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Arthropod diversity in pristine vs. managed beech forests in Transcarpathia (Western Ukraine)

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ABSTRACT

Pristine forests are generally assumed to be biodiversity hotspots. Is management detrimental to biodiversity? In some of the last European remains of pristine beech forest in Transcarpathia (Western Ukraine) the influence of forest management on arthropod biodiversity was assessed. Pitfall and flight interception traps were used to compare species numbers, abundances, Simpson diversity and species composition of beetles, spiders, millipedes and centipedes in pristine and managed forests.

For the sum of all identified species and most taxonomic groups, species numbers and Simpson diversity were not significantly different between the two management regimes. Species numbers, abundances, and species composition of different beetle families, spiders, millipedes and centipedes differed more between the three regions (Jaremcha, Mala Uholka, Shyrokyj Luh) than between pristine and managed forest plots within the same region. Neither red-listed beetle species nor specialized saproxylic beetles were more diverse in pristine forests. But the latter were more abundant in pristine plots, where the amount of dead wood was up to twenty times higher than in the managed plots.

We conclude that biodiversity in pristine beech forests is not generally higher than in managed beech forests. However, the much higher amount of dead wood in pristine forests provides a source habitat for saproxylic species spreading into managed forest plots in the same region, but not to distant forests, far from virgin forests, such as in Western Europe.

1. Introduction

Pristine or virgin forests always had and still have an aura of wilderness, naturalness, authenticity, and biodiversity. While the first three qualities unquestionably are accurate for unmanaged forests, can we also generally attribute high biodiversity to pristine forests? Tropical pristine rain forests harbour most of the world's biodiversity, especially if we consider all the millions of arthropod species yet to be detected (Mora et al., 2011). Accordingly, most people assume that pristine forests in temperate regions also show high species numbers and exclusive species, at least in comparison with managed forests in the same region.

There have been many studies on the influence of forest management on different components of forest biodiversity. In a meta-analysis of 49 published papers containing 120 individual comparisons of species richness between unmanaged

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and managed forests throughout Europe (Paillet et al., 2009), most of the papers dealt with forests, that had undergone more or less drastic changes of management in the past. The influence on biodiversity of the time since last management or management intensity was found to vary considerably between taxa and forest types. The claim that unmanaged forests in general contain more species than managed forests (Økland et al., 2003) could not be confirmed in several groups of organisms such as vascular plants (Schmidt, 2005), carabid beetles (Desender et al., 1999), and beetles in general (Väisänen et al., 1993). With regard to arthropod diversity in pristine forests the meta-analysis yielded no results for a comparison with that of managed forests.

Pristine or virgin forests, defined as forests, which have never been influenced significantly by humans, are rare in Europe, and this is particularly true for beech forests (*Fagus silvatica*) (Parviainen, 2005). On the other hand, beech is the most abundant deciduous forest tree in Central Europe (Peters, 1997), with global responsibility for conservation and provision of ecosystem services. Some remains of truly pristine beech forests can be found in Eastern Europe. They provide unique possibilities to assess the impact of forest management on biodiversity. The largest pristine stands of around 10 000 ha are under protection in the Transcarpathian Ukraine. Uholka–Shyrokyj Luh in Western Ukraine (Brändli and Dowhanytsch, 2003; Commarmot et al., 2013) is located in central Transcarpathia and belongs to the eight protected forest areas united in the Carpathian Biosphere Reserve. In the year 2007 the pristine forest of Uholka–Shyrokyj Luh was, together with smaller primeval forest remnants in Ukraine and Slovakia, declared as the UNESCO World Heritage site "Primeval Beech Forests of the Carpathians and the Ancient Beech Forests of Germany" (Trotsiuk et al., 2012). Past and present occasional anthropogenic impacts on these forests are thought to be low and do not seem to have a discernible impact on forest dynamics (Commarmot et al., 2013).

However, most of today's beech forests in Transcarpathia are intensely managed. In managed beech forests all trees are of about the same age and size. There are hardly any standing dead trees and only very few fallen stems on the ground.

Arthropod diversity in managed beech forests has often been compared with that of old, presently unmanaged beech forests (e.g., du Bus de Warnaffe and Lebrun, 2004; Topp et al., 2006; Müller et al., 2007; Müller et al., 2008; Sobek et al., 2009), but rarely with pristine beech forests (Chumak et al., 2005; Müller et al., 2005a,b; Topp et al., 2006; Kappes et al., 2009). Topp et al. (2006) compared litter-dwelling beetles in stands of pristine beech forests in Slovakia with different amounts of dead wood. They found that the influence of course woody debris within each forest type (beech and oak forests) was more important than any other environmental factor.

Most studies on arthropods in beech forests focus on saproxylic beetles because they depend on dead wood, which makes the main ecological difference between managed and unmanaged forests (e.g., Müller et al., 2007; Müller et al., 2008; Lachat et al., 2012; Gossner et al., 2013). For saproxylic beetles, species richness was better explained by factors occurring at plot level, such as dead wood or fungi, than by management intensity (Müller et al., 2008).

Considering the aspects of naturalness, wilderness, and authenticity, which are highly divergent in managed and pristine forests, and given the structural diversity in age and size of the dominant tree species, as well as the highly different amount of dead wood, we tested the hypothesis (Hypothesis I) that arthropod species numbers, species abundances and Simpson diversity must be significantly higher in pristine than in managed beech forests within the same region. We also tested the hypothesis (Hypothesis II) that management, or the lack of it, is more important for species composition than neighbourhood between inventoried stands. Hypothesis III is the expectation that pristine forests harbour many more rare, specialized and threatened species than managed forests.

2. Material and methods

2.1. Study sites

The study sites were located in the Carpathian Biosphere Reserve and the Carpathian National Natural Park, Ukraine (Fig. 1). All comparable sites roughly correspond in their elevation above sea level (500–900 m.a.s.l.; Table 1).However, the sites differed in vegetation structure and management practice. The pristine beech forests of Uholka and Shyrokyj Luh and Jaremcha consist of an almost pure *Fagetum* with poorly developed herbage (Appendix 1a). Considerably more dead and live wood was available in the pristine beech forests compared to the managed forests (Table 1). Similarly, trees in the pristine forests were of higher maximum age. In the pristine beech forests of Transcarpathia most of the understory also consisted of young beech trees and seedlings. There were hardly any flowering plants, and sightings or traces of vertebrates other than birds were extremely rare during fieldwork.

2.2. Collecting method

To collect surface-dwelling arthropods we used pitfall-traps, and for the collection of flying insects we employed a combination of window interception traps and yellow water-pan traps. At each of the 22 trap sites two pitfall traps and one combination trap were placed at distances of at least 10 m between traps. The pitfall traps consisted of a plastic funnel (15 cm aperture) recessed into the soil and mounted on top of a plastic bottle containing 2% formaldehyde solution (Obrist and Duelli, 1996). A roof 10 cm above the traps provided protection from rain and dry leaves. The combined window interception and yellow pan traps (Duelli et al., 1999) were placed at a height of 1.5 m above ground. They consisted of two sheets of plexiglass (42 cm × 50 cm) crossed at right angles, placed on top of a yellow plastic funnel with a surface diameter of 43 cm.

Fig. 1. Distribution of the six sampling sites (each consisting of 2–4 trap sites) within the three regions Mala Uholka, Shyrokyj Luh, and Jaremcha in Transcarpathian Ukraine. Map by M.L. Hobi, WSL.

Table 1
Number of trap sites, their location and typical forest measures in the two management types (pristine vs. managed forest).

Forest management type	Managed forests ($N = 8$)			Pristine forests ($N = 14$)						
Region	Jaremcha	Mala Uholka		Jaremcha			Mala Uholka			Shyrokyj Luh
Longitude (Decimal degrees)	24.565	23.635	23.641	24.561	24.561	24.561	23.635	23.635	23.635	23.733
Latitude (Decimal degrees)	48.445	48.178	48.18	48.446	48.446	48.446	48.182	48.182	48.182	48.336
Elevation (m.a.s.l)	900	570	500	870	870	870	600	600	600	825
Area (ha)	4.4	37	13	11	22	22	47	47	47	25
Max. tree age (yrs)	40	65	150	210	210	210	200	200	200	280
Live wood volume (m^3/ha)	140	400	500	415	485	485	610	610	610	590
Dead wood volume (m^3/ha)	4	1	4	6	10	10	73	73	73	76
Last harvesting	1973	1940	1850	–	–	–	–	–	–	–
Sampling year	2004	2004	2004	2001	2001	2004	1999	2001	2004	1999
N trap sites	2	4	2	1	1	2	2	2	4	2

The funnel was filled with water containing some drops of detergent to make insects sink quickly. The traps were emptied weekly from March to September. Most forest plots were sampled in 2004, others also in 2001 or in 1999 (Table 1). A total of 28 sampling periods (weeks) covered the main activity season of most taxa. The water in the funnels had to be refilled or replaced several times during summer.

The collected material per trap site (two pitfall traps and one combined window interception and yellow pan trap) was pooled and kept in 75% alcohol, sorted to higher taxa levels and distributed for species identification to Ukrainian specialists (see acknowledgements).

2.3. *Data evaluation*

The basic unit for all calculations is the pooled material from one *trap site*, consisting of two pitfall traps and one combined window interception and yellow pan trap. Usually, two trap sites were located within a *forest plot*, which is either managed or pristine beech forest. The forest plots belong to one of the three *regions*, Uholka, Shyrokyj Luh, or Jaremcha. The number of trap sites differs between managed (8) and pristine (14) forests, but since only the mean numbers of arthropods per trap site are compared, the uneven numbers of trap sites per region or management type have no influence on the results.

As dependent variables we tested the number of species, the log-transformed number of individuals and the inverse Simpson index (R package *vegan*, `diversity(x, ‘‘inv’’)`, Eq. (1)) for each of the following taxonomic groups: Araneae, Carabidae, Curculionidae, Staphylinidae, remaining Coleoptera, Myriapoda, and the total.

$$\frac{1}{\sum_{i=1}^{S} p_i^2}. \tag{1}$$

As independent variables we included treatment, region, area, age of oldest trees, volume of live and volume of dead wood. We performed linear mixed effect models (lme, from R package ''lme4'') including region or forest management type as well as year and number of trap site as nested random effects and employed the maximum likelihood method (examples given in Eqs. (2) + (3)).

```
lme(y.nspp ~ Manag, random = ~ 1 | Region/Year/Rep, method = "ML")          (2)
lme(y.nind ~ Region, random = ~ 1 | Manag/Year/Rep, method = "ML").         (3)
```

Normal data distribution was verified with a Shapiro–Wilk normality test, and the distribution of residuals judged with normal probability plots. Some independent variables were strongly correlated (Spearman Rank Correlation rho > 0.7; e.g. dead wood and management rho $= 0.861$). However, not knowing a priori which would show stronger effects, we refrained from arbitrarily excluding one. Consequently, to find best explaining variables among correlated ones, we compared those independent variables against each other, which had a significant effect by testing pairwise with an ANOVA for significant differences between models.

For illustration, means comparisons were visualized with box-plots (Fig. 2). Rarefaction curves of the total arthropod collections were additionally fitted to the clench equation (Soberon and Llorente, 1993) to allow for comparison of species numbers extrapolated to equal abundances.

To elucidate the effects of region and treatment on rare species and those typical of pristine forests, we also compared species richness and abundance of coleopteran species which were either red listed (Köppel et al., 1998), or found to be components of pristine forest ecosystems by Speight (1989), named by Mateleshko (2005) as useful in identifying forests of international importance to nature conservation, related by Müller et al. (2008) to silvicultural management intensity, or identified as indicator species for dead-wood amount by Lachat et al. (2012).

To test whether treatment (management vs. pristine forests) is more important for species composition than the location (region) of sampling sites, we analysed the community similarity between sampling sites using Bray–Curtis algorithm (Bray and Curtis, 1957) based on a distance matrix for each pair of sites (Legendre and Legendre, 1998). We then created a dendrogram of the relatedness of communities among the single sampling sites using a hierarchical cluster analysis based on Ward's minimum distance (Ward, 1963). All community data (site by species matrices) have been Hellinger-transformed to reduce the effect of dominant species particularly abundant in our interception traps and make the data appropriate for linear analyses (Legendre and Gallagher, 2001). We finally applied variation partitioning analysis to quantify the unique and joint contribution of Treatment and Region of the sampling sites to variation in community composition among sites (Legendre and Legendre, 2012).

All statistical analyses were performed using R 3.1.2 (R Core Team, 2014) by using packages *lme4* (Bates et al., 2014) and *vegan* (Oksanen et al., 2013).

3. Results

3.1. Effects on species diversity and abundance

All in all, 24,306 individuals from 637 arthropod species were identified and used for the analyses (Appendix 3). The focus here was on the insect order Coleoptera, represented by 504 species, separated into the three families Carabidae, Curculionidae, and Staphylinidae, and one group of all the other Coleoptera. Spiders are represented with 89 species, and 44 species of Myriapoda were collected. The main result seen on Table 2 is the fact that numbers of species and individuals are not as different between pristine and managed forests as expected (Hypothesis I). This holds true for all arthropod species together and for most of the separate taxa. Total species numbers compared with rarefaction for equal abundances did also not reveal any significant effects ($p > 0.05$, not shown). Except for Myriapoda, consistently higher mean numbers of individuals per sampling site were found in the 14 pristine forest trap sites, but due to the large standard deviation between trap sites that result is not statistically significant. Also, none of the average species numbers of the identified taxa were significantly different between pristine and managed forests, except in Curculionidae, where the effect could be better explained by the amount of dead wood. Significant differences, however, can be seen between the three regions, especially with respect to the number of trapped individuals. Spiders were most abundant in Jaremcha, whereas carabid beetles prevailed in Shyrokyj Luh and curculionids in Mala Uholka. Examples of box plots visualize the differences in species richness, abundance and diversity (Simpson Index) for effects of the factors treatment and region (Fig. 2).

The low influences of treatment (managed or pristine plots) and the stronger influence of Region are shown in Table 3. The only significant ($p = 0.04$) influence of management (correlated 0.861 with tree age and 0.860 with dead wood) is on the species numbers of Curculionidae, the abundance of Carabidae, and the Simpson diversity of all species, and that of the Staphylinidae. The factor Region, on the other hand, was a dominant factor for higher species numbers of Carabidae in

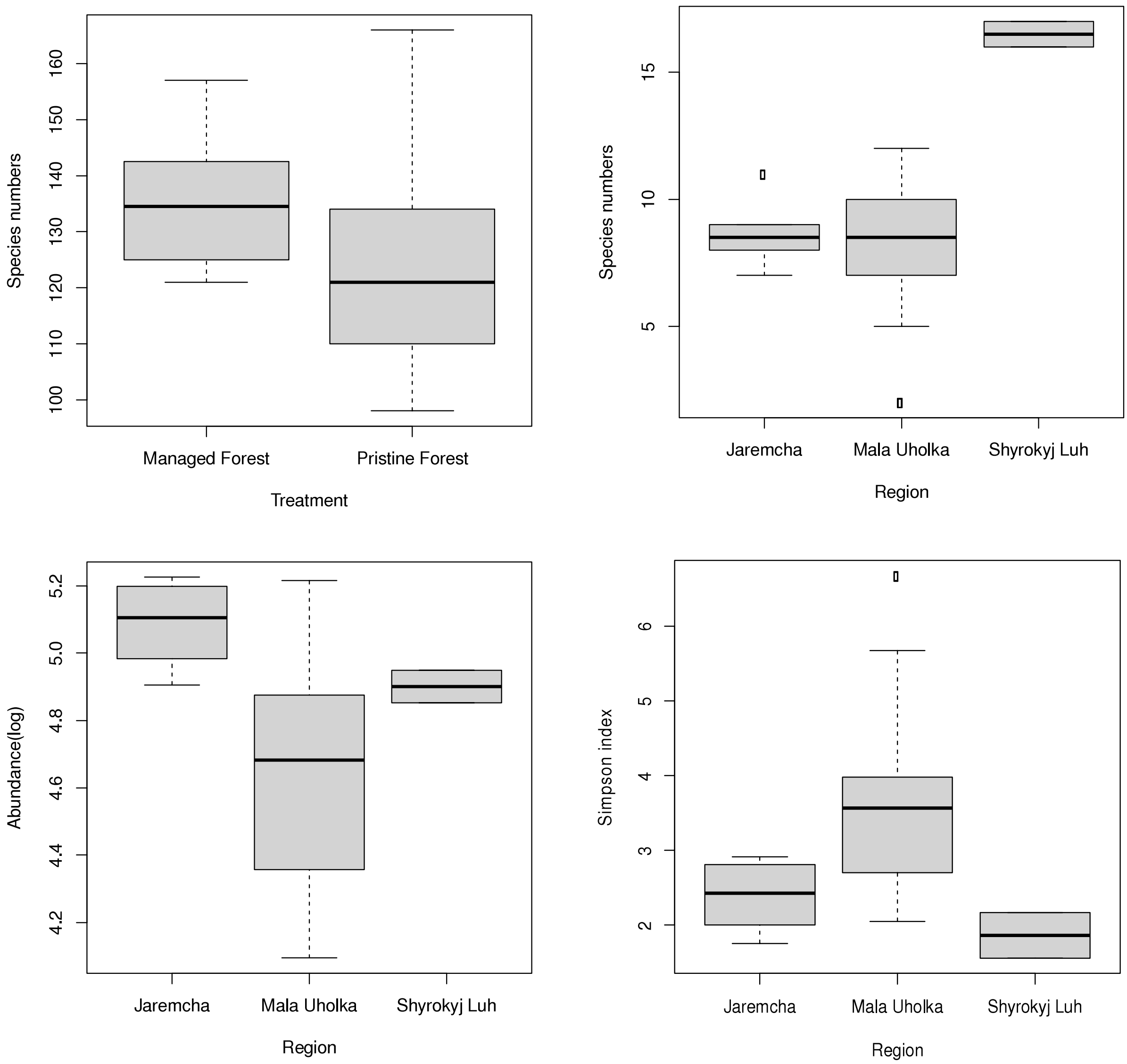

Fig. 2. Examples of boxplots illustrating data given in Tables 2 and 3, with median (solid line), interquartile range (grey box), 1.5 × interquartile range (whiskers) and possible extreme values (dots). (a) Total number of species does not differ significantly between treatments, (b) most carabid species were found in Shyrokyj Luh, (c) abundance of Araneae significantly differed between regions, (d) Simpson diversity of Curculionidae is significantly higher in Mala Uholka than in the other sites.

Shyrokyj Luh and Curculionidae in Mala Uholka, and lower species numbers of Other Coleoptera in Jaremcha, and Myriapoda in Mala Uholka. Even more significant was the factor Region for the number of individuals per trap site. All in all, Jaremcha had lower abundance, but for spiders, Jaremcha yielded the highest numbers of individuals. Jaremcha was also low in Myriapoda and the Other Coleoptera. No really dominant factor is discernible for Carabidae and Staphylinidae. Simpson diversity is best explained by the amount of dead wood, correlated (0.74) with management for All species and spiders, whereas the Simpson index for the Other Coleoptera, Curculionidae, and Myriapoda mainly depends on the region.

3.2. Effects on species composition

The second hypothesis (Hypothesis II), stating that treatment (managed forest) or the lack of it (pristine forest) is more important for species composition than regional affinities was tested with a cluster dendrogram (Fig. 3). Dendrograms were calculated for the sum of all species (Fig. 3(a)), as for the separate groups of arthropods (Fig. 3(b) carabid beetles; Appendices 1a–e for the other taxonomic groups) shown in Tables 2 and 3.

The dendrograms indicate the similarity among the trap sites with regard to their particular species composition. The expectation was that most trap stations in pristine forests build a block, and most stations in managed forests another block.

Table 2
Mean number of collected species and individuals and standard deviation (MN ± SD) are given for the treatments and the regions. (Statistics results are included in Table 3.)

		Total study	Forest type		Region		
			Pristine	Managed	Jaremcha	Mala Uholka	Shyrokyj Luh
Taxon	N sites	22	14	8	6	14	2
	Measure	N	MN ± SD	MN ± SD	MN ± SD	MN ± SD	MN ± SD
All	Nsp	637	124.2 (±18.3)	135.3 (±11.2)	118.3 (±7.9)	132.6 (±18.9)	127.0 (±7.0)
	Nind	24 306	1171.6 (±576.4)	987.9 (±272.6)	1240.3 (±552.0)	922.9 (±278.7)	1971.5 (±461.5)
Aranea	Nsp	89	19.7 (±3.8)	19.3 (±2.7)	19.8 (±4.0)	19.6 (±2.8)	18.5 (±5.5)
	Nind	2 753	130.0 (±43.9)	116.6 (±24.7)	162.2 (±19.6)	108.1 (±35.8)	133.5 (±6.5)
Carabidae	Nsp	36	9.8 (±3.6)	8.0 (±1.6)	8.7 (±1.2)	8.3 (±2.5)	16.5 (±0.5)
	Nind	1 467	90.4 (±94.8)	25.1 (±7.6)	54.7 (±18.6)	37.4 (±34.3)	307.5 (±16.5)
Curculionidae	Nsp	34	8.4 (±3.9)	5.8 (±1.3)	3.8 (±0.7)	9.0 (±3.2)	7.0 (±2.0)
	Nind	1 345	73.9 (±52.3)	38.9 (±21.3)	11.7 (±5.3)	82.4 (±43.8)	60.5 (±1.5)
Staphylinidae	Nsp	134	19.2 (±5.5)	20.0 (±5.0)	21.3 (±5.2)	18.1 (±5.0)	24.0 (±3.0)
	Nind	6 796	318.3 (±441.1)	292.5 (±377.1)	747.3 (±546.4)	83.1 (±47.2)	574.0 (±132.0)
Other Coleoptera	Nsp	300	51.7 (±12.1)	65.5 (±11.1)	47.5 (±4.6)	61.9 (±14.2)	48.0 (±1.0)
	Nind	8 681	418.5 (±253.9)	352.8 (±114.5)	163.2 (±27.4)	438.0 (±125.8)	785.0 (±275.0)
Myriapoda	Nsp	44	15.4 (±3.8)	16.8 (±3.3)	17.2 (±1.8)	15.8 (±4.3)	13.0 (±1.0)
	Nind	3 264	140.6 (±106.0)	162.0 (±28.9)	101.3 (±29.0)	173.9 (±97.9)	111.0 (±30.0)

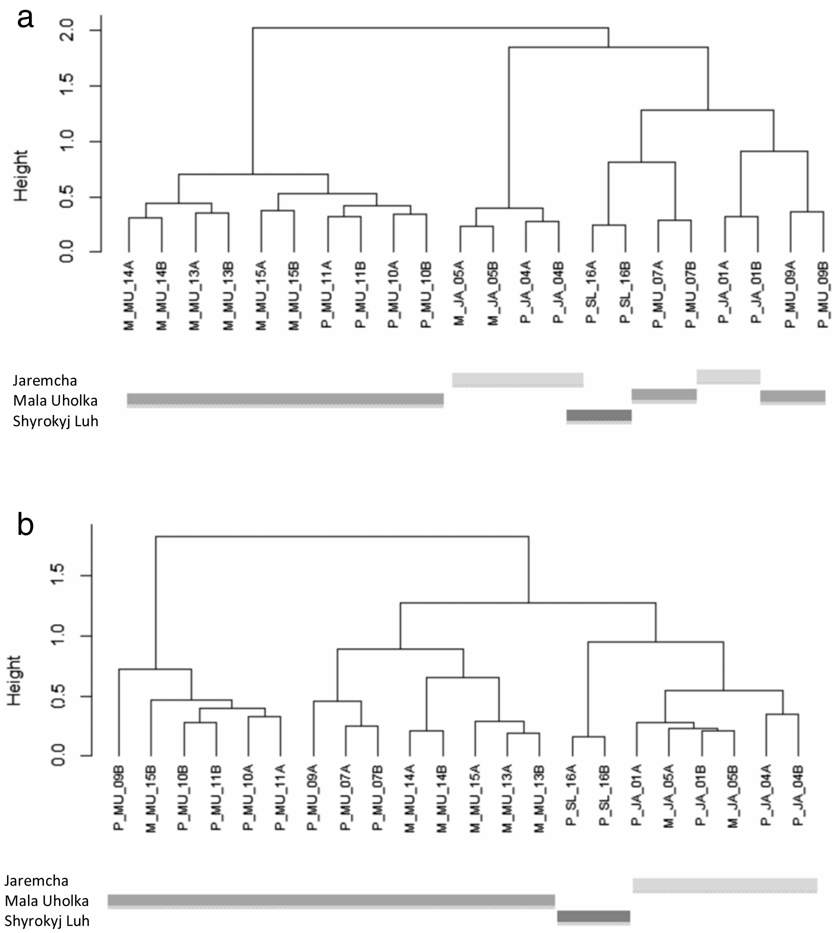

Fig. 3. Cluster analyses based on the similarity of species composition for (a) all taxa and (b) carabid beetles. The results show different distribution pattern of the influence of treatment (M = managed forests, P = pristine forests) among regions (JA = Jaremcha, MU = Mala Uholka, SL = Shyrokyj Luh).

Table 3
Results of lme analyses of effects on species numbers (N sp.), abundance (N ind.) and diversity (Simpson). Management (Manag), region, dead wood volume (VolDWoo), and age of oldest trees (AgeT) showed specific effects. Cells are filled in grey, where the effect of the corresponding variable proved dominant, as indicated by ANOVA of the respective lme results.

Group	Effect	N sp.	N ind.	Simpson
All species	Manag	n.s.	n.s.	*
	Region	n.s.	**	n.s.
	VolDWoo	n.s.	n.s.	*
	AgeT	n.s.	n.s.	n.s.
Aranea	Manag	n.s.	n.s.	n.s.
	Region	n.s.	***	n.s.
	VolDWoo	n.s.	n.s.	*
	AgeT	n.s.	n.s.	n.s.
Carabidae	Manag	n.s.	*	n.s.
	Region	*	*	n.s.
	VolDWoo	n.s.	*	n.s.
	AgeT	n.s.	*	n.s.
Curculionidae	Manag	*	n.s.	n.s.
	Region	***	***	**
	VolDWoo	**	**	n.s.
	AgeT	n.s.	n.s.	n.s.
Staphylinidae	Manag	n.s.	n.s.	*
	Region	n.s.	n.s.	n.s.
	VolDWoo	n.s.	n.s.	n.s.
	AgeT	n.s.	n.s.	*
Other Coleoptera	Manag	n.s.	n.s.	n.s.
	Region	**	***	***
	VolDWoo	n.s.	n.s.	n.s.
	AgeT	n.s.	n.s.	n.s.
Myriapoda	Manag	n.s.	n.s.	n.s.
	Region	*	***	*
	VolDWoo	n.s.	n.s.	n.s.
	AgeT	n.s.	n.s.	n.s.

Significance codes:
n.s. $p > 0.05$.
* $p \leq 0.05$.
** $p \leq 0.01$.
*** $p \leq 0.001$.

If neighbourhood of the trap sites (Region) is more important than the influence of management, the blocks would be built by the three regions. Our result is mixed: Assessing the sum of all species (less the singletons) the dendrogram (Fig. 3(a)) shows two clusters with mixed management (at Jaremcha and Mala Uholka) on the left hand site, and one cluster (on the right hand site) with mainly pristine forests, from all three regions. This means that some of the trap sites in pristine forests of the three regions are more similar to each other than to the neighbouring managed forest sites—and to the other pristine forest sites in their own region. But most of the pristine trap sites, both in Mala Uholka and Jaremcha, were more similar to the managed sites in the same region. Obviously, comparing the species composition gives a more complex image than the above box plots, where there was hardly any significant difference in species diversity between the two treatments.

The most consistent position within the dendrogram is found for the trap sites at Shyrokyj Luh, where no managed forest plots could be sampled. The two trap sites in pristine forest always align in the dendrogram with pristine forest sites of one or both other regions. They are almost never aligned in a cluster with managed forest. The only exception is the carabid fauna (Fig. 3(b)), where the species composition is almost the same in managed or pristine forests in the two regions with both managements, Mala Uholka and Jaremcha.

Similar to the dendrogram for all species, the dendrograms for Araneae and All Coleoptera (Appendices 1a, b) show a block of eight trap sites, all in pristine forest, and always with the two trap sites at Shyrokyj Luh. For the Staphylinidae and Myriapoda, (Appendices 1d, e) the block of pristine forest trap sites consists of six trap sites, again containing the Shyrokyj Luh sites. The least management-depending group are the curculionid beetles (Appendix 2c), but even there, the two sites of pristine forests at Shyrokyj Luh align with two pristine forest sites in Mala Uholka.

Table 4 corroborates the results of the species composition (cluster) analyses by showing that the region (i.e. the location of the trap sites in different regions) explains a higher proportion of variance in community composition compared to the treatment (i.e. managed vs. pristine forest stands) in all taxonomic groups.

Table 4
Variation partitioning with relative percentage variance explained as the adjusted R^2 (R^2_{adj}) of the unique and combined (∩) fractions of treatment (managed vs. pristine stands) and the three regions. The region explains between 1.7 (diplopods) to 8.6 (weevils) times more variance in community composition than treatment (forest management) for all taxonomic groups.

Taxonomic groups	Treatment (%)	M ∩ R (%)	Region (%)
All species	4	0	30
Aranea	7	1	27
Carabidae	5	0	24
Curculionidae	3	1	26
Staphylinidae	5	0	24
Other Coleoptera	4	0	29
Myriapoda	7	2	12

Table 5
Number of species (N sp.) and individuals (N ind.) of selected coleopteran groups (see also text) found under the managements and in the regions. Group relates to species of the Red List of rare and threatened saproxylic beetles in Central Europe (Köppel et al., 1998), the list of specialist beetles of the Carpathian pristine forests (Mateleshko, 2005), species mentioned in the list of particularly valuably saproxylic arthropods by Speight (1989), the list of "Urwald" relict species of Müller et al. (2005a), and the most recent list with 127 saproxylic indicator species by Lachat et al. (2012). Values in bold are significantly larger than the compared numbers.

Group	Var.	Treatment			Region			
		Managed forest	Pristine forest	Sig	Jaremcha	Mala Uholka	Shyrokyj Luh	Sig
Red list	N sp.	15.3 (±2.5)	13.7 (±3.0)	n.s.	12.0 (±2.4)	**15.4** (±**2.7**)	13.0 (±0.0)	*
	N ind.	51.6 (±18.7)	93.0 (±64.6)	n.s.	65.0 (±28.5)	83.9 (±67.3)	75.0 (±3.0)	n.s.
Mateleshko	N sp.	6.5 (±1.8)	4.6 (±2.2)	n.s.	**6.8** (±**1.3**)	4.9 (±2.3)	3.0 (±0.0)	*
	N ind.	14.9 (±5.5)	25.0 (±21.6)	n.s.	16.7 (±7.2)	22.2 (±21.9)	**29.0** (±**2.0**)	*
Speight	N sp.	0.9 (±0.6)	1.5 (±0.7)	n.s.	1.2 (±0.4)	1.2 (±0.9)	2.0 (±0.0)	n.s.
	N ind.	2.5 (±2.0)	10.9 (±14.3)	n.s.	6.5 (±3.8)	3.3 (±4.3)	**44.0** (±**2.0**)	**
Müller	N sp.	1.8 (±0.8)	1.1 (±0.5)	n.s.	1.0 (±0.6)	1.6 (±0.7)	1.0 (±0.0)	n.s.
	N ind.	9.8 (±7.5)	11.3 (±10.4)	n.s.	1.5 (±1.0)	**14.1** (±**9.4**)	**14.5** (±**3.5**)	**
Lachat	N sp.	8.0 (±2.4)	6.6 (±2.1)	n.s.	5.2 (±1.1)	**8.1** (±**2.3**)	**6.0** (±**1.0**)	**
	N ind.	121.8 (±74.4)	177.5 (±228.1)	n.s.	11.8 (±4.7)	**159.5** (±**102.7**)	**577.5** (±**283.5**)	***

Significance codes (sig):
n.s. $p > 0.05$.
* $p \leq 0.05$.
** $p \leq 0.01$.
*** $p \leq 0.001$.

3.3. Effects on species of conservation concern

We screened our species lists for species mentioned in published lists for particularly valuable, rare and threatened, or specialist beetles in Central Europe (e.g. Appendix 1b). The results shown in Table 5 do not support the third hypothesis, claiming that the number of species of conservation value is higher in pristine forests than in managed forests. In our study the average number of rare, threatened or specialist beetle species per trap was not significantly different in managed and pristine forests. In fact, the average figures for pristine forest sites were consistently but not significantly, lower than in managed forests. In the comparison between the three regions, species numbers also were not significantly different, apart from a slightly significant difference between Jaremcha and Mala Uholka for the list of indicative saproxylic beetles (Lachat et al., 2012), as well as more red listed species in the latter region.

The results are not much different for the number of individuals. They are consistently higher in the pristine forests, albeit never significantly. A regional comparison of the individuals of the listed species indicates that some saproxylic species must have been quite abundant in particular forest plots, notably at the two sites in the pristine forest of Shyrokyj Luh.

4. Discussion

In our study, arthropods from different families and different trophic guilds were not significantly influenced by management in beach forests. Their average species numbers per trap site, with one exceptions, were not higher in pristine than in managed forests. Not even the species composition was significantly different. And most surprisingly, not even the species considered to be old forest specialists, as well as species that are rare and threatened in Central Europe, were more diverse in pristine forests.

In the scientific literature on arthropods in pristine forests and natural forest reserves there is a strong focus on saproxylic beetles. This fascinating group is of prime conservation concern (Speight, 1989; Ranius and Jansson, 2000; Simila et al., 2002; Müller et al., 2005a; Davies and Semui, 2006; Müller and Gossner, 2010; Müller et al., 2010; Lachat et al., 2012; Müller et al., 2013). Of 1377 saproxylic beetle species known for Germany, 115 species (8%) are considered Urwald relict species (Müller et al., 2005a). Brunet and Isacsson (2009) sampled 180 saproxylic beetle species on beech snags in Sweden, of which

10% were on the red list, and more red-listed species were found in old-growth forests as compared to managed forests. Our pristine plots yielded roughly the same number of species considered to be Carpathian pristine forest specialists by Mateleshko (2005) as the managed plots. A maximum of three red-listed species per plot (Central European Red List of 1998, Köppel et al., 1998) were collected in our study, without a significant difference between managed and pristine plots. One reason for these low numbers might be the sampling methods used. Relict species in old forests tend to stay in their native micro-habitat and can best be sampled by specialists by sieving decayed wood or searching visually (Müller et al., 2005a). Also, one could speculate that our results might have been different with additional traps in the canopy. However, with only one tree species involved, differences in habitat quality are likely to be more pronounced at the forest floor (amount of dead wood, light) than in the canopy.

In our study, the amount of dead wood was much higher in pristine plots than in managed plots (Table 1). Still, the amount of dead wood, highly correlated with the factor management, did not show up as a prominent variable. In a study on saproxylic species in boreal forests in Fennoscandia (McGeoch et al., 2007), both quality and quantity of course woody debris were decisive factors for beetle diversity, whereas stand size, position, and distance to nearest reserves were irrelevant. The influence of the amount of dead wood on saproxylic beetles in beech forests was also investigated by Müller et al. (2007, 2008). No differences were found in the number of species and individuals, but dead wood amount had a strong influence on particular species specialized on forests close to pristine conditions. The authors suggest not using total species numbers to recognize degradation in forest species, but rather focus on rare and threatened species.

We argue differently here, with a broader spectrum of ecosystem services in mind. Since the major difference between managed and pristine beech forests is the size and the amount of dead wood, saproxylic beetles, which depend on dead wood, are rather obvious indicators for that aspect of beech forests. Or to put it the other way: What ecosystem services can saproxylic species deliver in a managed forest, where the removal of dead wood is the prime goal, i.e. the prime ecosystem service? Whether a lower amount of dead wood in managed forests is a sign of ecological degradation or reduced ecological sustainability is a matter of how one defines ecological degradation and sustainability. Carbon sequestration is an important ecological ecosystem service of forests. In managed forests, the stems are harvested as timber and either used in the constructing business, thereby storing CO_2, or they are used for burning, thereby replacing not renewable fossil fuels. In both cases, less carbon is released into the atmosphere, if compared to the situation in pristine forests, where dead wood is decomposed by saproxylics. In pristine forests, the sequestered CO_2 is released into the atmosphere in equal amounts to those sequestered by the living trees. Thus, with respect to ecological or economical ecosystem services, saproxylic beetles are rather questionable indicators.

Ecological resilience and sustainability in either pristine or managed beech forests depend on a multitude of interactions between a diverse and abundant community of species at all trophic levels. Rare and threatened saproxylic species are by definition not abundant and therefore can cause only few ecological interactions. Thus they have little ecological impact and provide indication mainly for cultural ecosystem services, such as spiritual enrichment, intellectual development, recreation, and aesthetic values (Harrison et al., 2010). For all other ecosystem services, total species numbers or the abundance and diversity of ecologically or economically relevant groups, such as pest antagonists or decomposers, are more adequate as indicator taxa. Nuckols and Connor (1995) for example report that damage caused by chewing insects was consistently higher on trees in natural forests than in urban or ornamental plantings. In a recent analysis, Lange et al. (2014) investigated the effects of forest management on Carabidae and Staphylinidae in different types of forests in Central Europe. The species diversity of the two predatory beetle groups was higher in older than in younger stands, and lower in unmanaged than in managed stands. But generally, the effect of management on the beetle communities was small, as in our study for these two beetle families. Gossner et al. (2014) found arthropods in general not to be reliable indicators of forest types in Germany, and that indicator species should be defined at the regional scale. In our study in Transcarpathia, we were not even able to find a decisive influence of management on regional specialists of unmanaged forests.

5. Conclusions

Arthropod biodiversity was not generally higher in pristine beech forests than in managed beech forests (Hypothesis I). Management had a lesser influence on species composition than expected (Hypothesis II). As the species compositions in managed and pristine beech forests did not differ significantly in our samples, remnant pristine beech forests in Transcarpathia can only marginally contribute to overall species diversity with source populations of rare and threatened saproxylic specialists (Hypothesis III).

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at http://dx.doi.org/10.1016/j.gecco.2014.11.001.

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