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Management Intensity and Forest Successional Stages as Significant Determinants of Small Mammal Communities in a Lowland Floodplain Forest

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Abstract: The conversion of forests from complex natural ecosystems to simplified commercial woodlands is one of the major causes of biodiversity loss. To maintain biodiversity, we need to understand how current management practices influence forest ecosystems. We studied the effects of forest successional stage and management intensity on the abundance, species richness, and assemblage composition of small mammals. Our results show that management intensity significantly contributes to reducing the number of species after clearcutting. We revealed that intensively managed clearings can make the dispersal or foraging activity of small mammals difficult and hence negatively influence their abundance and species richness. The significantly higher species richness of small mammal species was recorded within more extensively rather than intensively managed clearings. In contrast, we did not observe significant changes in species richness and abundance after intensive management in old-growth forests. Species *Clethrionomys glareolus* and *Apodemus flavicollis* reached the greatest abundance in old-growth forest patches. On the other hand, *Microtus arvalis* and *Microtus subterraneus* were species mainly associated with the successionally youngest forest stands. Our analysis suggests that intensive management interventions (i.e., vegetation destruction by pesticides and wood debris removal by soil milling) in clearings produce unhostile environments for majority of the small mammal species.

Keywords: rodents; insectivores; oak woodlands; forest management; species richness; forest age

1. Introduction

Nowadays, 34% of the Czech Republic area is covered by woodland of which most of the area is occupied by commercial forests [1]. Commercial forests are managed by different types of harvesting practices. The dominant forest management practice is using clearcutting as a logging technique, which is often followed by mechanical site preparation presented by soil milling (especially in lowland floodplain forests). Clearcutting also generates forest stands of different ages, introducing a mosaic of spatially divided stands to a landscape, which ranges from more open habitats to strongly shaded habitats (i.e., forest cycling). Only a small proportion of commercial forests are covered by old-growth forest stands [2]. A number of studies have demonstrated that even commercial forests provide good conditions for various species of organisms and thus support biodiversity [3–6]. The high number of species in managed commercial forests is largely due to the between site variations [7,8]. On the other hand, a number of studies have demonstrated that intensively managed forest plantations negatively influence the diversity of carabids [9,10], birds [11,12], moths [13], and plants [14]. The impact of commercial forests can also be seen in the composition and abundance of individual species [4,5,15]. For instance, most of the species of litter-dwelling arthropods in open habitats are small macropterous species with good dispersal abilities. On the other hand, closed canopy forest sites have a higher proportion of large carnivorous species [4,15,16].

Retaining the forest biodiversity is one of the main objectives of sustainable forestry [17]. The topic of sustainable forestry should be reflected mostly in the management of European forests because temperate biomes are found to be generally more disturbed than tropical biomes [18]. Central Europe's temperate forests have been identified as the ecosystems most impacted by human activity, e.g., only 0.2% of the Central European deciduous forests remain in a relatively natural state [18]. It is generally accepted that the maintaining high biodiversity of forests is important for sustaining and promoting ecosystem services in human communities, such as carbon storage, water retention, timber, recreation, and nutrient cycling [19]. Another result of greater biodiversity is the promotion of forest resistance and resilience to human-induced pressures such as global climate change [20]. This natural capacity to mitigate environmental changes is mainly caused by a sufficient species pool with important roles in ecosystem processes, such as pollinators, seed dispersals, predators, herbivores, and decomposers [20].

Forest heterogeneity is a key factor influencing species diversity and composition [21–23]. Heterogeneity can be manifested on spatially different scales [24]. On a landscape scale, commercial forests planted in stands of different ages generate a heterogeneous mosaic of spatially divided stands [4,25]. On a stand scale, forests can be influenced by either the complexity of vertical vegetation structure or by the formation of different microhabitats [22,23]. The main difference between commercial and natural forests is that clearcutting significantly decrease forest complexity, mainly at the local scale, because it removes all live and dead wood and gets rid of the herb layer by applying herbicides. On the other hand, biodiversity can be sustained by forest cycling, maintaining spatial heterogeneity on the landscape scale [3–5].

Overall, it is well documented that management type and forest stand age are important factors influencing biodiversity and community structure in commercial and noncommercial forests [25–28]. On the other hand, the combined effect of forest management intensity and stand age has only been sporadically tested on small mammals [29]. Thus, this paper reports the effect of management intensity and forest successional stage on small mammal assemblage.

In this study, we mainly focus on comparing assemblages and the diversity of small mammals in commercial forests at varying age stages and management. We hypothesize that: (i) an intensive type of management in the form of mechanical soil preparation will decrease the biodiversity of forest clearings; (ii) an intensive type of management in the form of cutting understory vegetation will decrease biodiversity in the old-growth forests, and (iii) differently old stands will be invaded by different assemblages of small mammals.

2. Materials and Methods

2.1. Study Area

The study area is situated in the South Moravian Region of the Czech Republic along the alluvium of the lower reach of the River Svratka in the vicinity of the villages of Vranovice and Ivaň (48°57′57 N, 16°36′23 E). The floodplain forests in the alluvium of the lower reach of the River Svratka are important floodplain forest complexes in the Czech Republic, providing heterogeneous conditions in an otherwise unified landscape of southern Moravia [14]. The largest part of the monitored area (25 km^2) is covered by hardwood floodplain forest vegetation, *Fraxino-Quercion roboris*, often with altered tree layers [30]. The study area is dominated mostly by forest plantations of oak *Quercus robur* L. The other plantations are ash *Fraxinus excelsior* L., hornbeam *Carpinus betulus* L., black alder *Alnus glutinosa* L., and black walnut *Juglans nigra* L. The plantations are of various ages, from young to matured. All studied locations were commercial forests, afforested with at least 90% representation of *Quercus robur* used for timber harvesting, except extensive (natural) old-growth forest stands, where logging activities were forbidden. The geological substrate is characterized as black soils on loess. The territory belongs to the Thermophyticum phytogeographical region [31]. The average annual temperature is 9.2 °C and the average annual rainfall is 550 mm. Its surrounding landscape is composed mainly by agriculture fields (cereals, sunflowers, oil seed rape).

2.2. Study Design and Sampling

Study sites were divided into 6 age categories and two management type categories. Age categories were as follows: (a) 1 year, (b) 3 years, (c) 10 years, (d) 20 years, (e) 60 years, (f) 120 years. Two types of management of forest clearings (1 year) and old-growth forest (120 years) were recognized: (a) Intensive (commercial) and (b) extensive (natural). There was herbicide application and wide-area mechanical soil preparation (e.g., soil milling, stump removal) on intensively managed clearings. Extensive clearings were without soil preparation and herbicide application. There was only hand-operated mowing of unwanted vegetation during the summer. Intensive (commercial forest, artificially planted) old-growth forests were characterized by a dominant representation of *Quercus robur*, stands were more open due to logging activities, and the habitat structure was homogeneous. On the other hand, extensive (natural) old-growth forests were highly heterogeneous, with various tree species (naturally regenerated) typical for floodplain forests. The logging operations were forbidden in these habitats.

The study sites of various ages and management intensity were distributed randomly in the study area, with a mean distance between sites (stands) of 625 m (SD = 455,82; range = 280–1850 m). All study sites (forest stands) were of similar size (1 ha). Every age category/management type had three spatial replications, totaling 24 study sites.

The sampling was conducted during the vegetation period of 2016 using 2 different collecting methods at each study site. First, trapping by snaps was carried out during spring (3–6 May) and autumn (2–5 November). Snap traps were laid in line of 20 traps each, approximately 3 m apart such that the total length of each line was about 60 m across the center of each study site. Traps were baited with peanut butter and exposed for 3 successive nights. They were checked once per day in the morning and the bait was replaced if necessary (when eaten away or washed away by precipitation). Secondly, pitfall traps (plastic 500 mL jars, 9 cm in diameter, depth 15 cm), filled up to one-third with a solution of 4% formaldehyde with a few drops of detergent as a killing and preserving agent, were used. In the center of each study site, 5 pitfall traps placed 10 m apart such that the total length of each line was about 50 m. The traps were installed on 10 April and deactivated on 27 September. Traps were emptied monthly. After collecting, the samples were preserved in 70% ethanol. All aspects of trapping complied with EU Council Directive 86/609/EEC on experimental use of animals.

2.3. Evaluation of Environmental Characteristics

In order to assess the influence of forest management on the environmental characteristics and small mammal communities, we measured 5 environmental variables during July 2016: (a) Herbaceous cover, (b) shrub cover, (c) height of litter, (d) amount of woody debris, and (e) canopy openness. The herbaceous and shrub coverage was estimated by eye as a percentage proportion within five 5 × 5 m squares randomly placed within each of the studied site. Woody debris was divided into fine woody debris (FWD) of between 1–10 cm in diameter and coarse woody debris (CWD) of over 10 cm in diameter [32]. FWD was present as fine and thicker twigs in a relatively thin layer on the surface of the soil. CWD was represented by tree stumps, fallen trunks, and thick branches covering the surface of the soil. The quantity on the plot was estimated as the percentage cover on the soil surface within five 5 × 5 m squares randomly placed within each of the studied sites. The height of litter was measured as the thickness from 5 random samples per study site in centimeters using a ruler. The litter depth of each site was determined as the mean of these 5 samples. Canopy openness was classified for each study site using hemispherical images captured 1 meter above the ground for 1 day to rule out seasonal effects (14 July 2016). These images were analyzed and the relative proportion of canopy openness was estimated using the software Gap Light Analyser 2.0 [33].

2.4. Statistical Analyses

2.4.1. Regression Analysis

To analyze the effect of the site preparation after clearcutting (extensive/intensive) in young stands and the natural regeneration/artificial thinning in old-growth forest on small mammal species richness and abundance, a generalized linear mixed-effects model (GLMM) with negative binomial error distribution was used [34]. Based on the experimental design (at each site, samples were collected by repeated measures in time), a mixed model was designed as a random intercept and slope model in which locality was included as the random intercept effect and month was included as the random slope effect. The partial effect of each explanatory variable was tested with the likelihood ratio (LR) analysis of deviance using a chi-square statistic. The likelihood ratio analysis tested whether the deviance of the full model significantly increased after each explanatory variable was excluded from the model. Data were analyzed in the R program [35].

2.4.2. Multivariate Data Analysis

The assemblage change of the small mammal communities in relation to management intensity in old-growth forests, soil preparation practices after clearcutting, and forest successional stages were visualized by partial canonical correspondence analysis (pCCA) with the study month as covariable. We set the month as covariable to eliminate possible systematic or successional change in species composition that would take place on all plots regardless of treatment. In addition, small mammals were sampled sequentially from May to November. Therefore, we maintained the time autocorrelation of individual records using cyclic shifts. The abundances of each species were transformed by a decimal logarithm. The significance of the canonical axis was tested with a restricted Monte Carlo permutation test for the time series with 2000 permutations. To test the effect of forest characteristics on small mammal species composition, locality and successional age were used as covariables. It this case, randomization was restricted by randomizing time records within each locality separately using cyclic shifts. The significance of each explanatory variable was then tested by the forward selection procedure. All ordination analyses were conducted by the statistical software CANOCO, v. 5 [36].

3. Results

3.1. Species Richness and Abundance

A total of 771 individuals belonging to 10 different species were collected (Table 1). Rodents were the most abundant group, comprising 76% of the total number of individuals collected, with the dominant species being *Microtus arvalis*. Insectivora were the other abundant group, which encompassed 24% of the total number of individuals collected, with the dominant species being *Sorex minutus*. Overall, three different families were presented: Soricidae, Muridae, and Cricetidae. The number of species significantly differed only between intensively and extensively managed clearings (glmmANOVA, LRT = 3.947, p = 0.0469). The plots with intensively prepared soil after clearcutting significantly decreased the number of species in comparison to extensively managed plots after clearcutting (Figure 1). Moreover, the small mammal species richness and abundance were not significantly different among the chronosequences of forest stands in different stages of succession or between intensively and extensively managed old-growth forests. The analysis of the species response curve also revealed that only one out of ten sampled species had significantly higher predicted abundance in the plots with intensively managed clearings. On the other hand, two species had significantly higher predicted abundance in intensively managed old-age forest stands (Table 1).

Table 1. Summary table of the analysis of the species response curve visualizing species responses to an environmental gradient (i.e., management intensity) on the first ordination axis. Species response curves were fitted by generalized linear models with Poisson error distribution and a control for overdispersion. Positive scores of species among old-growth forest patches represent a positive association with extensive forest management and vice versa. Positive scores of species among clearing patches represent a positive association with intensive forest management and vice versa.

Species	Abundance		Scores on the First CCA Axis	Explained Variance	F	*p*
	Intensive	Extensive				
Old-Growth Forest						
Apodemus flavicollis	35	9	−0.216	16.4	5.2	<0.01
Apodemus sylvaticus	2	7	0.987	16.6	3.5	0.037
Clethrionomys glareolus	44	29	0.016	2.8	0.84	0.599
Crocidura leucodon	0	6	1.062	32.3	9.0	<0.001
Microtus arvalis	8	3	−0.325	5.4	1.3	0.288
Sorex araneus	5	3	−0.078	2.4	0.43	0.651
Sorex minutus	14	11	−0.109	9.0	3.2	0.047
Clearings						
Apodemus flavicollis	6	14	0.041	0.1	0.03	0.852
Apodemus sylvaticus	46	11	1.092	18.3	12.6	<0.001
Clethrionomys glareolus	0	12	−0.771	35.1	21.4	<0.001
Crocidura leucodon	1	18	−0.695	25.2	0.63	0.571
Micromys minutus	0	2	−0.262	1.8	0.32	0.572
Microtus arvalis	27	103	−0.095	3.2	3.7	0.056
Microtus subteraneus	1	3	0.157	0	0.008	0.928
Neomys anomalus	0	3	−0.668	14.1	5.2	0.024
Sorex araneus	0	27	−0.366	7.3	5.7	0.018
Sorex minutus	1	34	−0.501	12.8	11.2	<0.01

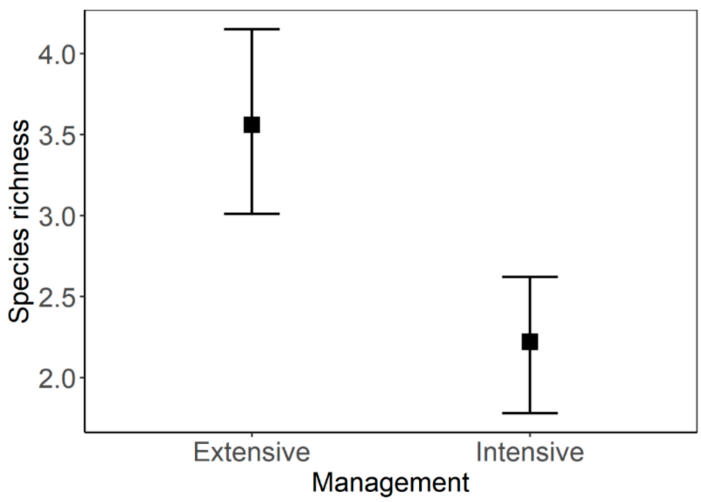

Figure 1. Effect of extensive (without soil preparation) and intensive (mechanical soil preparation) site preparation after clearcutting on small mammal species richness. Error bars represent ± 95% confidence interval.

3.2. Species Assemblage

The small rodent assemblages significantly differed between intensively and extensively soil preparation of clearings (pseudo-F = 8.6, p = 0.004) (Figure 2a). After partialing out the effects of covariables, the management intensity explained 6.72% of the variance of the species data. Assemblages in adult forest stands also differed between intensive and extensive forest management (pseudo-F = 2.6, p = 0.021) (Figure 2b). After partialing out the effects of covariables, the management intensity in old-growth forest explained 2.07% of the variance of the species data. Based on the forest characteristics passively projected into the ordination space, extensively managed adult forests (i.e., naturally regenerated) were characterized by a high amount of litter, low canopy openness, and high shrub coverage, while intensively managed old forests were characterized by less shady conditions and a low amount of litter (Figure 2b). Among the measured forest properties, the percentage of woody debris was found to be the most influential for small mammal assemblages (pseudo-F = 2.4, p = 0.002) and explained 1.6% of the variance of the species data. We detected the highest abundances of the Soricidae family in the plots with high abundances of fine woody debris (Figure 3). In addition, the CCA revealed difference between assemblages of small mammals in the forest stands under different successional stages (pseudo-F = 4.0, p = 0.004) (Figure 4). After partialing out the effects of covariables, the successional stage of the forest stands explained 6.87% of the variance of the species data. Species related to successionally youngest plots were typical ruderal open habitat species such as *Microtus arvalis* and *Microtus subterraneus*. On the other hand, species that occurred in the old stands represent typical forest species, *Apodemus flavicollis* and *Clethrionomys glareolus*.

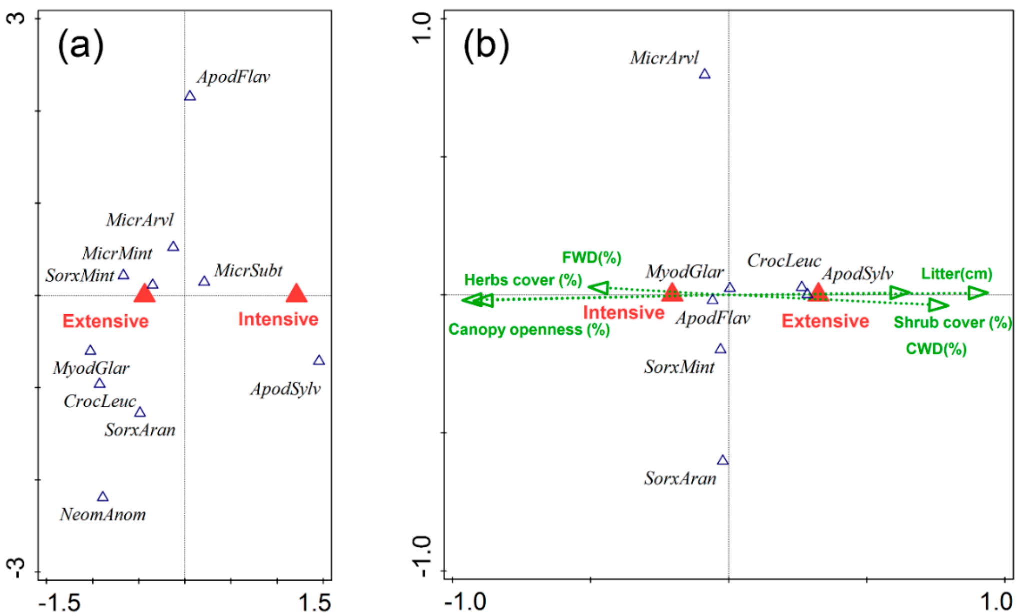

Figure 2. Partial canonical correspondence analysis biplot with the study month as a covariable showing (**a**) the change in small mammal assemblages at intensive (mechanical soil preparation after clearcutting) and extensive (without soil preparation) study plots; (**b**) differences within small mammal assemblages according to different management intensity (intensive—artificial thinning; extensive—natural regeneration) in old-growth forest stands. Forest characteristic were passively projected onto the ordination diagram. *ApodFlav*, *Apodemus flavicollis*; *ApodSylv*, *Apodemus sylvaticus*; *MicrSubt*, *Microtus subterraneus*; *MicrArvl*, *Microtus arvalis*; *MicrMint*, *Micromys minutus*; *MyodGlar*, *Clethrionomys glareolus*; *CrocLeuc*, *Crocidura leucodon*; *NeomAnom*, *Neomys anomalus*; *SorxAran*, *Sorex araneus*; *SorxMint*, *Sorex minutus*.

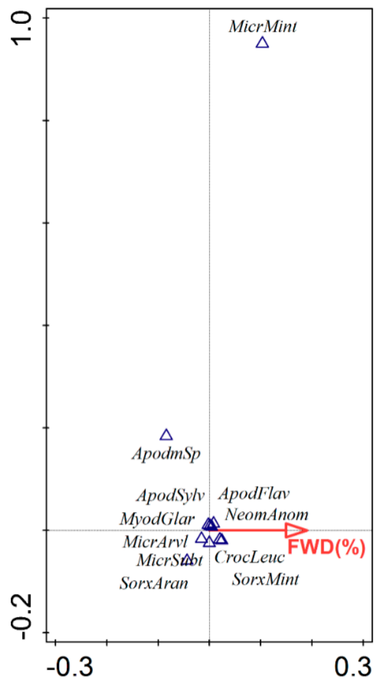

Figure 3. Partial canonical correspondence analysis biplot showing the effect of fine woody debris on small mammal species composition with the locality and successional age as a covariable. *ApodFlav*, *Apodemus flavicollis*; *ApodSylv*, *Apodemus sylvaticus*; *MicrSubt*, *Microtus subterraneus*; *MicrArvl*, *Microtus arvalis*; *MicrMint*, *Micromys minutus*; *MyodGlar*, *Clethrionomys glareolus*; *CrocLeuc*, *Crocidura leucodon*; *NeomAnom*, *Neomys anomalus*; *SorxAran*, *Sorex araneus*; *SorxMint*, *Sorex minutus*.

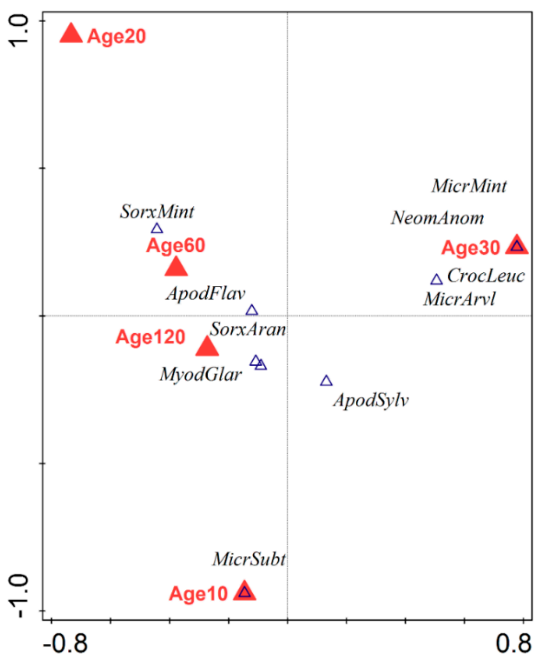

Figure 4. Partial canonical correspondence analysis biplot with the study month as a covariable showing the change in small mammal assemblages in relation to different forest successional stages. *ApodFlav*, *Apodemus flavicollis*; *ApodSylv*, *Apodemus sylvaticus*; *MicrSubt*, *Microtus subterraneus*; *MicrArvl*, *Microtus arvalis*; *MicrMint*, *Micromys minutus*; *MyodGlar*, *Clethrionomys glareolus*; *CrocLeuc*, *Crocidura leucodon*; *NeomAnom*, *Neomys anomalus*; *SorxAran*, *Sorex araneus*; *SorxMint*, *Sorex minutus*.

4. Discussion

In this study, we analyzed the effect of forest successional stage and management intensity on abundance, species richness, and assemblage composition of small mammals in lowland floodplain forest stands. We found evidence of a marked effect of mechanical soil preparation after clearcutting on species richness and assemblage composition. The majority of species reduced their abundance in response to intensively managed clearings. On the other hand, the opposite trend was observed in old-growth forest stands. Among the studied abiotic characteristics of the forest, we revealed that only fine woody debris significantly influenced small mammal composition. There was evidence that insectivorous mammal species have a tendency to forage in habitats with highly accumulated wood biomass.

4.1. Responses of Species Richness and Abundance to Forest Managements

We demonstrated that intensively managed forest clearings (i.e., mechanical soil preparation after clearcutting) had detrimental effects on the number of small mammal species. Our results are in contrast with works indicating only small effects or no effect of clearings on small mammal species richness or assembly composition [3,37]. The results of the meta-analysis also revealed that the species of small mammals increased in abundance after clearcutting [29]. We assume that vegetation destruction by pesticides and wood debris removal by soil milling are important factors leading to the loss of suitable habitats to find shelter, food, or nesting places. All insectivores and rodent species except *Apodemus sylvaticus* seemed to avoid intensively managed clearings. This is not so surprising, considering that *Apodemus sylvaticus* occurs more in open habitats and is a generalist with regard to habitat requirements, with wide ecological tolerances [38]. On the other hand, more species showed significant associations with intensively (i.e., thinning management applied) rather than extensively (i.e., naturally regenerated) managed adult forests. This could be explained by seed and plant biomass production, which is generally lower in shady than light forests [26,39,40].

Moreover, we did not observe a significant decrease in species richness and abundance during the chronosequence of different aged forest stands [41–43]. This could be explained by the small number of species we sampled and by the great ability of small mammals to migrate between forest stands of different successional stages [37]. Small mammals are characterized by intensive breeding with high litter production, population fluctuation, and very active foraging patterns [44,45]. These characteristics allow rapid reproduction and spread to the surrounding landscape with roughly equivalent environmental conditions.

4.2. Responses of Species Assemblage to Forest Managements

Small mammal assemblages significantly changed along the chronosequence of forest stands in different stages of succession. We therefore claim that forest stands with different successional stages create unique environmental conditions with the specific assemblage of small mammal species. Moreover, our result contradicts the assumption that the high forest is a less preferred habitat for *C. glareolus*, possibly due to its lack of food and scarce herb layer [39]. On the other hand, some authors have found that *C. glareolus* is positively affected by large, highly connected patches of old-growth forest [29,46,47]. It has been documented that *Clethrionomys glareolus* prefers forests with a thick herb layer and thin crown canopy [40]. We assume that *C. glareolus* may have great flexibility in food selection, which allows it, under certain circumstances, to dominantly colonize old-growth forests [48]. Another potential explanation why bank vole preferred old-growth forests is that some of the forest stands were intensively managed (i.e., artificial thinning) and an increased amount of light could have a positive effect on the herb layer. In addition, fine woody debris was the only environmental characteristic that significantly influenced small mammal assemblage. We observed that insectivorous mammal species had a tendency to forage in habitats with a high accumulation of wood biomass. It is well known that thick and heterogeneous layers of forest litter with presence of woody debris are colonized by a large number of invertebrates [49].

Results regarding the composition of small mammal assemblages in intensive and extensive managed forest stands showed significant differences. In old-growth forests, the abundance of *Apodemus flavicollis* and *Apodemus sylvaticus* showed significantly opposite patterns, which is likely related to their different ecological requirements [50]. *Apodemus flavicollis* was significantly associated with intensively managed old-growth forest characterized by increased light availability. Specific conditions of thinned forest stands are probably related to the large production of seeds, which are a major food source for *Apodemus flavicollis* [51]. To the contrary, higher abundance of *Apodemus sylvaticus* in extensive managed forests may be related to its lower specialization in feeding on tree seeds and its submissive position toward *Apodemus flavicollis* [39,52].

In forest clearings, the composition of assemblages significantly changed in response to intensive or extensive management. We also revealed that intensively managed clearings can make the dispersal or foraging activity difficult and hence significantly influence the species composition. Vegetation destruction by pesticides and wood debris removal by soil milling was of sufficient intensity to significantly negatively affect the abundance of majority of individual species in the assemblage. New assemblages formed after the disturbance were dominantly formed only by *Apodemus sylvaticus*, while the rest of the species showed a negative association with intensively managed clearings.

5. Conclusions

Our study showed that intensive management interventions in clearings significantly contribute to the decrease of species number and abundance in forest stands. Our results also suggest that, in some circumstances (i.e., mechanical site preparation presented by soil milling on a large area), intensively managed clearings may create a migration barrier for the most of small mammal species. Thus, we conclude that the soil preparation after clearcutting produces an unhostile environment for the majority of small mammal species and therefore active forest management, increasing habitat complexity (e.g., accumulation of dead wood or preservation of standing dead trees) in lowland floodplain forests is needed. We also suggest that some trees (i.e., nonvigorous low-quality trees) per hectare (at least 5–10 trees) should be retained at the stand level to mitigate the effects of timber harvesting on organisms [53].

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