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A Comparison of the Formation Rates and Composition of Tree-Related Microhabitats in Beech-Dominated Primeval Carpathian and Hyrcanian Forests

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Abstract: Primeval forests in the temperate zone exist only as a few remnants, but these serve as important reference areas for conservation. As key habitats, tree-related microhabitats (TreMs) are of intense interest to forest ecologists, but little is known about their natural composition and dynamics in different tree species. Beech forms a major part of the temperate forests that extend from Europe, home to European beech *Fagus sylvatica* L. (Fs), eastward to Iran, where Oriental beech *Fagus orientalis* Lipsky (Fo) is the dominant species. In this study, we compared TreMs in primeval forests of both species, using data from Fo growing in 25 inventory plots throughout the Hyrcanian forest belt in Iran and from Fs growing in a 9 ha permanent plot in the Uholka Forest of Ukraine. TreMs based on 47 types and 11 subgroups were recorded. Beech trees in the Hyrcanian forest had a higher mean diameter at breast height (dbh) than beech trees in Uholka and contained twice as many TreMs per hectare. Although the mean richness of TreMs per TreM bearing tree was similar in the two species, on the basis of the comparison single trees in two groups ($n = 405$ vs. 2251), the composition of the TreMs clearly differed, as the proportions of *rot holes*, *root-buttress concavities*, and *crown deadwood* were higher in the Hyrcanian Forest, and those of *bark losses*, *exposed heartwood*, and *burrs and cankers* higher in Uholka Forest. Estimates of TreMs dynamics based on dbh and using Weibull models showed a significantly faster cumulative increase of TreMs in Fo, in which saturation occurred already in trees with a dbh of 70–80 cm. By contrast, the increase in TreMs in Fs was continuous. In both species, the probability density was highest at a dbh of about 30 cm, but was twice as high in Fo. Because of limitations of our study design, the reason behind observed differences of TreM formation and composition between regions remains unclear, as it could be either result of the tree species or the

environment, or their interaction. However, the observed differences were more likely the result of differences in the environment than in the two tree species. Nevertheless, our findings demonstrate that the Hyrcanian Forest, recently designated as a natural heritage site in Iran, is unique, not only as a tertiary relict or due to its endemic trees, herbs and arthropods, but also because of its TreMs, which form a distinct and rich habitat for associated taxa, including endemic saproxylic species.

Keywords: TreMs; *Fagus orientalis*; *Fagus sylvatica*; primeval forest

1. Introduction

Since the seminal work by Speight [1] on saproxylic invertebrates and their conservation, conservationists have increasingly recognised the importance of deadwood as a critical habitat for endangered forest species worldwide [2,3]. This awareness has resulted in the development of diverse strategies for deadwood enrichment, as well as the creation of set-asides in boreal and temperate forests and even in production forests [4–6]. Experts of many forest taxa have pointed out that living trees as well as deadwood provide a number of microhabitats. These include cavities for birds [7], hollow trees with wood molt for specialists such as the hermit beetle (*Osmoderma eremita* Scopoli) [8], bark shelter as roosting sites for bats [9], rot holes as habitats for lichens and bryophytes [10], water-filled holes in trees (dendrotelms) as habitat for diptera and beetles [11], and the suspended soil used by mites and other small organisms in tree canopies [11]. Moreover, veteran trees often harbour multiple microhabitats, thus providing a functionally rich habitat [12,13], but even snags can host crucial and complementary microhabitats [12,14].

Möller [13] classified most of the microhabitats of saproxylic beetles using an approach developed as a monitoring tool for European beech forests [15]. The classification is essentially a general catalogue of tree-related microhabitats (TreMs) and is based on a hierarchical approach [16] that allows standardised inventories and comparisons among forests and tree species with respect to their microhabitats. TreMs regularly develop in primeval forests, mainly in fallen trees, in trees damaged by ice breaks, or the attacks of insects and fungi and in senescent trees. As trees differ in their life-spans and their resistance to harsh climates or decomposing organisms, their decay and thus the development of TreMs can vary widely between trees of a given age and species, but also as a function of site quality [14,17,18]. However, because studies on TreMs are relatively new and data on TreMs in primeval forests are rare, the current understanding of TreM diversity and composition in managed and primeval forests is limited [12,19,20].

With its high shade tolerance and competitive advantage, European beech (*Fagus sylvatica*) dominates many temperate broadleaf forests in Europe, in zones ranging from the plains to the montane. However, only a small proportion of these forests can be classified as primeval as most primeval forests were destroyed by the effects of several thousands of years of anthropogenic pressure on forest habitats [21,22]. A few larger primeval forest patches survived in the Carpathians in Eastern Europe [23,24]. In addition to anthropogenic pressure, the diversity of European beech forests has been affected by the post-glacial recovery of refuges in the Mediterranean area [25], which has altered both the community composition and the genetic diversity of forest species [26,27].

Oriental beech (*Fagus orientalis*) occurs from eastern Greece over the Caucasus to the eastern part of the Hyrcanian Forest, located south of the Caspian Sea. The clear species status of Oriental beech was only recently determined in genetic analyses [28]. Like the European beech, the Oriental beech is shade-tolerant and tends to dominate in montane regions with sufficient precipitation. Regeneration occurs via small patch dynamics, following the breakdown of over-mature trees [29–31]. Similar to the European beech, the majority of Oriental beech forests have been heavily affected by human land-use, partly due to the long cultural histories of the native region of these trees. In Iran, beech forests grow along the Hyrcanian Forest belt, south of the Caspian Sea. The protection conferred by neighbouring

deserts and high alpine mountains in the south has allowed the survival of large primeval beech forests [32]. As tertiary relicts, these forests have given rise to several endemic plant and animal species [33,34].

UNESCO valued the primeval forests of the Carpathians and Iran by designating them as “Primeval Beech Forests of the Carpathians” and “Hyrcanian Forests”, respectively. Despite this recognition, both forests are under serious threat. In the Carpathians, illegal logging is commonly conducted in natural beech forests [35]. In Iran, authorities initially followed recommendations aimed at protecting the forests, but then allowed the removal of dying and damaged trees, including snags. Both give rise to TreMs and therefore to habitats for endangered species. Recently, following interventions by scientists and conservationists, the harvesting of living trees, including sanitary felling, and the removal of deadwood have been stopped [36,37], but in Iran, the number of trees with TreMs is currently very low.

Primeval temperate forests serve as an important reference baseline for integrative management strategies [38]. Studies of beech forests have focussed on their stand structure [23,24,29]; the amount and composition of deadwood [39]; and the composition of fungi, bryophytes [40–42], and beetles [34,43–45]. By contrast, the composition and dynamics of TreMs in natural forests of European and Oriental beech remain poorly explored.

In this study, the composition and dynamics of TreMs in natural forests of European and Oriental beech were described and compared using data collected in primeval forests along the Hyrcanian belt and in the largest primeval forest of European beech, found in Ukraine. Because these congeneric species are closely related, similarities in the composition and dynamics of their TreMs were expected.

2. Material and Methods

2.1. Study Regions and Design

The Hyrcanian forest in Iran forms a belt along the southern edge of the Caspian Sea. Differences in elevation result in different vegetation zones, with Oriental beech forests found between 800 and 2000 m a.s.l. (above sea level). At this elevation, the mean annual temperature range is 8–12 °C and mean precipitation ranges from 1200 to 1400 mm, with a decreasing trend from west to east [32]. Cambisols are the most common soil under *Fagetum* communities. The humid climate favours the growth of the beech trees, which reach heights of up to 47 m. The forest still harbours large primeval forests with an impressive diversity of globally threatened species and endemic species, for example, saproxylic beetles [34,37]. In this study, data on TreMs in Oriental beech were collected in five larger forests (seven stands, each with a size of 5–100 ha and 1–5 plots per stand) of three provinces (Table S1). The minimum distance between two plots was 100 m. The 25 plots were located within the beech-dominated zone of the Hyrcanian Forest. They had an elevational range of 854–1790 m a.s.l. and a geographical west–east extent of >500 km, thus covering the full distribution range of Oriental beech in Iran. Single plots had an area of 0.1 ha. Although the slope was not measured, most of the plots were located on steep slopes (see Supplementary Figure S1). Trees with a diameter at breast height (dbh) ≥ 7 cm were included in the sample. In addition to the 405 beech trees with a dbh ranging from 7 to 139 cm, six velvet maples (*Acer velutinum* Mast.), three Caucasian alders (*Alnus subcordata* C.A.M.), six ironwoods (*Parrotia persica* C.A.M.), and one wild service tree (*Sorbus torminalis* (L.)) were studied as well. For each tree, all of its TreM types were recorded. Sampling was conducted by two of the authors (R.J. and R.W.), using a binocular (10 \times) when necessary. The Uholka-Shyrokyi Luh primeval forest of Ukraine is located in the Carpathians, over an area of >10,000 ha. Its elevation ranges from 400 to 1300 m a.s.l. The mean annual temperature is 7.7 °C and mean annual precipitation is 1130 mm (at 430 m a.s.l.). The forest is dominated by European beech on acidic cambisols [46] and was designated as a UNESCO World Heritage site in 2007. The Uholka Forest is the largest of the transnational UNESCO World Heritage “Primeval Beech Forests of the Carpathians and the Ancient Beech Forests of Germany” and it harbours a rich diversity in species recognised as indicators of

old-growth [44]. Data on the TreMs of this primeval forest were collected in September 2015 from the 9 ha permanent research plot established in 2000 by a Swiss-Ukrainian team [47] and regularly assessed thereafter. The large research plot is located in the lower zone of the forest. Local conditions, including a weak slope, thick soil and sufficient precipitation, are very favourable for beech growth and lead to large trees with a height of >50 m. The 2251 evaluated beech trees ranged in size from 7 to 129 cm dbh. TreMs were registered in all plots according to the same TreM typology (see Tables S1 and S2).

2.2. Statistical Analyses

In our samplings, species admixed with the two *Fagus* species at both study sites accounted for 5% of all inspected trees. These trees were removed from the analysis before the analyses of the TreMs. TreMs recorded in the field were compared for their correspondence with the 47 TreM types published by Larrieu et al. [16]. The resulting TreM list was then simplified to obtain sufficient data for modelling. The 11 TreM subgroups were roughly similar to the 15 groups described in Larrieu et al. 2018 (see Table S1) and are referred to herein simply as TreMs. To standardise samples, trees with a dbh of <7 cm were removed from the Uholka sample. Finally, the individual *Fagus* trees were used as observation units. Hence, the two species groups were large enough to test with glms and estimate of the confidence bands for most of the dependent variables. The differences in the abundances of TreM types between the two tree species were identified by fitting a generalised linear mixed model (glmer) with a binomial distribution in lme4 [46] and in a multiple post-hoc comparison using the function glht in multcomp [48]. Potential differences in the dynamic of TreMs between the two *Fagus* species were determined by applying the Weibull model as recently developed for TreM modelling. This approach allowed modelling of the cumulative distribution, hazard rate function, and probability density function [17].

The Weibull model can be expressed as

$$F(d, \lambda, k) = 1 - e^{-(\lambda d)^k}, \quad (1)$$

and the terms of the equation are defined as follows:

F is the cumulative distribution and corresponds to the probability that the first TreM appeared before the tree reached its actual dbh. It was calibrated on the data (for a given dbh, F corresponds to the proportion of trees with at least one TreM).

h is the hazard rate function and corresponds to the probability that a tree has no TreMs at dbh D but will acquire its first TreM when it reaches D + dD. Although h cannot be calibrated directly on the data, it can be deduced from F.

f is the probability density function corresponding to the probability of any tree acquiring its first TreM at a dbh between D and D + dD. The difference between f and h is that, in the former, whether the tree will have a TreM at dbh D is unknown; for h, the fact that the tree had no TreM at D is known. f cannot be calibrated directly on the data but can be deduced from F.

The notation used in this study was a slight modification of that of Courbaud et al. [20]. Thus, λ as used herein corresponds to $1/\lambda$ used by those authors. It was changed for our study because, in the model calibration process, this resulted in better sampling of prior λ values. Gamma prior distributions were used for λ and k. The MCMC calibration process was based on 50,000 iterations. A satisfactory model calibration was indicated by Rhat values slightly >1.

3. Results

The diameter range of beech in Uholka and Hyrcanian forests was similar, but the mean of the latter species was higher due to the larger number of individuals in the Uholka Forest with a dbh of <20 cm (Table 1, Figure S2). More TreMs were found in Hyrcanian beech trees (100 TreM trees/ha) than in Uholka beech trees considering all trees >7 cm dbh, but also trees >20 cm dbh (Table 1). However, the mean number of TreMs per TreM-bearing tree was similar in the two species.

Table 1. Summary of the comparisons of tree-related microhabitats (TreMs) borne by *Fagus sylvatica* and *Fagus orientalis* in primeval forests in Ukraine and Iran, respectively. *p*-values are based on a post-hoc test of a binomial model that included all inspected beech trees. Significant larger values are shown in bold. dbh: mean diameter at breast height, Fo: *F. orientalis* Lipsky, Fs: *Fagus sylvatica* L.

	Fo Iran	Fs Ukraine	
Total investigated area	2.5 ha	9.0 ha	
Investigated admixed tree species (<i>n</i>)	19	114	
Investigated <i>Fagus</i> trees ≥ 7 cm	405	2251	
Mean (min, max) dbh of <i>Fagus</i> trees	44.3 (7–139)	32.3 (7–129)	
Percentage of TreM-bearing trees ≥ 7 cm	60%	31%	
Percentage of TreM-bearing trees ≥ 20 cm	78%	60%	
TreM richness per TreM-bearing tree for 11	2.15 (1.63)	2.04 (1.51)	
TreM subgroups (all 47 TreM types)			
TreM density/ha			<i>p</i> -value
• Woodpecker cavity	3.20	0.89	<i>p</i> < 0.001
• Rot hole	22.80	8.89	<i>p</i> < 0.001
• Dendrotelm	4.00	1.11	<i>p</i> < 0.001
• Root concavity	66.8	28.1	<i>p</i> < 0.001
• Bark loss	0.40	16.1	<i>p</i> = 0.024
• Exposed heartwood	4.80	10.1	n.s.
• Crack	0.00	9.33	n.s.
• Crown deadwood	30.0	9.33	<i>p</i> < 0.001
• Burr and canker	2.40	8.11	n.s.
• Polypore	2.00	12.9	n.s.
• Sap run	0.00	1.33	n.s.

The distribution of simplified TreM types was very different between the two areas, with larger proportions of *rot holes*, *root concavity* and *crown deadwood* in the Hyrcanian Forest compared with the Uholka. Conversely, beech in Uholka had larger proportions of *bark loss*, *cracks*, *burr and canker*, and *polypores* (for a distribution of detailed TreM categories see Table S3). The specific composition of TreMs in the Hyrcanian Forest was rather consistent among the three provinces (Table S4). Overall, TreM types were more equally distributed in the Uholka than in the Hyrcanian Forest (Figure 1). In the Hyrcanian Forest, there were significantly more TreMs per hectare for *woodpecker holes*, *rot hole*, *dendrotelm*, *root concavity*, and *crown deadwood* whereas in Uholka Forest only *bark loss* occurred significantly more often (Table 1).

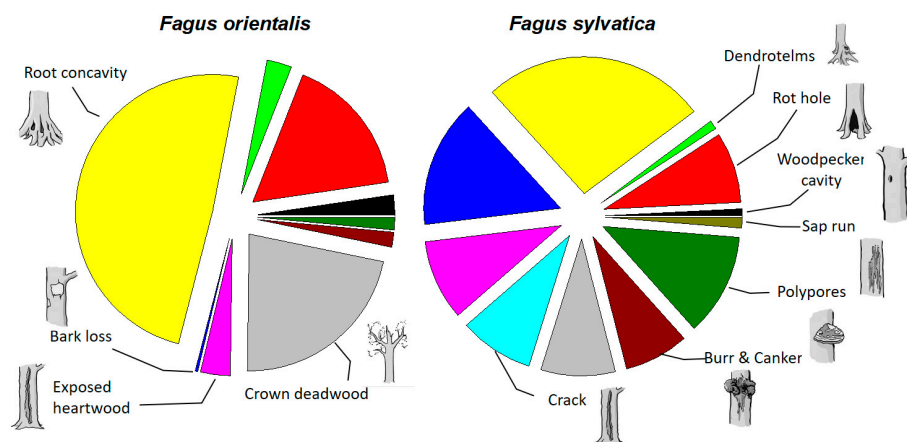


Figure 1. Distribution of the 11 TreM subgroups in Oriental beech and European beech from primeval forests in Iran and Ukraine, respectively. Colours used to indicate the TreMs are the same for the two beech species.

The Weibull modelling approach showed clear differences in the dynamics of both sampling groups. Overall, the probability of the appearance of the first TreM before the tree reached its actual dbh (cumulative probability) increased much faster in Oriental beech of the Hyrcanian Forest and resulted in an asymptotic curve, whereas the probability in European beech in Uholka increased continuously (Figure 2). The probability density was highest for both species at a dbh of about 30 cm but was twice as high for beech in the Hyrcanian Forest. The probability density was quite flat for beech in the Uholka Forest, indicating that trees here acquired their first TreM at a large range of sizes. It was quite narrow around a size of 30 cm for beech in the Hyrcanian Forest, indicating that most trees of this species acquired their first TreM when they had a dbh of about 30 cm.

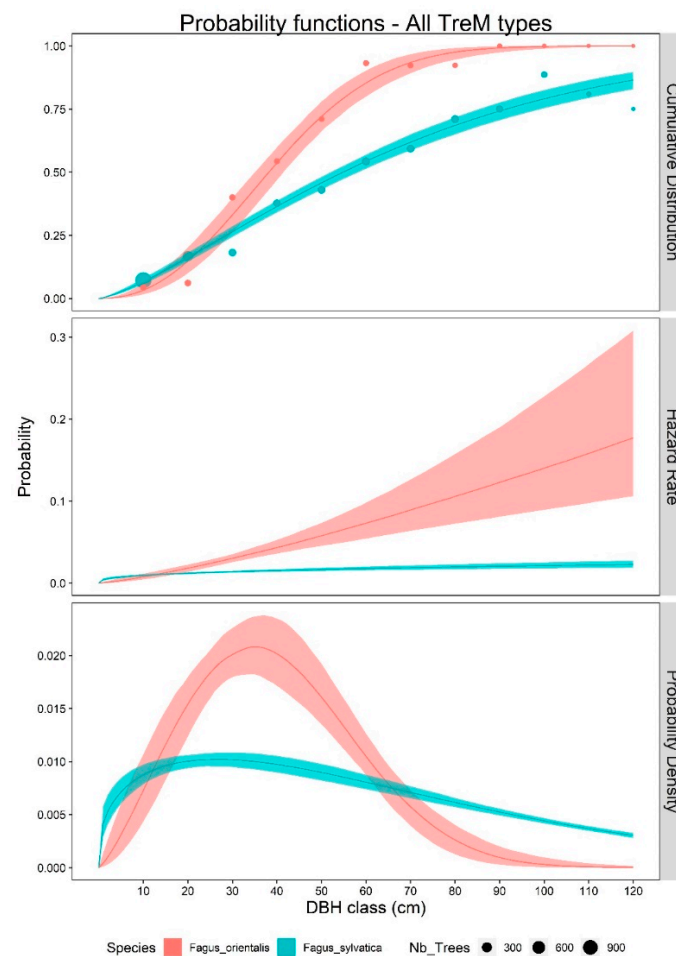


Figure 2. Relationships for the three models of TreM formation based on the 11 TreM subgroups. The cumulative distribution function shows the probability that at least one TreM will form on the tree before it reaches diameter d . The hazard function is defined as the rate of TreM formation at diameter d , conditional on the absence of TreMs until diameter d . The probability density function shows the diameter at which a tree acquires its first TreM. Confidence bands correspond to 95% predictive intervals. Non-overlapping confidence bands indicate significant differences between the two species.

The 11 simplified TreMs were modelled for areas (Figure 3), but for both, the model calibration was not satisfactory for exposed *heartwood*, and in the Hyrcanian Forest for *bark loss*, *exposed heartwood*, *cracks*, and *sap run*. For the models with a satisfactory calibration, the non-overlapping confidence intervals of *woodpecker holes*, *crown deadwood*, *root concavity*, and *rot holes* increased more rapidly in the Oriental beech of the Hyrcanian Forest, and those of *burr and canker* and *polypores* in European beech of the Uholka Forest.

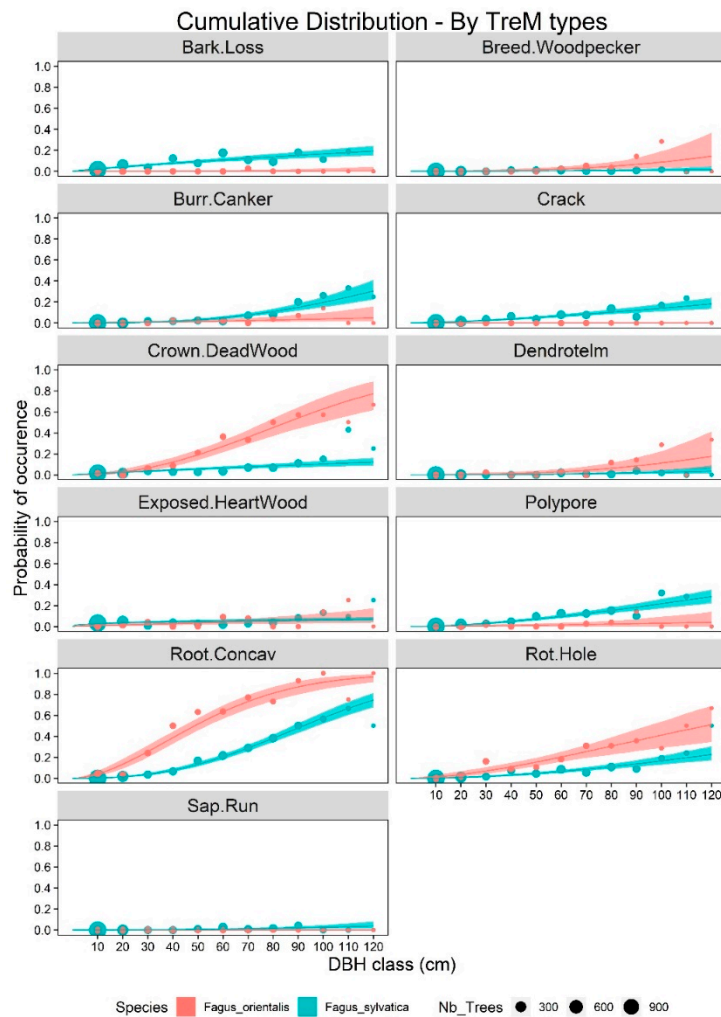


Figure 3. The cumulative distribution function for single TreM subgroups. Confidence bands correspond to 95% predictive intervals. Non-overlapping confidence bands indicate significant differences between the two species.

4. Discussion

Our comparison of Oriental beech and European beech in the two world heritage sites, the Hyrcanian Forest and Carpathian beech forests, respectively, revealed a number of significant differences in the TreMs of the two species. First, the TreM composition was very different, with high proportion of *rot holes*, *root buttress concavities*, and *crown deadwood* in Oriental beech and a more even distribution of the different TreM types in European beech. The two species also differed significantly in terms of the number of specific TreM types per hectare. Second, for all TreMs, their development was much faster in Oriental beech than in European beech. However, before these differences and their implications for the occurrence of endemic species can be discussed, the limitations of the two datasets must be pointed out. Thus, in the Ukraine, only one stand was sampled, whereas in Iran numerous plots were sampled but the total area was smaller (2.5 ha vs. 9 ha in Uholka). Moreover, the Ukrainian forest had a larger number of small trees (Figure S2). Whether the differences between the study sites affected our results and conclusions is unclear. In addition, it should be noted that our dataset did not allow testing for differences between the two species, because of a lack in spatial replicates in the Ukraine forest. Nonetheless, the number of individual species sampled was sufficient to estimate formation functions of TreMs and to test for differences in the composition between the two groups based on single trees. The difference in total numbers of trees and of small trees in particular was unlikely to have distorted our findings to any great extent, because Weibull functions are calculated on the basis of standardised

dbh values, and small trees bearing fewer TreMs had little effect on the overall TreM composition. The main challenge is that large primeval forests are very rare and therefore so are data from these forests. In the following sections, we discuss potential explanations for our findings while keeping in mind the limitations in our study's design.

4.1. TreM Variation Due to Tree Species

Because studies of TreM are relatively new, in contrast to those of deadwood, little is known about the differences in TreM types between forests, in forests differing in their management type (production forests vs. unmanaged or primeval forests), or in different tree species [12,20]. Studies in France have shown a difference in the number and composition of TreMs in beech, oak, fir, and spruce [12,20]. The focus of the present study was two very closely related and morphologically similar tree species that evolved distinctly in two widely separated locations beginning about 8.7 Ma ago [28]. Most of the TreMs examined in our simplified approach were saproxylic, such as some types of decaying wood, or might be a starting point for saproxylic habitats, such as some dendrotelms and some root-buttress concavities. Hence, the observed differences in the TreMs may have been a function of the tree species or of ecophysiological differences between the beech trees in the Uholka and Hyrcanian forests [49,50]. Different ecophysiological adaptations, such as drought tolerance, of beech trees in the two study areas could lead to differences in the amount of crown deadwood [49]. Moreover, tree species differ in their growth dynamics and decay rates, both of which are reflected in the physical structure of the trees and the chemical composition of their wood compounds [51]. Kahl et al. [52] showed significant differences in the decay rates of 13 tree species growing in Central Europe, including European beech but without genus replicates (each genus was represented only by one tree species). The decay rate of the next closest relative, *Quercus petraea* (Matt.) Liebl., was clearly lower. That same study attributed differences in the decay rates of different tree species to species-specific chemical/physical variations in laccase/endocellulase expression, the occurrence of heartwood, the wood ray height, and the log-specific richness of saproxylic beetles and fungi [52]. Hence, differences in the chemical and physical parameters of different tree species may affect the decay rates of the trees and the formation of saproxylic TreMs, even in two closely related *Fagus* species. However, this aspect has not been well studied. Another indirect effect of the tree species may be colonisation by different fungi. Heilmann-Claussen et al. [53] investigated the fungal communities of many tree species, including European beech, and showed clear differences in their composition, mostly between gymno- and angiosperms and weaker relationships at lower taxonomic levels. Similarly, an experimental study of fungal communities revealed a strong host specificity [51]. The authors found that European beech shared more species with the genus *Betula* than with more closely related broadleaves. The host fidelity of fungi is largely independent of microclimate conditions, as recently demonstrated [51]. It can therefore be assumed that the observed patterns in host fidelity are also relevant for the deadwood attached to living trees, for example, *crown deadwood* or *exposed heartwood*. On the other hand, Fo and Fs are much more similar than any of the species investigated in previous studies. Furthermore, although we did not compare the fungi associated with Fo and Fs, our field investigations of the wood-inhabiting fungi of Iran revealed that most of the fungi known from European beech are also present in the fungal communities of Oriental beech, including *Fomes fomentarius* (L.), the principal decomposer of *Fagus* wood. However, whether *F. fomentarius* is as predominant a parasite on living Oriental beech as it is on European beech is unclear.

A further possible reason for the differences in the rate of TreM formation in Fo and Fs is the tree growth rate, as faster tree growth might accelerate TreM formation. However, this would not explain the different curves, because TreM development was standardised to dbh in all models and tree growth conditions in the investigated area of Uholka Forest were suitable for the growth of beech.

4.2. Trem Variation Due to the Environment

Alternatively, our findings can be explained by environmental differences between the two study sites, especially the difference in climate. The Hyrcanian Forest is warmer and more humid than the Carpathian forests. Thus, in the former both the growth of individual trees and the success of fungal attacks after wounding should be increased. This explanation is supported by personal observations in our sampling plots while we gathered tree cores. Indeed, to reconstruct the age of the plots, we drilled the largest living tree without a visible TreM per plot. Although not visible on the outside, >90% of the tree's trunk drilled was rotten inside and showed accelerated decay due to fungi.

On a tree per hectare basis, Oriental beech was characterised by many more *woodpecker holes*, *root concavities*, *rot holes*, and *crown deadwood* than determined in European beech. This pattern was robust across provinces in Iran. This may have been a species-specific feature but also independent thereof. Woodpeckers in beech forests attack rotten heartwood or even initiate a fungal infection [54]. Fungal effects might also be promoted by a large number of *rot holes*, whose development in Oriental beech starts close to the ground rather than from debarked areas of the tree, as observed in European beech. Hence, most *rot holes* in Oriental beech are connected to the soil, which would explain the generally more decayed trunk status of the larger Oriental beech trees in our study. Rotting occurring close to the ground may be a consequence of the environmental effects of run off, which together with stones on the nearby ground contributes to the formation of root buttress cavities. This is supported by recent findings of Asbeck et al. [19]. They found a clear effect of elevation in the Black Forest region in Germany on elevated *root buttress cavities* in beech, fir, and spruce forests. They interpret this because of higher rock falls, soil movements, and tree swaying in steeper slopes of higher elevations, an explanation that would fit very well with our results, with *Fagus orientalis* growing in Iran more in steeper slopes of higher elevations. Thus, our results of more root buttress cavities seems more likely an effect of the environment than of tree species. However, whether the difference is species-specific or environmentally driven remains to be further clarified in stratified studies of tree-related microhabitats in both beech species under different topographies. Regarding the increase in crown deadwood, the most plausible explanation again might be the accelerated decay inside the largest trees, favoured by the humid climate. Rotting within the tree, the huge crowns of Oriental beech and the heavy autumn snowfall that is common in the Hyrcanian forest could together result in broken crown parts.

Courbaud et al. [17] compared the development of TreMs in European beech and silver fir (*Abies alba* Miller) in stands in the Pyrenees that had not been managed for the last 100 years. Hence, a TreM curve similar to that resulting from European beech in the Carpathians could be reasonably expected. However, the curves obtained in our study and those reported by Courbaud et al. [17] did not match. Furthermore, the curve of TreM development of European beech in the Pyrenees more closely resembled that of silver fir from the same site than the curve of European beech in the Carpathians; it was also more similar to the curve of Oriental beech. In a same way, Winter et al. [55] compared the probability of TreMs as a function of tree diameter in European beech and in Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) from Germany and the United States. In addition to the absence of a consistent tree species-specific pattern, the difference between trees from the United States vs. those from Germany was more important than the tree species, despite the comparison of a broadleaf with a conifer. These results concerning TreMs in different species and regions point to the environment as a more important determinant of TreM formation than the tree species itself.

4.3. Are Tree-Related Microhabitats Critical for Endemic Saproxylics?

An understanding of the importance of specific microhabitats for biodiversity requires studies of their communities. Möller [13] extensively described the link between microhabitats and >1000 insect species. In Iran, such studies are lacking, despite the high diversity of threatened and endemic saproxylic species [37]. In this section, we discuss the specific composition of TreMs in the Hyrcanian Forest in light of the habitat requirements of rare old-growth indicator species and endemic saproxylic beetles in the forest. The endemic elaterid species *Limoniscus wittmeri* Chassain is a

close relative of *Limoniscus violaceus* Müller, an inhabitant of base rot holes in Europe [56]. However, *L. violaceus* is extinct in most parts of Europe, such that in the areas where it still persists it is now protected by an EU habitat directive. Although rot holes have become rare structures in the majority of European forests, they are common in the primeval forests of the Ukraine (≈ 9 per ha) and abundant in the primeval forests of Oriental beech in Iran (≈ 23 per ha). The presence of *L. wittmeri* in the same forests was recently reported [46] and highlights the importance of these primeval forests and their abundance of rotted out cavities. Two other cerambycid species, *Parandra caspica* Ménétriés and *Paraclytus raddei* (Ganglbauer), are endemic to the Hyrcanian Forest, where they occur at high densities. Both species regularly use the rot holes of beech for their development and thus indicate the high quality of the Hyrcanian's primeval forests in terms of tree cavities [34,37]. Another specific TreM in the Hyrcanian Forest is the deadwood of tree crowns. In shady beech forests, this TreM provides a relatively rare, dry, and sun-exposed habitat. The abundance of crown deadwood may explain the regular occurrence of the jewel beetle *Dicerca fritilla* in these beech forests.

4.4. Implications for Nature Conservation in Broadleaf Forests

Current management policies for commercial forests in Europe include the promotion of biodiversity by incorporating natural features into the forests [42,43,57], such as the retention of deadwood as well as TreM-bearing trees. For the latter, targets are typically 5–10 trees per hectare [19]. In the reference forests of our study, the number of TreM-bearing trees was much higher. This difference might explain the rarity of many forest specialist species in Europe's managed forests and their restriction to small areas containing large numbers of veteran trees, as well as an abundance of deadwood [58]. Our finding of site- and region-specific differences in TreM dynamics and composition in both World Heritage areas complements earlier reports of beech forest diversity. Moreover, in the design of measures directed at conserving the overall diversity in beech forests, this study supports a research approach based on regions that differ in their soil, climate, and tree mixtures, rather than on different local stands within a single region [45,59].

5. Conclusions

A comparison of TreMs in primeval forests of European beech in the Carpathians and of Oriental beech in the Hyrcanian Forests of Iran revealed characteristics of both forest types that can be used as a reference for near-to-nature or retention forestry. However, an understanding of the mechanisms underlying the different patterns of TreM formation and composition will require standardised data from the same tree species in different environments. Our study did not allow a determination of the role played by tree species in explaining the observed differences, as it included only two primeval forest regions. Globally, there are few remaining temperate primeval forests in Europe, which hampers the inclusion of replicates in studies of broadleaf forests. Further investigations of Oriental beech in the Caucasus region or Azerbaijan and of TreMs in different beech forests of the Alps and Carpathians will contribute to elucidating the mechanisms underlying the regional differences in TreMs. Insights might also be obtained from studies of fungi, as the most important decomposer group in deadwood, such as by standardised sampling and sequencing. Nevertheless, our results add to those obtained in biodiversity research in the Hyrcanian Forest, which showed that the Oriental beech forests are unique not only because of their endemic tree species (e.g., *Parrotia persica*), diversity of endemic herbs [33], and saproxylic beetles [37], as well as the presence of the Persian leopard [60], but also in terms of their TreM profile.

Supplementary Materials: The following are available online at <http://www.mdpi.com/1999-4907/11/2/144/s1>, Figure S1: pictures from all Iranian plots, Figure S2: dbh distribution in both study areas, Table S1: Overview of Iranian plots, Table S2: classification of TreMs, Table S3: TreMs 47 types, Table S4: TreM composition in different provinces of Iran.

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