaten more sensitive species (Chytrý and Danihelka, 1993; Benes et al., 2006).

This study assesses the relative effects of stand openness and game density on richness and species composition of carabid beetles (Carabidae), spiders (Araneae), harvestmen (Opiliones), centipedes (Chilopoda), millipedes (Diplopoda) and woodlice (Isopoda: Oniscidea) in the Milovický Wood, southeastern Czech Republic. The wood harbours a rich fauna and flora and its managers still locally maintain traditional coppice management. A part of the wood is used for intensive game keeping, allowing comparison of impacts of high versus low ungulate densities simultaneously with impacts of stand openness.

2. Materials and methods

2.1. Study area

The Milovický Wood (Fig. 1; 48°49'N, 16°42'E, alt. 250 m) represents the largest complex of Pannonian thermophilous woods in the Czech Republic. It covers over 20 km² of rolling hills built by base-rich sediments and covered by quaternary deposits, situated in a region of warm and relatively dry climate (mean annual temperature: 9 °C, mean precipitation: 550 mm) at a crossroad between the Hercynian highlands, the Carpathians and the lowlands of Pannonia.

Until the mid-20th century, the wood was managed by coppicing, a management technique in which wood is harvested in short rotation to be used as fuel (locally: 20–40 years) and subsequently regenerates vegetatively from stumps and roots. Later on, the technique was abandoned in favour of singling, i.e. selecting most vigorous of coppice branches in order to achieve a structure akin to generative high forest. As hopes to produce good timber soon failed, two large game parks for red deer (*Cervus elaphus*), fallow deer (*Dama dama*) and mouflon (*Ovis ammon*), covering ca. 17 km², were established there in the 1960s (Fig. 1). The stocking was quite high until the early 1990s, when conservation concerns led to a reduction of game densities to the current ca. 0.5 deer per hectare (details: Benes et al., 2006).

A majority of the wood consists of mature (>80 years) singled oak coppice. Prevailing trees are oaks (*Quercus petraea*, *Q. pubescens*) and hornbeam (*Carpinus betulus*), accompanied by ash (*Fraxinus excelsior*), lime (*Tilia platyphyllos* and *T. cordata*) and elm (*Ulmus laevis*). To promote regeneration of oak, over 200 ha of fenced "regeneration blocks", have been established in the last few years. Proceeding by strips 30–50 m wide and not exceeding one hectare in area, they are sequentially thinned to canopy cover of 10–30%. It is expected that in most years, oak should germinate from seeds in the thinned stands. The thinning promotes vigorous regrowth of coppice species such as *Acer campestre*, *Corylus avellana*, *Crataegus* spp., and *Sorbus torminalis*. For a few years, the thinned panels resemble a traditional coppice with standards management, under which there are, amongst a lower layer harvested in short interval, sparsely growing mature trees, or standards, grown for timber. However, in contrast to the true coppice with standards, the mature trees are removed following an oak mast in the wood.

2.2. Study design

We sampled epigeic fauna using pitfall traps, set in a factorial 2 * 2 design under two levels of OPENNESS (dense vs. sparse stands) and two levels of GAME (game vs. no game). The dense stands were the singled oak coppice, all ca. 80 years old; the sparse stands with no game were fenced panels thinned to ca. 30% of canopy cover to facilitate oak regeneration; and the sparse stands with game were those coppiced to provide deer browse. We selected four sites for each of the four combinations, each with five traps, summing to sixteen sites and 80 traps.

We recorded the following additional variables for each trap: (i) percent cover of canopy layer, shrub layer (in 2 m

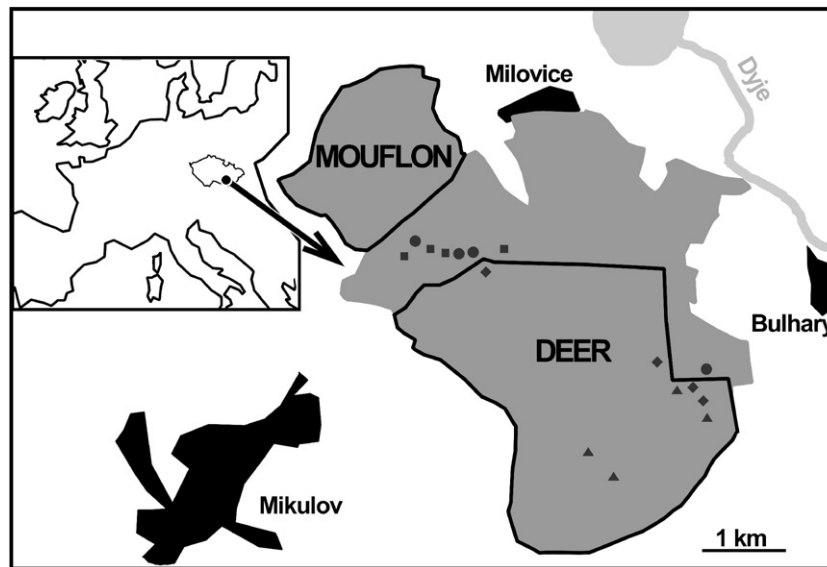


Fig. 1 – Map of the Milovický Wood, showing positions of trapping sites. Different symbols stand for the four combinations of OPENNESS and GAME factors: dense-game (diamonds), sparse-game (triangles), dense-no game (squares) and sparse-no game (circles).

height) and herb layer, estimated, respectively, in 20 m, 10 m and 5 m diameter circles around each trap; (ii) presence of all canopy layer species in 10 m diameter circles; (iii) presence of all shrub layer species in 5 m diameter circles; and (iv) percentage cover of forbs and grasses in 5 m diameter circles. All these variables were recorded on one date (1 May 2005) to rule out seasonal effects. In addition, latitudinal and longitudinal coordinates were taken for each trap.

2.3. Sampling of epigeic invertebrates

The traps were plastic cups of 1 l volume, 12 cm in diameter, containing a 4% solution of formaldehyde. Within sites, they were spaced at 8–10 meters in approximately straight lines, located in central parts of each stand, at a minimum distance of 30–40 m from other management types. They were exposed for three periods (1–23 May, 7–30 July, 9 September–2 October, all 2005) and were covered by lids for interim periods.

Throughout this paper, “arachnids” refer to spiders (Araneae) plus harvestmen (Opiliones), and “myriapods-isopods” refer to centipedes (Chilopoda), millipedes (Diplopoda) and woodlice (Isopoda: Oniscidea). Nomenclature follows Hurka (1996) for carabids; Buchar and Ruzicka (2002) for spiders; Klimes (2000) for harvestmen; Enghoff (2004) for millipedes and centipedes; and Schmalzfuss (2003) for woodlice.

2.4. Classifying the species

A straightforward approach to assess conservation value of the sampled species would be to compare their rarity and/or threat status (i.e., decline) (e.g., Benes et al., 2006; Tropek and Konvicka, 2008). This was not feasible in this case, because neither standard monitoring nor comprehensive distribution maps of the groups under study exist for the Czech Republic, with the exception of spiders (Buchar and Ruzicka, 2002). An alternative option was classifying the species into

“habitat quality categories”, designed by Buchar (1983) (originally for spiders) to assist monitoring of habitats. This scheme classifies all species into relics (‘restricted to natural, undisturbed habitats’), adaptive (‘able to colonise both undisturbed and moderately disturbed habitats’), and eurytopic (‘colonising even heavily anthropically disturbed sites’). Hurka et al. (1996) expanded this scheme for carabids, Klimes (2000) for harvestmen, Tuf and Laska (2005) for centipedes, and Tuf and Tufova (2008) for millipedes and woodlice. An updated classification for arachnids by Buchar and Ruzicka (2002) used here occasionally mentions >1 category per species. To obtain unequivocal categories, we applied the stringent criterion that species falling in >1 category were considered as belonging to the weaker one (e.g., those belonging to adaptive and relic were considered adaptive).

2.5. Analyses

We analysed carabids, arachnids, and myriapods-isopods separately but following identical approaches.

Species accumulation curves for the four OPENNESS–GAME combinations were constructed using the software EstimateS 8.0 (Colwell, 2006), and 95% confidence limits (Winfrey et al., 2007) were used to compare differences in their shapes.

Analyses of variance on log-transformed data, computed using the general linear models module in Statistica 7.0, were used to compare numbers of species and numbers of individuals per trap in different treatments. We used full-factorial repeated measures design with factors OPENNESS and GAME plus OPENNESS * GAME interaction, and with trapping PERIOD as a within-effect factor. To control for the effects of spatial positions of the traps, the latitudinal (x) and longitudinal (y) coordinates of each trap, both centered to zero mean and unit variance, plus the x * y interaction, were forced to the model as (numeric) covariates.

Relative representation of species belonging to the eurytopic, adaptive and relic categories was compared using contingency tables. We compared numbers of species, and summed numbers of individuals belonging to the categories, caught in each of the OPENNESS–GAME combinations.

Species composition was analysed using canonical correspondence analysis (CCA) (CANOCO v 4.5), which ordinated the species composition of samples according to external predictors and tests for effects of the predictors using a Monte-Carlo test (999 permutations) (Leps and Smilauer, 2003). Each trap/period was treated as a sample. To account for spatial and temporal non-independence, we used a split-plot permutation design with the periods of trap exposure considered as time series and the lines of five traps considered as line transects.

We used CCA to ask four questions. The first one addressed the effect of OPENNESS and GAME, both separately and in combination. We also applied a variance partitioning procedure, which assesses the independent effects of individual variables by successively entering competing variables as covariate terms. Second, we asked how the composition of samples was affected by canopy, shrub and herb covers and composition; following tests for the groups of variables describing stand structure (i–iv in Study design, above), we used the CANOCO forward-selection procedure to obtain models combining these variables, herein abbreviated as STAND. The third set of models addressed potential spatial non-independence. These SPATIAL models were based on forward selection of x and y coordinates of each trap, their second-order polynomials and all possible interactions. Finally, we asked if the patterns related to OPENNESS and GAME would hold after controlling for STAND and SPATIAL effects. This was tested via partial-CCA with STAND and SPATIAL as covariables.

3. Results

3.1. Species richness

We trapped 54 species and 2377 individuals of carabids, 86 species and 5164 individuals of arachnids (Araneae 79/5030, Opiliones 7/134) and 31 species and 545 individuals of myriapods-isopods (Diplopoda: 11/165, Chilopoda 7/100, Isopoda 6/280). Four carabids, eleven carabids and six myriapods-isopods are classified as relic species (Table 1, Appendix 1).

As shown by patterns of species accumulation (Fig. 2), the highest richness of carabids occurred in dense-game stands, closely followed by sparse-no game stands. Sparse-game and dense-no game stands contained similar and

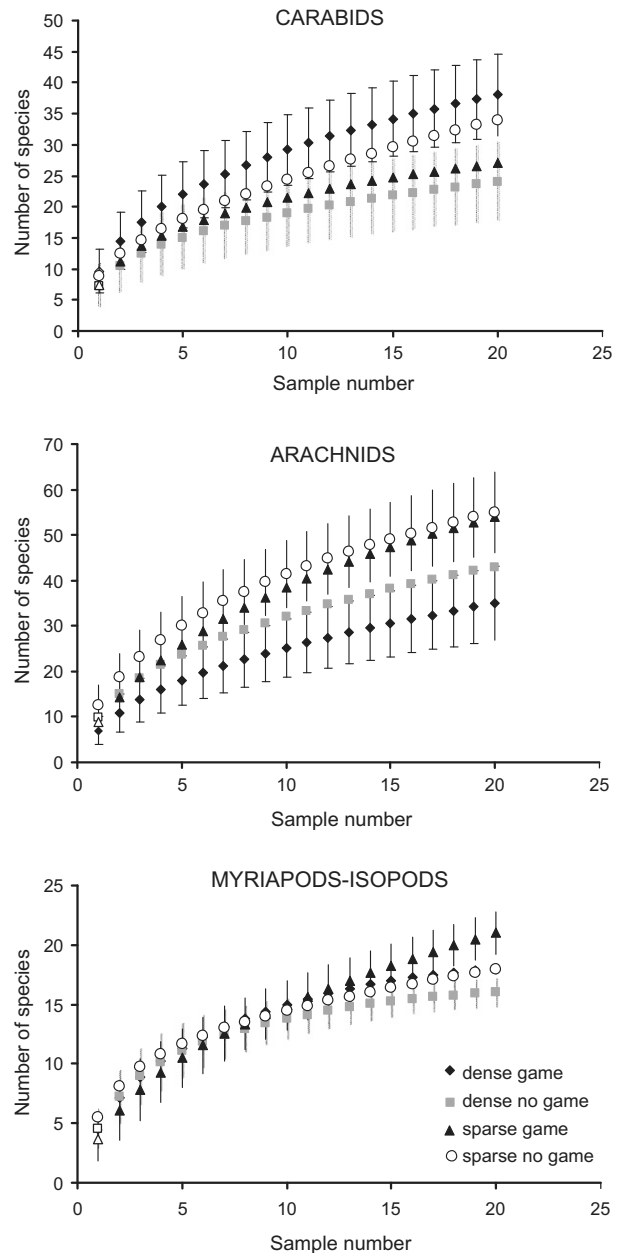


Fig. 2 – Species accumulation curves for pitfall catches of carabids, arachnids and myriapods-isopods trapped under four different combinations of OPENNESS and GAME in the Milovicky Wood. The bars are 95% confidence limits, depicted only for selected curves that are discussed in the text.

Table 1 – Summary data on pitfall traps catches from the Milovicky Wood

	Sparse-game Species/individuals	Sparse-no game Species/individuals	Dense-game Species/individuals	Dense-no game Species/individuals
Carabids	27/591	34/615	38/933	24/455
Arachnids	54/1063	55/2334	35/729	43/1197
Myriapods-isopods	21/100	18/274	18/192	16/183

considerably lower numbers of species. In arachnids, sparse-game and sparse-no game stands contained approximately equally high species richness, dense-no game stands were intermediate, whereas dense-game stands were poorest. In myriapods-isopods, the sparse-game stands returned the steepest curve not approaching an asymptote, whereas the curves for the other three situations had similar shapes, reaching asymptotes near the 15th sample.

In the analyses of variance controlled for spatial position of the traps (Table 2), the numbers of carabid species and individuals did not differ with regard to OPENNESS and GAME, but displayed a significant interaction. Sparse-no game stands hosted more carabids than sparse-game stands, whereas dense stands hosted similar numbers of species irrespective of GAME (Fig. 3a). The species richness of arachnids did not differ among the analysed situations, but sparse stands hosted more individuals than dense stands (Fig. 3b). More myriapod-isopod species were trapped in sparse stands (Fig. 3c). All three groups also displayed a prominent seasonality (Table 2). Numbers of species (all groups) and individuals (carabids and myriapods-isopods) were highest in spring and lowest in autumn.

3.2. Species composition

The four situations did not differ in relative representation of eurytopic, adaptive and relic species of carabids ($\chi^2_{6,df} = 1.61, p = 0.95$), arachnids ($\chi^2_{6,df} = 1.44, p = 0.96$) and myriapods-isopods ($\chi^2_{6,df} = 2.14, p = 0.91$). However, they differed with respect to numbers of individuals in the habitat quality categories in the case of carabids ($\chi^2_{6,df} = 264.44, p < 0.0001$) and arachnids ($\chi^2_{6,df} = 315.57, p < 0.0001$), but not myriapods-isopods ($\chi^2_{6,df} = 9.75, p = 0.14$). A surplus of individuals of eurytopic carabids originated from dense-game stands and a surplus of individuals of relic carabids originated from sparse-game and

sparse-no game stands. In arachnids, there was a surplus of individuals of adaptive species in sparse-no game stands (Fig. 4).

In the ordinations, both OPENNESS and GAME significantly affected the species composition of carabids and arachnids, whereas only OPENNESS affected myriapods-isopods (Table 3). For both carabids and arachnids, each of the tested factors displayed a significant effect even after setting the second factor of interest as a covariable.

For carabids (Fig. 5a), the first ordination axis distinguished between sparse and dense stands, whereas the second axis distinguished between game and no game. Species associated with sparse stands included, e.g., *Notiophilus rufipes*, *Carabus cancellatus* and *Cicindela campestris*. Species such as *Pterostichus melanarius* and *Harpalus affinis* displayed an association with dense stands. Species associated with game included, e.g., *Carabus granulatus*, *Abax parallelepipedus* and *Pterostichus oblongopunctatus*, whereas most species from sparse stands seemed to avoid high game density (*Notiophilus rufipes*, *Carabus ullrichi*). Out of four relic species, *Harpalus picipennis* and *Notiophilus rufipes* were associated with sparse stands, *Amara anthobia* with dense stands, whereas *Leistus rufomarginatus* did not display a clear association.

For arachnids (Fig. 5b), the first axis again distinguished between dense and sparse stands. Stands with game were more similar to dense stands according to arachnid composition, whereas stands without game were more similar to the sparse ones. Dense stands were suitable for such typical woodland species as *Centromerus sylvaticus* and *Harpactea rubicunda*, some widespread generalists (e.g., *Neriene clathrata*) and, unexpectedly, even a species associated with rocky steppes (*Megalephyphantes pseudocollinus*). Sparse stands hosted species typical for warm grasslands (e.g., *Xysticus lineatus* and *Ozyptila scabricula*), forest edges (e.g. *Ceratinella major*) and warm woodlands (e.g., *Ozyptila blackwalli* and

Table 2 – Results of repeated-measures ANOVAs comparing numbers of species and individuals of carabids, arachnids and myriapods–isopods trapped in Milovicky Wood. Full factorial 2 × 2 model with factors GAME and OPENNESS, repeated-measure factor PERIOD, and spatial positions of traps (x, y, x * y) forced to the model

	df	Carabids				Arachnids				Myriapods–isopods			
		Species		Individuals		Species		Individuals		Species		Individuals	
		F	p	F	p	F	p	F	p	F	p	F	p
Intercept	1	727.11	****	468.59	****	214.58	****	244.46	****	102.36	****	34.43	****
GAME	1	0.63	n.s.	0.01	n.s.	1.17	n.s.	0.29	n.s.	1.55	n.s.	0.77	n.s.
OPENNESS	1	1.91	n.s.	2.63	n.s.	2.82	n.s.	7.06	**	6.07	*	1.99	n.s.
GAME * OPENNESS	1	18.05	****	14.03	****	0.55	n.s.	0.97	n.s.	0.15	n.s.	1.42	n.s.
x	1	1.71	n.s.	0.17	n.s.	0.35	n.s.	0.01	n.s.	14.48	***	4.21	n.s.
y	1	4.18	n.s.	1.24	n.s.	1.10	n.s.	4.47	n.s.	2.23	n.s.	3.39	n.s.
x * y	1	0.01	n.s.	1.95	n.s.	1.42	n.s.	0.78	n.s.	0.38	n.s.	0.74	n.s.
Error	73												
PERIOD	2	21.91	****	9.56	***	31.07	****	49.61	n.s.	8.05	***	4.36	*
PERIOD * GAME	2	0.21	n.s.	0.20	n.s.	1.86	n.s.	0.78	n.s.	0.34	n.s.	3.44	*
PERIOD * OPENNESS	2	0.28	n.s.	3.74	*	1.37	n.s.	2.29	n.s.	0.46	n.s.	1.70	n.s.
PERIOD * GAME * OPENNESS	2	3.16	*	6.71	**	0.74	n.s.	0.47	n.s.	0.14	n.s.	0.87	n.s.
PERIOD * x	2	6.95	**	5.85	**	0.39	n.s.	0.01	n.s.	1.91	n.s.	3.09	*
PERIOD * y	2	3.19	*	3.74	*	1.56	n.s.	3.11	*	1.07	n.s.	1.81	n.s.
PERIOD * x * y	2	3.34	*	2.33	n.s.	0.55	n.s.	0.29	n.s.	1.79	n.s.	1.02	n.s.
Error	146												

n.s.: p > 0.05, *p < 0.05, **p < 0.01, ***p < 0.001, ****p < 0.0001, *****p < 0.00001.

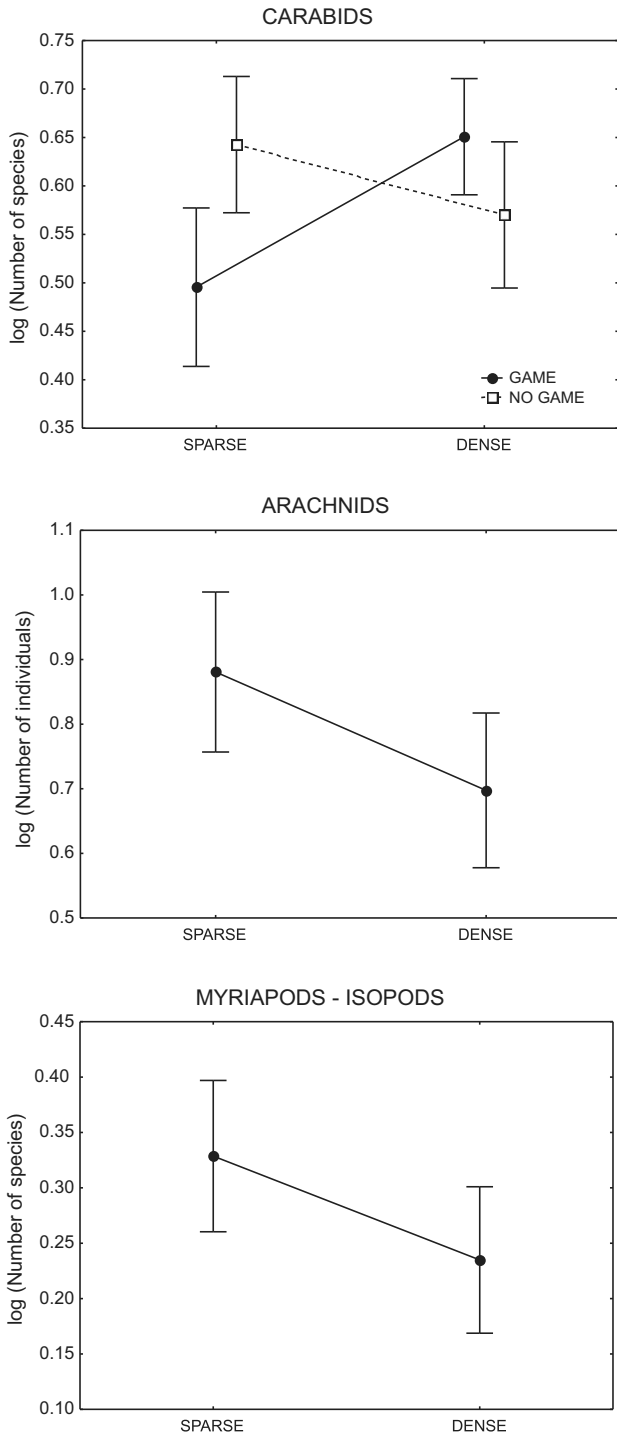


Fig. 3 – Results of repeated-measure ANOVA comparing carabids (numbers of species, A), arachnids (numbers of individuals, B) and myriapods–isopods (numbers of species, C) trapped under two levels of OPENNESS and GAME in the Milovicky Wood. Log-transformed mean numbers per trap and period with associated 0.95 confidence intervals are shown. See Table 2 for associated statistics.

Trichoncus affinis). Practically all relic arachnids inclined towards sparse stands, except for two species, *M. pseudocollinus* and *Scotina celans*. On the second axis, relic spiders such as

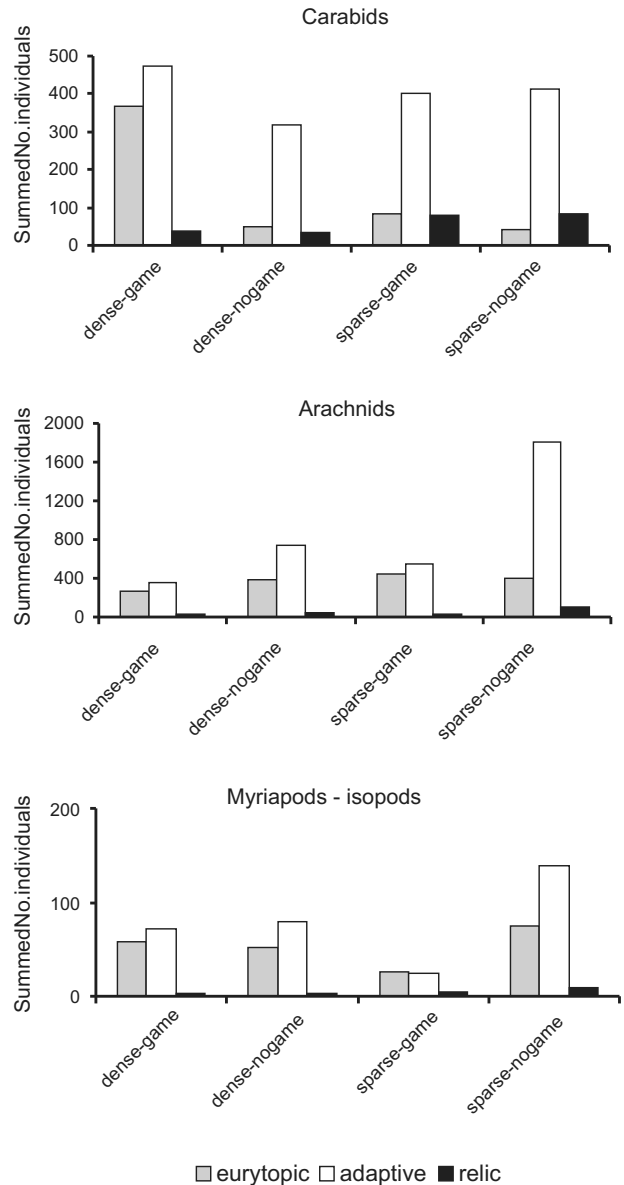


Fig. 4 – Summed numbers of individuals of carabids, arachnids and myriapods–isopods, trapped under four different combinations of OPENNESS and GAME and belonging to four habitat quality categories. Note that the combinations differed in representation of habitat association categories of carabids and arachnids, but not myriapods–isopods.

Ozyptila brevipes and *Xysticus robustus* displayed a preference for game, whereas such relic species as *Ozyptila blackwalli* and *S. celans* seemed to avoid high game density.

For myriapods-isopods (Fig. 5c), species associated with sparse stands included the relic chilopod *Stenotaenia linearis* and relic diplopods *Cylindroiulus arborum* and *Craspedosoma transsilvanicum*. A majority of species associated with dense stands were widespread adaptive species (e.g. *Ligidium hypnorum*, *Unciger transsilvanicus* and *Leptoiulus proximus*), exceptions being the xerophilous millipede *Brachyiulus bagnalli*. The relic species *Lithobius lucifugus* was captured only in two individuals, always with game.

Table 3 – CCA analyses ordering the species composition of pitfall catches of epigeic invertebrates in the Milovicky Wood

Model ^a	Carabids			Arachnids			Myriapods–isopods											
	Eig ₁	% ₁	p	Eig _{all}	% _{all}	p	Eig ₁	% ₁	p	Eig _{all}	% _{all}	p						
~GAME	0.082	1.49	***				0.079	0.90	***				0.047	0.69	n.s.			
~OPENNESS	0.078	1.46	***				0.115	1.30	**				0.085	1.24	***			
~OPENNESS + GAME	0.086	1.57	***	0.158	2.88	***	0.115	1.30	***	0.194	2.20	***	0.094	1.75	***	0.12	1.75	***
~GAME OPENNESS	0.080	1.38	***				0.079	0.91	***				0.035	0.52	n.s.			
~OPENNESS GAME	0.076	1.42	***				0.115	1.32	***				0.073	1.07	***			
STAND ^b	0.090	1.64	***	0.243	4.42	***							–	–	–	–	–	
SPATIAL ^c	0.149	2.71	***	0.175	3.19	***	0.100	1.14	***				–	–	–	–	–	
~OPENNESS STAND	0.030	0.57	n.s.				0.047	0.55	n.s.				0.039	0.59	n.s.			
~OPENNESS SPATIAL	0.076	1.43	***				0.101	1.16	***				–	–	–			
~OPENNESS STAND + SPATIAL	0.022	0.43	n.s.				0.044	0.52	n.s.				–	–	–			
~GAME STAND	0.061	1.16	***				0.077	0.90	***				0.032	0.48	n.s.			
~GAME SPATIAL	0.040	0.75	*				0.080	0.92	*				–	–	–			
~GAME STAND + SPATIAL	0.020	0.39	n.s.				0.055	0.65	n.s.				–	–	–			
~OPENNESS + GAME STAND	0.061	1.16	***	0.091	1.73	***	0.079	0.92	*	0.118	1.38	*	0.046	0.69	n.s.	0.071	1.06	n.s.
~OPENNESS + GAME SPATIAL	0.080	1.50	***	0.110	2.07	***	0.110	1.26	**	0.154	1.77	***	–	–	–	–	–	
~OPENNESS + GAME STAND + SPATIAL	0.028	0.55	n.s.	0.042	0.82	n.s.	0.059	0.69	n.s.	0.095	1.11	n.s.	–	–	–	–	–	

Eig₁ – eigenvalue of the first ordination axis; Eig_{all} – sum of all canonical eigenvalues; %₁ and %_{all} – percentage variation in species data accounted for by first and all ordination axes, respectively.

p – assessed via Monte-Carlo permutation tests: n.s. p > 0.05; *p < 0.05; **p < 0.01; ***p < 0.001.

a Model terms following ~ are explanatory variables, those following | are covariables.

b Obtained via a forward selection from variables describing each trap. Carabids ~ canopy cover + shrub cover + cover of grasses + *Acer campestre* (tree) + *A. campestre* (shrub); Arachnids ~ canopy cover + *Lonicera* sp. (shrub); Myriapods–isopods: ~ shrub cover + *Populus tremula* (tree).

c Obtained via a forward selection from variables describing spatial position of each trap. Carabids: ~y + y²; Arachnids: ~x; Myriapods and isopods: no model selected.

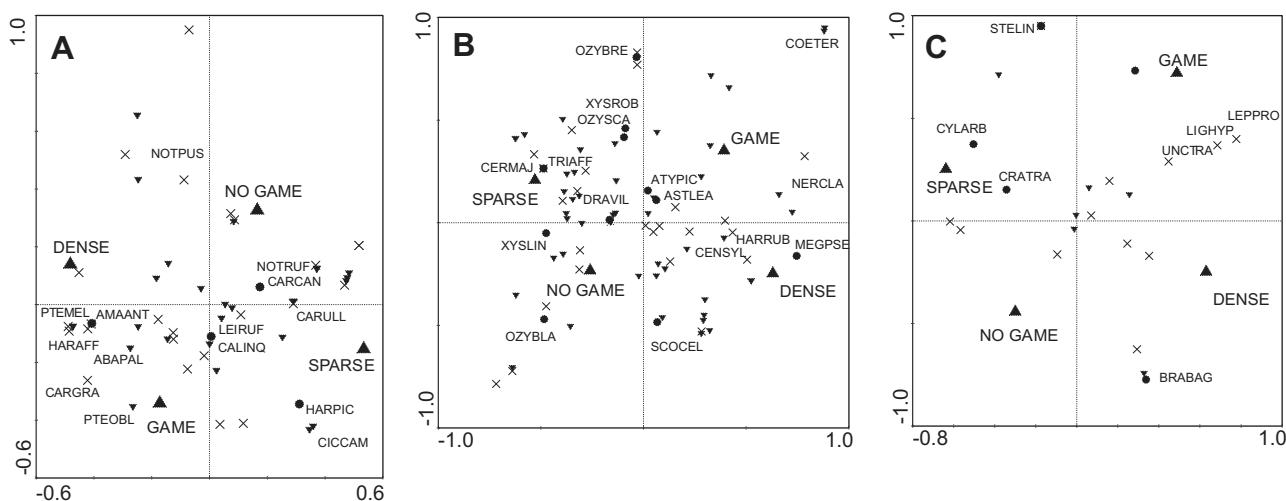


Fig. 5 – CCA ordinations of species composition of pitfall catches of carabids (A), arachnids (B) and myriapods–isopods (C) from the Milovicky Wood – models with GAME and OPENNESS as explanatory variables (~GAME + OPENNESS). Positions of all species are shown, different symbols stand for relic (filled circles), adaptive (filled triangles) and eurytopic (X-crosses) species. Abbreviations of species names are given for relic species and other species mentioned in the text.

Canopy and shrub covers were the strongest STAND predictors, entering the models for carabids (both) and arachnids (canopy cover) and arachnids and myriapods–isopods (shrub cover) (Table 3). The importance of canopy and shrub covers is also apparent from the partial ordinations, as OPENNESS lost its significance after treating the STAND predictors as covariables in the ordinations. SPATIAL variables affected

only carabids and arachnids. However, in contrast to STAND models, inclusion of SPATIAL covariables did not suppress the significant effects of OPENNESS and GAME for carabids and of OPENNESS for arachnids. It follows that for the species composition of carabids and arachnids, OPENNESS remained significant even after controlling for spatial positions of sites.

4. Discussion

Open and sparse stands within a European lowland deciduous wood differ in richness and species composition of three groups of epigeic invertebrates, and a majority of species considered as relic, and thus being of conservation concern, prefers sparse stands. However, details of the patterns differ among the three groups. Further differences among the groups arose with respect to response to ungulate density.

Carabids reached highest species richness and abundance in dense stands with game and in sparse stands without game. However, whereas practically all the species occurring in dense stands with game were widespread generalists (=eurytopic species), the sparse-no game stands hosted a considerable proportion of adaptive and relic species. In arachnids, sparse stands hosted higher numbers of individuals and in addition, species of conservation concern avoided high game densities. In myriapods-isopods, sparse stands hosted a higher number of species.

4.1. Mechanisms

A likely mechanism for the high species richness of sparse stands is the increased structural diversity, compared to even-aged dense stands. The sparse stands contain mature trees, scrub, tall and short herbaceous vegetation, and even bare ground. They are likely more akin to highly heterogeneous old-growth than even even-aged plantations (e.g., Latty et al., 2006). Niemela et al. (1996) showed, for boreal forests, that forest ground invertebrates strongly respond to small scale (10–15 m) heterogeneity. Oxbrough et al. (2005, 2006) documented the positive role of stand heterogeneity, including open spaces, for woodland spiders in Britain. Grgic and Kos (2005) reached similar conclusions for centipedes in Slovenia. Heterogeneous woodland architecture also increases the richness and density of herbivorous insects (e.g., Greatorex-Davies et al., 1993, 1994; Gittings et al., 2006), likely enhancing the prey supply for predatory carabids, arachnids and myriapods.

The role of prey supply is neatly illustrated by the high richness and abundance of carabids in dense-game stands. These catches mainly consisted of generalist small bodied-predators, often encountered in shady stands (cf. de Warnaffe and Lebrun, 2004) and likely attracted to the high density of larvae developing in ungulate faeces. In contrast, catches from sparse stands contained numerous carabids preying on larger-bodied herbivorous insects (cf. Trautner, 1996). Arachnids always displayed lower abundance in dense stands. This was likely due to less developed herb and shrub layers, because even many 'epigeic' spiders use herbs or shrubs for hunting (e.g., Buchar, 1968). A good case were crab spiders (Thomisidae) which included several relic species (e.g., *Ozyptila blackwalli*, *Xysticus lineatus*), all inclining towards sparse stands.

For the detritivorous diplopods and woodlice, the essential resource is plant litter (Poser, 1990; Jabin et al., 2004; Jabin et al., 2007; Topp et al., 2006). The more heterogeneous vegetation, the more diverse litter both in terms of amount and composition (Koivula et al., 1999; Gongalsky et al., 2005). A higher utilisation of rare litter types by detritophagous soil

fauna was documented experimentally (Seeber et al., 2006). The consumption of plant material by ungulates necessarily decreases litter amount and diversity.

4.2. Management and conservation implications

The preference of a significant proportion of woodland epigeic fauna for sparse stands is consistent with the notion that the recent biodiversity of lowland woods have been moulded by centuries and millennia of traditional woodland use. It is also consistent with the theories that natural woodlands of temperate Europe would be sparser than recent close-canopy high forests (Vera, 2000). What is routinely labelled as 'woodland fauna' in fact forms two rather distinct groups – a group of species depending on sparse woodlands and a group of species of dense, shady and humid stands. Indeed, these two groups are sometimes distinguished in descriptive literature (cf. Buchar, 1983; Hurka, 1996) and even bear different names in some national terminologies (e.g., 'Hainarten' vs. 'Waldarten' in German, translatable as 'grove species' and 'forest species'). Decocq et al. (2004) reached a similar conclusion for forest ground herbs. Gradual closing of lowlands forests, brought about by the shift of modern forestry towards growing even-aged high forests, is negatively affecting the specialised epigeic fauna of sparse woodlands, while supporting species preferring, or tolerating, dense stands.

We are not aware of other quantitative studies illustrating this pattern for epigeic invertebrates of lowlands of Central Europe. In contrast, the importance of traditional management for epigeic woodland invertebrates is increasingly recognised from Southern Europe, e.g. from Spain (Taboada et al., 2006) and Greece (Argyropoulou et al., 2005). Unlike in more northerly areas, traditionally managed woodlands still comprise considerable areas in Southern Europe (Grove and Rackham, 2001) and the transition towards growing even-aged stands is happening in recent years, so that currently practising ecologists are personally witnessing the ensuing biodiversity changes. In Central and Western Europe, the main transition had occurred a century ago. It had been so pervasive that at present, the coppiced panels in the Milovický Wood, maintained to benefit deer, represent the only substantial areas of active coppices in the entire Czech Republic.

Educated in a paradigm of dense climax woodlands, many Central European naturalists simply missed the connection between increasing rarity of sparse woodlands insects (the 'grove species') and increasing woodland closure. Many authors recognised that a considerable proportion of temperate woodland biodiversity prefers edge habitats (e.g., carabids: Magura, 2002; birds: Paquet et al., 2006), without addressing the crucial issues where edge species would occur in pre-cultural conditions and why would there be so many of them, given that edge habitats are, by definition, smaller than core habitats. This paradox is easily resolved by the assumption that the core habitats of the past consisted of relatively sparse stands.

A considerable proportion of our catches from sparse stands also consisted of species classified as 'thermophilous' or 'steppe specialist' by Central European authors (e.g., spiders *Xysticus lineatus* and *Ozyptila scabricula*, chilopod *Stenotania linearis*, diplopod *Cylindroiulus arborum*). Benes et al. (2006)

observed a similar pattern for butterflies in the same wood. Clearly, the recent dichotomy between woodland and grassland fauna is to a large extent artificial due to relatively recent woodland closure. For centuries and millennia, the lowland woodlands likely harboured more diversified conditions, including grassland-like glades.

The negative impacts of ungulates on species richness and the preferences of relic species might be disappointing for colleagues advocating reestablishment of woodland grazing as a restoration strategy for woodland habitats (e.g., Van Wieren, 1995; Kirby, 2004). Grazing had traditionally accompanied coppicing or alternated with it. However, compared to the high game densities at our study sites, facilitated by supplementary feeding (Benes et al., 2006), the densities of domestic animals traditionally grazed in woodlands had been rather low and seasonally varying. To use ungulates for opening up woodlands, the densities would have to be considerably lower than in recent intensive deer parks and measures such as temporary fencing would have to be applied.

In conclusion, restoring of traditional short-rotation coppicing (or coppicing with standards) would benefit relic epigeic invertebrates of European lowland woods. Generous restoration measures seem to be necessary for conservation areas, if they are to retain the biodiversity for which they were established. This might locally suppress populations of some of the species associated with dense stands, but this concern is rather unsubstantiated, as even-aged high forests will still be favoured by commercial forestry. The minimum-intervention strategy now preferred for lowland woodland reserves is probably impoverishing specialised relic fauna, and should be urgently reconsidered in favour of traditional management practices.

Key to species abbreviations (for Fig. 5)

Carabids: ABAPAL – *Abax parallelepipedus* (Piller & Mitterpacher, 1783); AMAANT – *Amara anthobia* A. et G. B. Villa, 1833; CALINQ – *Calosoma inquisitor* (Linnaeus, 1758); CARCAN – *Carabus cancellatus* Illiger, 1798; CARGRA – *Carabus granulatus* Linnaeus, 1758; CARULL – *Carabus ullrichi* Germar, 1824; CICCAM – *Cicindela campestris* Linnaeus, 1758; HARAFF – *Harpalus affinis* (Schrank 1781); HARPIC – *Harpalus picipennis* (Duftschmid, 1812); LEIRUF – *Leistus rufomarginatus* (Duftschmid, 1812); NOTPUS – *Notiophilus pusillus* G. R. Waterhouse, 1833; NOTRUF – *Notiophilus rufipes* Curtis, 1829; PTEMEL – *Pterostichus melanarius* (Illiger 1798); PTEOBL – *Pterostichus oblongopunctatus* (Fabricius, 1787).

Arachnids: ATYPIC – *Atypus piceus* (Sulzer, 1776); CENSYL – *Centromerus sylvaticus* (Blackwall, 1841); CERMAJ – *Ceratinella major* Kulczyński, 1894; COETER – *Coelotes terrestris* (Wider, 1834); DRAPPUM – *Drassyllus pumilus* (C. L. Koch, 1839); DRAVIL – *Drassyllus villicus* (Thorell, 1875); HARRUB – *Harpactea rubicunda* (C. L. Koch, 1838); MEGPSE – *Megalepthyphantes pseudocolinus* Saaristo, 1997; NERCLA – *Neriere clathrata* (Sundevall, 1830); OZYBLA – *Ozyptila blackwalli* Simon, 1875; OZYBRE – *Ozyptila brevipes* (Hahn, 1826); OZYSCA – *Ozyptila scabricula* (Westring, 1851); SCOCCEL – *Scotina celans* (Blackwall, 1841); TRIAFF – *Trichoncus affinis* Kulczyński, 1894; XERMIN – *Xerolycosa miniata* (C. L. Koch, 1834); XYSLAN – *Xysticus lanio* C. L. Koch, 1835; XYSLIN – *Xysticus lineatus* (Westring, 1851); XYSLUC –

Xysticus luctator L. Koch, 1870; XYSROB – *Xysticus robustus* (Hahn, 1832).

Myriapods-isopods: BRABAG – *Brachyiulus bagnalli* (Brolemann, 1924); CRATRA – *Craspedosoma transsylvanicum* Verhoeff, 1897; CYLARB – *Cylindroiulus arborum* Verhoeff, 1928; GEOLIN – *Geophilus linearis* C. L. Koch, 1835; LEPRO – *Leptoiulus proximus* (Nemec, 1896); LIGHYP – *Ligidium hypnorum* (Cuvier, 1792); LITLUC – *Lithobius lucifugus* L. Koch, 1862; UNCTRA – *Unciger transsylvanicus* (Verhoeff, 1899).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.biocon.2008.01.005](https://doi.org/10.1016/j.biocon.2008.01.005).

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