

## Article

# Re-Inventories at Two Study Sites in the Oberpfalz (Bavaria, Germany): Increase in RWA Nests, Herb Biodiversity and Dead Wood in Sustainably Managed Forests

Gabriele M. Berberich <sup>1,\*</sup>  and Martin B. Berberich <sup>2</sup> <sup>1</sup> Wissenschaftlich-Technisches Redaktionsbüro Dr. Berberich, Am Plexer 7, D-50374 Ertstadt, Germany<sup>2</sup> IT-Consulting Berberich, Am Plexer 7, D-50374 Ertstadt, Germany; mb@berberichweb.com

\* Correspondence: gb@berberichweb.com

**Abstract:** A large-scale re-inventory of red wood ant (RWA; *Formica rufa*-group) nests and a comparative analysis of their presence/absence data was carried out for the first time in 2023 at two study sites in the Oberpfalz, NE Bavaria, Germany, to investigate the suspected decline of nests, their relationship with forestry aspects, and possible changes in spatial distribution due to tectonic activity (GeoBio-Interactions). We inventoried, in two sustainably managed forests, outstanding nest occurrences (5393 nests including 5276 active nests) and an increase of  $\approx 8\%$  over 4–7 years. Our results do not support claims that the number of nests in the Oberpfalz is in sharp decline. RWA preferred mature and medium–mature pine-dominated forests. Standing and downed dead wood did not negatively affect nests. The number of nests with woodpecker cavities and the diversity of the herb layer increased. Nests clusters in NW–SE direction suggest a strong interaction between nest distribution and active tectonics. Our (re-)inventory approach combined with the extensive photo database is a valuable tool for (a) monitoring the entire forest habitat including natural restocking, herb biodiversity, woodpecker cavities, and dead wood in, at, and around nests, and (b) identifying GeoBio-Interactions. Such an approach will lead to more realistic counts of RWA nests and provide scientific evidence of the current situation of nests occurrence. We suggest seven to eight years as an appropriate time interval for re-inventories.



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**Keywords:** re-inventory; red wood ants; dead wood; woodpecker; forest habitat; sustainably managed forests; tree age; tree species; natural restocking; GeoBio-Interactions; Erbendorfer fault line

## 1. Introduction

Global tectonic, magmatic, and geologic processes are essential drivers of biodiversity patterns in all ecosystems (e.g., [1,2]). The resulting type, structure, composition, thickness, and physicochemical properties of the bedrock influence the nutrient supply, water retention, plant growth, composition, and productivity of forests, one of the prevalent ecosystems on land. Understanding the tectonic and lithologic controls on ecology and biology is therefore of fundamental importance [3,4].

Forests are long-lived ecosystems with multiple functions: (a) highly important economic factor and raw material supplier for forest-based industries, (b) climate regulator, (c) protector against and moderator of natural hazards, (d) conservator of biodiversity, natural cycles, and provider of habitats for flora and fauna, and (e) provider of natural experiences and recreational areas for humans, e.g., [5,6]. However, forest ecosystems are threatened. Management (e.g., intensive use), as well as natural influences (e.g., climate change, loss of biodiversity and habitats), affect the ability of forests to recover after disturbances [7]. Habitat loss, invasive species or climate change have also been suggested to negatively affect insect diversity and promote species decline in forests [8,9]).

Sustainable forest management (SFM) aims to support the forest and the multifunctional forest sector to (a) secure and improve the growth and stability of forest stands,

(b) develop sustainable, economically, and ecologically balanced management practices, and (c) ensure the long-term integrity and biodiversity of forest ecosystems [5]. Two forestry aspects, dead wood (DW) and red wood ants (*Formica rufa*-group; hereafter RWA), are considered as indicators of sustainable forest management. Dead wood is an important habitat for a wide range of organisms and plays a key role in carbon, nutrient, and hydrological cycles, and influences ecosystem processes. In many managed forests, DW such as decaying standing or downed trees, roots, and branches are scarce due to their removal [10]. RWA are important forest species (e.g., [11]), related to, but not limited to, habitat biodiversity (e.g., [12]) and pest regulation (e.g., [13]). Furthermore, RWA are bioindicators of hidden active tectonic systems [14–19] and geogenic gases (“GeoBio-Interactions”), a prerequisite for their settlement [20–23]. Declines (e.g., [24,25]), but also population increases (e.g., [26,27]), have been reported for RWA. RWA are also considered endangered in Germany, although statistically sound long-term monitoring was discontinued in the 1980s [28,29]. Consequently, it is currently not possible to make any statements on the urgently needed conservation status of this species. To fill this knowledge gap, the two densely forested study sites (a) Münchsgrün (MG) and (b) Falkenberg (FB) in the tectonically active Oberpfalz (NE Bavaria, Germany) were re-investigated for the first time with respect to different forestry aspects and possible GeoBio-Interactions [14,18,30,31].

In this comparative analysis, not only was the number of RWA nests counted but the ecosystem around a RWA nest was also monitored and documented in a photo database [14,18,30]. We asked six interrelated questions: (1) Are presence/absence data of RWA nests comparable to the two previous inventories? (2) What is the influence of changing forest composition (related to, e.g., tree species, tree age, natural restocking, herb layer) on RWA nests? (3) Does the enrichment of dead wood (standing and/or downed trees, lying branches) in, on, and around a nest during SFM influence RWA nest settlements and nest growth? (4) Was the number of woodpecker cavities (WpC) created by predation on the entire nest surface different from previous inventories? (5) What influence do tectonic structures have on RWA nest distribution (GeoBio-Interactions)? (6) What are the best time intervals for re-inventories? A novel and key aspect of our approach is to evaluate the presence/absence data and the spatial distribution of RWA nests with previous inventories in order to test the postulated decline of RWA in the Oberpfalz region, taking into account the impact of sustainable forest management and increased seismic activity in this region.

## 2. Materials and Methods

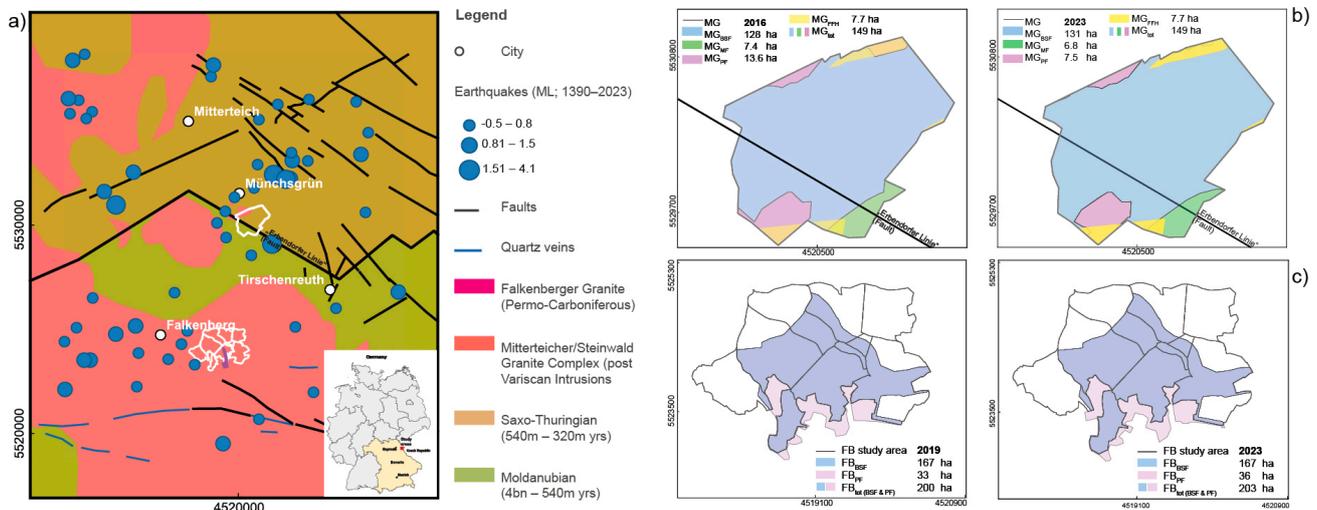
### 2.1. Location and Geologic Setting

Bavaria is one of the most densely forested states in Germany, with 2.56 million hectares accounting for one-third of its total area. The Bavarian State Forest (BSF) is the main forest owner in the two re-inventoried study sites MG and FB, both under the responsibility of the Waldsassen forest division; smaller shares belong to private owners (private forests; PF) or municipalities (municipal forests; MF; [14]). In addition, more than one third of the state forest area in Bavaria is currently classified as at least of the following protection categories: Natura 2000, nature reserves, or natural forests [32–34].

MG and FB are located in the Oberpfälzer Lake district between the towns of Mitterteich, Tirschenreuth, and Falkenberg (NE Bavaria, Germany; Figure 1a). The gently NE–SW sloping (MG) and partially rugged (FB) terrains are located between 470–550 m a.s.l. and are characterized by low mean annual temperature, short vegetation period, and high precipitation rate [14].

Since the Paleozoic, intricate tectonic, magmatic, and geologic processes have shaped both sites. Two different basement units, the Saxo-Thuringian (in the north) and the Moldanubian (in the south), are separated by a large, tens-of-kilometers-long fault system, the “Erbendorfer Line”, that mainly strikes NW–SE and cuts the MG study area in the SW into two sections (Figure 1a). Permo-Carboniferous granite intrusions, the (a) Mitterteicher/Steinwald Granite Complex and (b) Falkenberger Granite Complex, were formed after the collapse of the Variscan orogen. During the Alpine orogeny, rifting (e.g., Eger

rift system), volcanism, subsidence, and uplift were dominant. Today, a NW–SE to NNW–SSE-oriented compressional stress field and weak to moderate shallow crustal earthquakes ( $<20$  km;  $M_L \leq 3.5$  Richter scale) characterize this region [14].



**Figure 1.** Tectonic setting of both study sites with (a) major tectonic units, faults (black lines), and earthquake events (blue dots) taken from literature [35–43]. The inset shows the location of both sites in Bavaria, Germany, close to the Czech border; (b) Münchsgrün (MG) and (c) Falkenberg (FB) study areas detailing mapped sites for the 2016/2019 inventories and the 2023 re-inventory [14].

## 2.2. Mapping Approach and Data Collection

The re-inventory followed the approach developed by Berberich et al. [14,18,30,31] and already applied in the 2016 (MG) and 2019 (FB) inventories [14]. To provide a scientific comparison between the 2016/2019 and 2023 inventories and data collection, the same field methodology was applied: all 352 ha of the mapped area (Figure 1b,c) were walked and mapped by the same observers. To ensure an area-wide inventory, tracks were recorded during mapping with transect spacing  $<10$  m. Mapping was conducted in April, May, and October at both sites and across all inventories to compare forest composition and herbaceous layer.

The fieldwork was divided into two main steps to investigate the presence/absence data of RWA nests: (a) Re-inventory of all RWA nests previously mapped in 2016 and 2019. The GPS coordinates of all these RWA nests were transferred to a GPS receiver (Garmin 60CSx). Previously mapped nests were revisited and mapped with a second GPS receiver (Garmin 62S) together with surrounding forest parameters, and (b) Inventory of new nests including their surrounding forest parameters with the second GPS receiver.

The following parameters were collected in the field:

1. Nest height (NH; classified into five classes: start-ups: 0.01–0.10 m, short: 0.11–0.50 m, medium: 0.51–1.00 m, tall: 1.01–1.50 m, very tall: 1.51–2.00 m; Table 1);
2. Nest diameter (ND; classified into five classes: small: 0.01–0.50 m, medium: 0.51–1.00 m, large: 1.01–1.50 m, very large: 1.50–2.00 m, and extra-large  $> 2.01$  m; Table 1);
3. Activity ( $n_{act}$ ) or inactivity of RWA nests ( $n_{inact}$ ; nest structures were still present, but no ant activity was observed during the inventory; therefore, the nest was considered dead);
4. Location of RWA nests (e.g., within the forest, forest roads, forest edges);
5. Number of woodpecker cavities (WpC) on the entire nest surface created by predation, e.g., by the Green Woodpecker (*Picus viridis*; divided into three classes: class 1: 1–5 cavities; class 2: 6–10 cavities; class 3:  $>10$  cavities);
6. All visible herbs at, on, and around each RWA nest (within 1.5 m of the nest);
7. Tree species at, on, and around each RWA nest (within 1.5 m of the nest);

8. Qualitative information on standing or lying dead wood (DW; classified into three classes: DW-1: standing DW (dying, decaying or biotope trees), DW-2: downed DW (small and large branches of varying diameter lying on or around a nest), and DW-3: downed DW of class 2 with additional decaying logs of at least 15 cm in diameter intentionally enriched by foresters as part of sustainable forest management (Figure 2). There were too few stumps for an additional class 4 “dead tree stumps” because RWA nests on, around, and on top of tree stumps (partially) covered the stumps with nest material;
9. Cleared plots (CP) due to forest management;
10. Finally, at least two photographs (landscape and normal format) of each nest were taken and stored in a photo database. These photographs were used to compare and re-identify (a) active nests ( $n_{actR}$ ), (b) forest composition, (c) dead wood classes, and (d) herbaceous layers mapped during the 2016/2019 campaigns;
11. Random sampling of RWA species in the field ( $\approx 10\%$  of mapped RWA nests) identified mainly *F. polycтена*, as *F. rufa* and *F. polycтена* are difficult to distinguish without a stereomicroscope.



**Figure 2.** Examples of dead wood classes 1–3 in (a) MG and (b) FB study area: DW-1: biotope trees (weathered red signature “A” in MG is a marker for the RWA nest) and dying standing tree, DW-2: branches of different size and diameter as downed DW, and DW-3: downed DW with additional tree trunks. Photo credit: M.B. Berberich.

Additional forest parameters on (1) primary tree species ( $TS_{prime}$ ), (2) medium tree age (mTA; classified into five general tree age classes: newly planted ( $\leq 20$  years), young (21–40 years), early mature (41–60 years), medium mature (61–80 years), mature ( $\geq 81$  years), and (3) information on ownership type (BSF; MF; PF) were obtained from the 10-year forest inventory and management plan (forest database) of the Bayerische Staatsforsten AöR, Regensburg [44].

Finally, the total number of nests ( $n_{tot}$ ) in all inventories and the spatial distribution of RWA nests were examined.

During this 2023 re-inventory,  $\approx 131$  ha ( $MG_{BSF}$ ) and  $\approx 170$  ha ( $FB_{BSF}$ ) were mapped in the BSF. The same adjacent areas of the PF and MF, previously inventoried in 2016/2019, were also included in this re-inventory due to the high abundance of RWA nests. The total mapped areas are 149 ha ( $MG_{tot}$ ) and 203 ha ( $FB_{tot}$ ; Figure 1b,c) in 2023.

**Table 1.** Descriptive statistics of total nest numbers ( $n_{tot}$ ), numbers of active nests ( $n_{act}$ ), numbers of active re-identified nests ( $n_{totR}$ ), nest height (NH), and diameter classes (ND) for the MG (2016/2023) and FB (2019/2023) inventories. Increase in active nest numbers ( $\Delta n_{act}$ ) and percentages are set in bold. – = not present.

Year	Study Area	Numbers								(a) Nest Height (NH) Classes of Active Nests ( $n_{act}$ )					(b) Nest Diameter (ND) Classes of Active Nests ( $n_{act}$ )				
		$n_{tot}$	$n_{act}$	$n_{actR}$	$\Delta n_{tot}$	Difference ( $\Delta$ ) for MG (2016/2023) and FB (2019/2023)				Start-Ups	Short	Medium	Tall	Very Tall	Small	Medium	Large	Very Large	Extra-Large
						% $n_{tot}$	$\Delta n_{act}$	% $n_{act}$	$\Delta n_{actR}$										
2016	MG	2326	2292	–	–	–	–	–	–	277	1208	632	153	22	947	696	393	173	83
2023	MG	2555	2513	1336	229	9.8	221	<b>9.6</b>	<b>58.3</b>	117	1496	706	165	29	836	829	594	199	55
2019	FB	2830	2607	–	–	–	–	–	–	406	1453	607	138	3	1175	738	493	129	72
2023	FB	2838	2763	1712	8	0.3	156	<b>6.0</b>	<b>65.7</b>	353	1683	622	96	9	1131	822	591	168	51

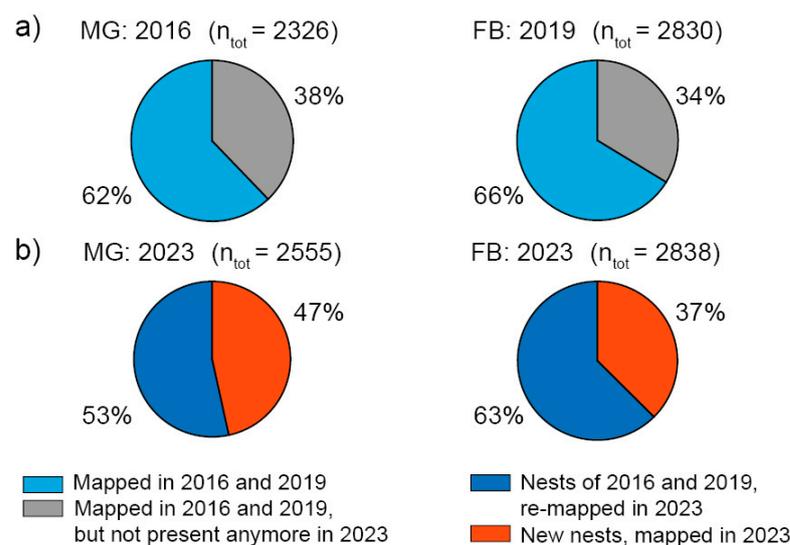
### 2.3. Data Analysis

Octave 8.4.0, MATLAB 2023b (online), and QGIS 3.34 were used for the analyses. Uniform or random distributions or clusters were analyzed using nearest neighbor distribution statistics in MATLAB 2023b (online). For  $MG_{BSF}$  and  $FB_{BSF}$ , a Multivariate ANalysis Of Variance (MANOVA), one-way ANOVA, Kruskal–Wallis-Test, and multiple comparison with a Bonferroni-adjusted post hoc analysis were applied to physical nest parameters (NH, ND) of active nests, medium tree age (mTA), and woodpecker cavities (WpC) to examine patterns of multiple dependent variables. Information on tree species and medium tree age (mTA) was only available for BSF [44]. Density plots of RWA nests were generated to provide insight into their underlying spatial distribution and possible changes over time using the code developed by He [45]. This code generated a bivariate plot of scattered point data (RWA nests) by setting the number of equally spaced bins to 20. Color-coded graphs show that multiple RWA nests in the same location result in the highest concentrations of the numerical variable (hotspots), colored in red. Flora Incognita, a freely available mobile image-based application, was used to automatically identify wild plants in the field [46].

## 3. Results

### 3.1. Presence/Absence Data of RWA Nests

A total of 5393 RWA nests ( $n_{tot}$ ) were mapped across the sites. This re-inventory clearly shows an overall increase in total nest numbers ( $n_{tot}$ ) of  $\approx 10\%$  in MG and stable situation in FB ( $\approx +0.3\%$ ). In the 2023 inventory,  $\approx 58\%$  of RWA nests ( $n_{tot}$ ) mapped in 2016 and 2019 were re-identified;  $\approx 42\%$  were newly mapped nests. About one third of the nests ( $n_{tot}$ ) mapped in 2016/2019 could not be re-mapped for various reasons (Figure 3; Tables 1 and 2): (a) natural processes: some RWA nests disappeared because the colony died due to natural causes, including nest destruction by, e.g., wild boars ( $\approx 2.5\%$ ) and other unidentified processes after the 2016/2019 inventories; (b) thickets: In 2023,  $\approx 4\%$  of the nests at both sites could not be re-mapped due to access constraints. These nests were now located in very dense thickets, so their status-quo is uncertain; (c) Pond management (FB): In 2019, 22 nests were mapped on the banks of a fish pond. Pond management caused the water level to rise, submerging these nests. They could not be re-mapped in 2023. Only nests that were active in 2023 will be discussed below.



**Figure 3.** Gain and loss of RWA nests ( $n_{tot}$ ) for the (a) MG and (b) FB study area for the 2016/2019 inventories and the 2023 re-inventory.

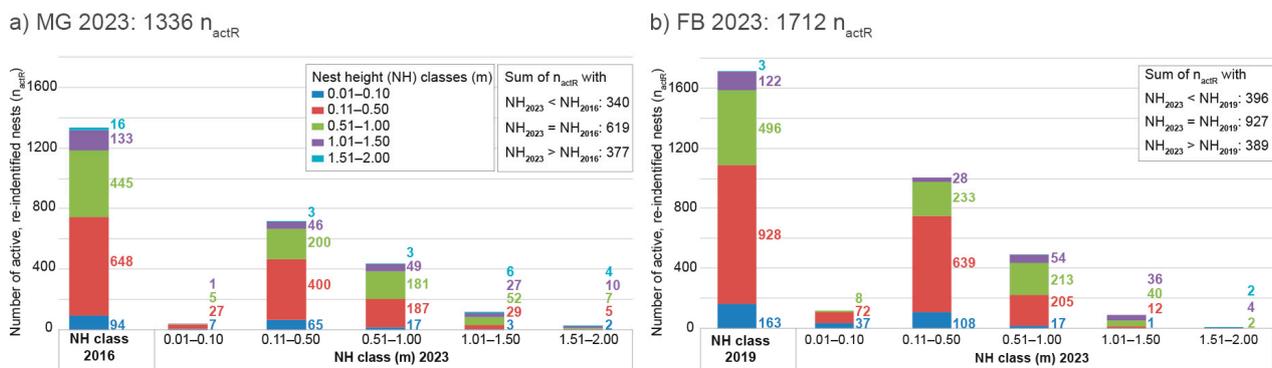
**Table 2.** Descriptive statistics of total mapped area ( $ha_{tot}$ ), forest owners (BSF, MF, PF) holding a share of the mapped area, numbers of active nests ( $n_{act}$ ) in BSF, MF, PF, and Fauna-Flora-Habitat (FFH) areas, numbers of active nests ( $n_{act}$ ) in natural restocking (NR) and on partly cleared and cleared plots (CP) for the 2016, 2019, and 2023 inventories for (a) MG and (b) FB study area; – = not present.

Year	Mapped Area $ha_{tot}$	State Forest (BSF)		Municipal Forest (MF)		Private Forest (PF)		FFH Area *		Number of Active Nests ( $n_{act}$ )				Number of $n_{act}$ in BSF, MF, and PF		
		ha	%	ha	%	ha	%	ha	%	$\Sigma n_{act}$	BSF	MF	PF	FFH *	NR	CP
<b>(a) MG</b>																
2016	149	128	85.9	7.4	5.0	13.6	9.1	7.7	5.2	2292	2110	89	93	89	44	120
2023	149	131	87.9	6.8	4.6	11.2	7.5	7.7	5.2	2513	2213	121	179	105	280	357
<b>(b) FB</b>																
2019	200	167	83.5	–	–	33	16.5	–	–	2607	2221	–	386	–	331	57
2023	203	167	82.3	–	–	36	17.7	–	–	2763	2332	–	431	–	294	182

\* Area and nests related to the FFH area “Waldnaabtal between Tirschenreuth and Windisch-Eschenbach” (DE6139371) are integrated into those of BSF, MF and PF areas and nests.

Active RWA nests ( $n_{act}$ ) were 2513 (MG;  $\approx 10\%$  increase) and 2763 (FB;  $\approx 6\%$  increase). An increase in the numbers of nests ( $n_{act}$ ) was also observed in the differently owned forests: BSF ( $\approx 5\%$ ), MF ( $\approx 36\%$ ), and PF ( $\approx 93\%$ ; Tables 1 and 2). In particular, small active nests ( $ND < 0.5$  m) showed a high percentage in all inventories (MG  $\approx 72\%$ ; FB  $\approx 64\%$ ), and their sum increased by  $\approx 9\%$  in both study areas (Table 1). Most active nests were located in forest stands and natural regeneration areas (MG:  $\approx 67\%$ ; FB:  $\approx 54\%$ ), and up to a quarter (MG:  $\approx 16\%$ ; FB:  $\approx 26\%$ ) along forest roads and skid trails. Open areas such as meadows, fields, or pond banks were not preferred by RWA nests (MG:  $\approx 3\%$ ; FB:  $\approx 14\%$ ).

Nearly two thirds of active nests mapped in 2016/2019, and their forest habitat, were re-identified ( $n_{actR}$ ) at both study sites using the GPS records and the 2016/2019 photo database. More than  $\approx 50\%$  (MG:  $\approx 57\%$ ; FB:  $\approx 53\%$ ) of start-ups and short nests survived since the last inventories and were re-identified in 2023. Overall, nest heights developed positively: In 2023, half of the re-identified nests showed the same NH class (MG:  $\approx 46\%$ ; FB:  $\approx 54\%$ ) or even developed into larger nests (MG:  $\approx 28\%$ ; FB:  $\approx 23\%$ ). Approximately a quarter of the  $n_{actR}$ s were smaller than those mapped in 2016/2019 (Figure 4).

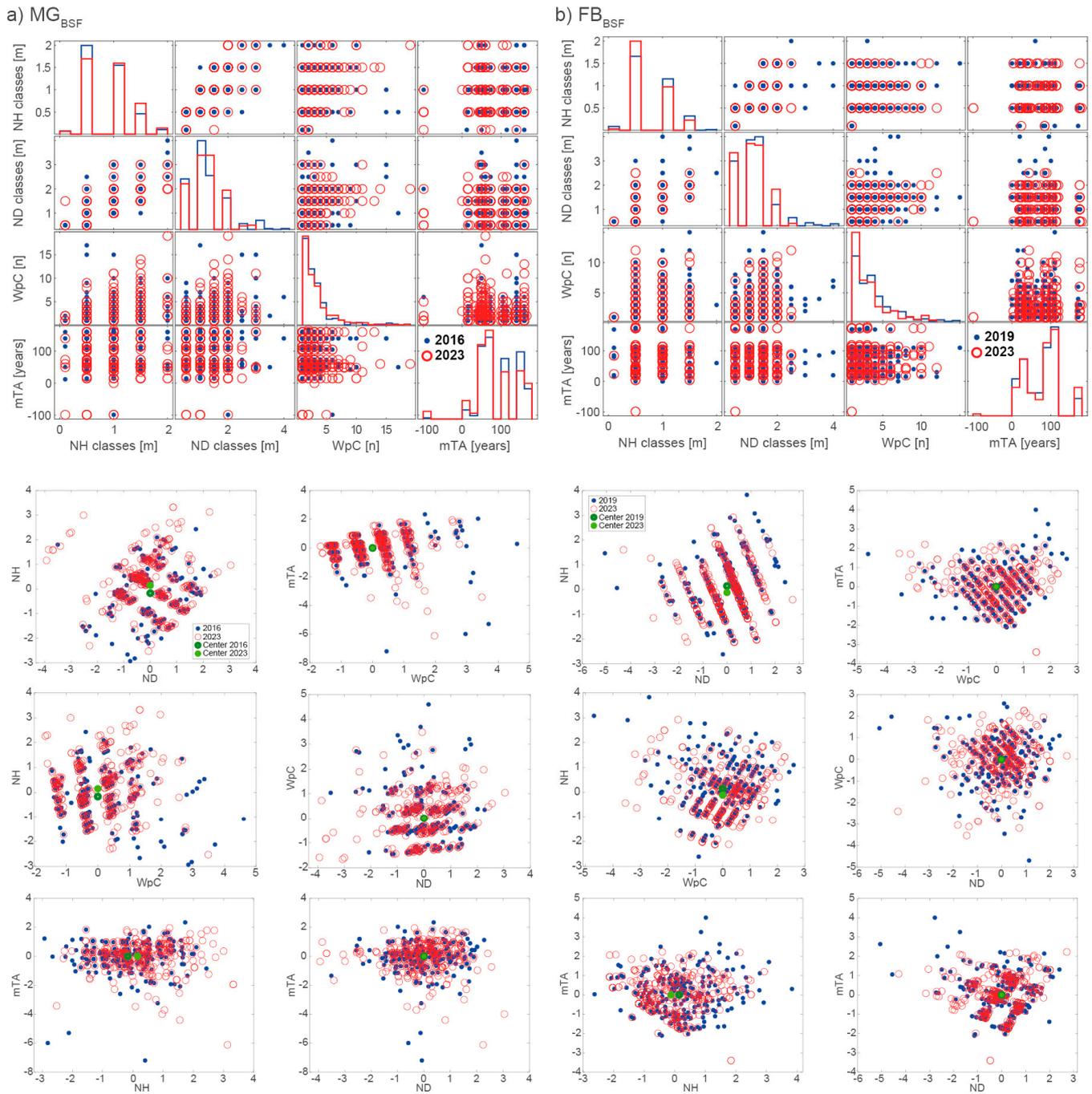


**Figure 4.** Growth of active, re-identified nests ( $n_{actR}$ ) between the 2016/2019 inventories and the 2023 re-inventory for (a) MG and (b) FB study area.

We observed an  $\approx 5\%$  increase in the number of active nests between the two inventories in  $MG_{BSF}$  and  $FB_{BSF}$  (Table 2). The statistically significant results of the MANOVA for  $MG_{BSF}$  and  $FB_{BSF}$  for the 2016/2019 to 2023 inventories confirm that the data are dependent and non-random ( $d = 1$ ;  $p < 0.05$ ; Wilk's  $\lambda$ : 0.976 ( $MG_{BSF}$ ) and 0.983 ( $FB_{BSF}$ ); Table 3). The Wilk's lambda results indicate a small group separation in 2023. This result is supported by the grouped plot matrices and grouped scatterplots of the first two canonical variables of the MANOVA (Figure 5), which show that changes over time of the inventories were associated with (a) small separations between groups, (b) a shift to larger NH and ND, (c) an increase in  $WpC$ , and (d) a shift of  $mTA$  to more early mature forests for  $MG_{BSF}$  due to timber harvesting and a recent assessment of tree age classes and to more mature forests in  $FB_{BSF}$  for 2023. The Kruskal–Wallis zero  $p$ -value confirms that all data come from the same distribution at the 1% level of significance (Table 4). Bonferroni-adjusted posthoc test showed significant differences in all tested parameters (Table 5).

**Table 3.** Results of the MANOVA for the 2016/2019 inventories and the 2023 re-inventory for (a)  $MG_{BSF}$  and (b)  $FB_{BSF}$ .

Study Area	d	p	dfW	dfB	dfT	Wilk's $\lambda$	$\chi^2$
(a) $MG_{BSF}$	1	0.004	627	1	628	0.976	15.351
(b) $FB_{BSF}$	1	0.035	601	1	602	0.983	10.360



**Figure 5.** Results of MANOVA for active nests for nest height (NH), nest diameter (ND), medium tree age (mTA), and woodpecker cavities (WpC), showing a grouped plot matrix (top) and six grouped scatter plots of the first two canonical variables and their centers (bottom) for the 2016/2019 inventories and the 2023 re-inventory for (a)  $MG_{BSF}$  and (b)  $FB_{BSF}$ . Tree ages with a signature of  $-100$  represent no trees or clearings around a nest. Blue: 2016/2019 data; red: 2023 data.

**Table 4.** Results of Kruskal–Wallis ANOVA test and results of multiple comparison with Bonferroni-adjusted post-hoc analysis for the 2016/2019 and 2023 inventories for physical nest parameters (NH, ND) of active nests, medium tree age (mTA) for TS<sub>prime</sub>, and woodpecker cavities (WpC) for (a) MG<sub>BSF</sub> and (b) FB<sub>BSF</sub>. LL = Lower Limit and UL = Upper Limit for the 95% confidence interval for the true mean difference; A-B = difference between the estimated group means;  $p = p$ -value.

(a) MG: 2016						(a) MG: 2023					
Kruskal–Wallis ANOVA test											
Source	SS	df	MS	Chi-sq	Prob > Chi-sq	Source	SS	df	MS	Chi-sq	Prob > Chi-sq
Groups	$4.24 \times 10^{10}$	3	$1.41 \times 10^{10}$	6598.6	0	Groups	$5.36 \times 10^{10}$	3	$1.79 \times 10^{10}$	7054.3	0
Error	$1.49 \times 10^{10}$	8911	$1.7 \times 10^6$			Error	$2.01 \times 10^{10}$	9697	$2.07 \times 10^6$		
Total	$5.73 \times 10^{10}$	8914				Total	$7.38 \times 10^{10}$	9700			
Multiple comparison with Bonferroni-adjusted post-hoc analysis											
Group A	Group B	LL	A-B	UL	$p$	Group A	Group B	LL	A-B	UL	$p$
NH	ND	$-1.024 \times 10^3$	$-8.264 \times 10^2$	$-6.289 \times 10^2$	$1.5378 \times 10^{-27}$	NH	ND	$-1.232 \times 10^3$	$-1.023 \times 10^3$	$-8.152 \times 10^2$	$1.0916 \times 10^{-37}$
NH	WpC	$1.997 \times 10^3$	$2.194 \times 10^3$	$2.392 \times 10^3$	$6.002 \times 10^{-188}$	NH	WpC	$2.356 \times 10^3$	$2.564 \times 10^3$	$2.772 \times 10^3$	$8.141 \times 10^{-231}$
NH	mTA	$-4.205 \times 10^3$	$-4.001 \times 10^3$	$-3.798 \times 10^3$	0	NH	mTA	$-4.665 \times 10^3$	$-4.448 \times 10^3$	$-4.230 \times 10^3$	0
ND	WpC	$2.823 \times 10^3$	$3.021 \times 10^3$	$3.218 \times 10^3$	0	ND	WpC	$3.379 \times 10^3$	$3.587 \times 10^3$	$3.795 \times 10^3$	0
ND	mTA	$-3.379 \times 10^3$	$-3.175 \times 10^3$	$-2.971 \times 10^3$	0	ND	mTA	$-3.641 \times 10^3$	$-3.424 \times 10^3$	$-3.207 \times 10^3$	0
WpC	mTA	$-6.399 \times 10^3$	$-6.196 \times 10^3$	$-5.992 \times 10^3$	0	WpC	mTA	$-7.228 \times 10^3$	$-7.011 \times 10^3$	$-6.794 \times 10^3$	0

Table 4. Cont.

(b) FB: 2019						(b) FB: 2023					
Kruskal–Wallis ANOVA test											
Source	SS	df	MS	Chi-sq	Prob > Chi-sq	Source	SS	df	MS	Chi-sq	Prob > Chi-sq
Groups	$6.03 \times 10^{10}$	3	$2.01 \times 10^{10}$	7432.2	0	Groups	$6.9933 \times 10^{10}$	3	$2.3311 \times 10^{10}$	7757.3	0
Error	$2.11 \times 10^{10}$	10,034	2,106,794.5			Error	$2.5446 \times 10^{10}$	10,577	2,405,817.6		
Total	$8.15 \times 10^{10}$	10,037				Total	$9.5379 \times 10^{10}$	10,580			
Multiple comparison with Bonferroni-adjusted post-hoc analysis											
Group A	Group B	LL	A-B	UL	<i>p</i>	Group A	Group B	LL	A-B	UL	<i>p</i>
NH	ND	$-1.254 \times 10^3$	$-1.049 \times 10^3$	$-8.439 \times 10^2$	$1.1475 \times 10^{-40}$	NH	ND	$-1.467 \times 10^3$	$-1.254 \times 10^3$	$-1.041 \times 10^3$	$1.5177 \times 10^{-53}$
NH	WpC	$2.034 \times 10^3$	$2.239 \times 10^3$	$2.445 \times 10^3$	$2.024 \times 10^{-181}$	NH	WpC	$2.245 \times 10^3$	$2.458 \times 10^3$	$2.671 \times 10^3$	$1.249 \times 10^{-202}$
NH	mTA	$-4.667 \times 10^3$	$-4.454 \times 10^3$	$-4.240 \times 10^3$	0	NH	mTA	$-5.111 \times 10^3$	$-4.888 \times 10^3$	$-4.664 \times 10^3$	0
ND	WpC	$3.083 \times 10^3$	$3.289 \times 10^3$	$3.494 \times 10^3$	0	ND	WpC	$3.499 \times 10^3$	$3.712 \times 10^3$	$3.925 \times 10^3$	0
ND	mTA	$-3.618 \times 10^3$	$-3.404 \times 10^3$	$-3.191 \times 10^3$	0	ND	mTA	$-3.858 \times 10^3$	$-3.634 \times 10^3$	$-3.410 \times 10^3$	0
WpC	mTA	$-6.906 \times 10^3$	$-6.693 \times 10^3$	$-6.480 \times 10^3$	0	WpC	mTA	$-7.570 \times 10^3$	$-7.346 \times 10^3$	$-7.122 \times 10^3$	0

**Table 5.** Descriptive statistics of total mapped area ( $ha_{tot}$ ) for forest owners (BSF, MF, PF), numbers of active nests ( $n_{act}$ ) in BSF, MF, and PF, numbers of re-identified active nests ( $n_{actR}$ ) in BSF, MF, and PF, dead wood classes 1–3 (DW), numbers of active nests with DW ( $n_{actDW}$ ), and ratio of active nests with dead wood per ha for the 2016, 2019, and 2023 inventories for (a) MG and (b) FB. – = not present.

Year	BSF						MF						PF								
	$ha_{tot}$	n	n/DW Classes			Sum $n_{actDW}$	$n_{actDW}/ha$	$ha_{tot}$	$n_{actDW}$	n/DW Classes			Sum $n_{actDW}$	$n_{actDW}/ha$	$ha_{tot}$	n	n/DW Classes			Sum $n_{actDW}$	$n_{actDW}/ha$
			1	2	3					1	2	3					1	2	3		
<b>(a) MG (<math>n_{act}</math>)</b>																					
2016	128	2110	57	495	410	962	8	7.4	89	0	9	14	23	3	13.6	93	1	29	15	45	3
2023	131	2213	63	436	454	953	7	6.8	121	2	12	17	31	5	11.2	179	4	64	27	95	8
<b>(a) MG (<math>n_{actR}</math>)</b>																					
2023	131	1336	31	220	232	483	4	6.8	70	0	5	11	16	2	11.2	51	0	13	9	22	2
<b>(b) FB (<math>n_{act}</math>)</b>																					
2019	167	2221	40	880	447	1367	8	–	–	–	–	–	–	–	33	386	5	181	15	201	6
2023	167	2332	55	653	426	1134	7	–	–	–	–	–	–	–	36	431	4	141	24	169	5
<b>(b) FB (<math>n_{actR}</math>)</b>																					
2023	167	1446	34	412	268	714	4	–	–	–	–	–	–	–	36	266	3	96	10	109	3

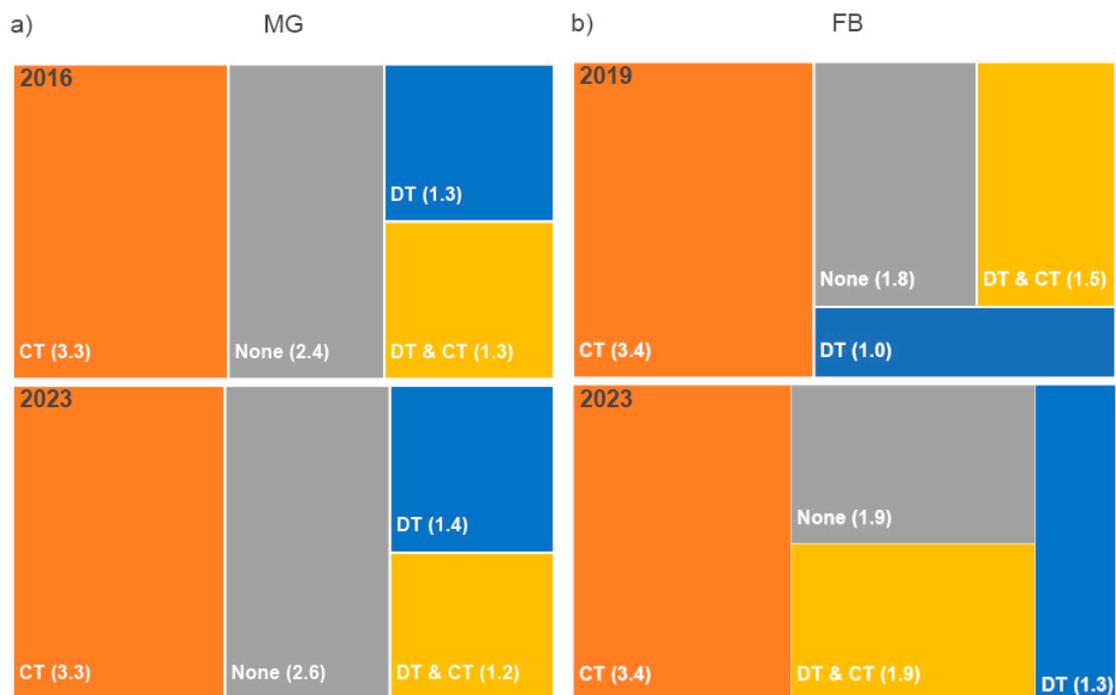
As observed in 2016/2019, RWA nests were spatially clustered in 2023 (nearest neighbor ratio < 1:  $MG_{BSF}$ : 0.53;  $FB_{BSF}$  0.41) and Z-statistic <  $-1.96$  ( $Z_{MG}$ :  $-62.76$ ;  $Z_{FB}$ :  $-82.17$ ) at the 95% significance level [14].

### 3.2. Interconnection of Forest Composition and RWA Nests

#### 3.2.1. Tree Species and Age

Information on primary trees ( $TS_{prime}$ ) and medium tree age (mTA) was only available for BSF [44], but not for municipal (MF) or privately (PF) owned forests. Therefore, these forestry aspects are discussed only for  $MG_{BSF}$  and  $FB_{BSF}$ . In agreement with the BSF, the mTA was selected for all analyses.

The coniferous forest at RWA nests consists mainly of pine (*Pinus sylvestris*;  $MG_{BSF}$ :  $\approx 66\%$ ;  $FB_{BSF}$ :  $\approx 58\%$ ) and spruce (*Picea abies*;  $MG_{BSF}$ :  $\approx 30\%$ ;  $FB_{BSF}$ :  $\approx 41\%$ ) as  $TS_{prime}$  in all inventories. Mature ( $\geq 81$  years) pine-dominated forests were the preferred location for RWA nests on average at both sites ( $MG_{BSF}$ :  $\approx 45\%$ ;  $FB_{BSF}$ :  $\approx 44\%$ ). In this age class, nest sizes ranged from start-ups to tall nests in both inventories. The proportion of RWA nests (start-ups to medium-sized nests) in medium mature (61–80 years) pine forests was robust for MG ( $MG_{BSF}$ :  $\approx 12\%$ ), but was reduced by half in  $FB_{BSF}$  (2019:  $\approx 13\%$ ; 2023:  $\approx 6\%$ ). Start-ups, short nests and medium-sized nests were also observed in mature ( $\geq 81$  years) spruce-dominated forests, but at lower proportions. In  $MG_{BSF}$ ,  $\approx 18\%$  of all nests were recorded in early mature (41–60 years) spruce forests. In  $FB_{BSF}$ , the numbers of start-ups to medium-sized nests quadrupled in young (21–40 years) spruce-dominated areas. Compared to 2019, fewer start-ups, short nests and medium-sized nests were observed in newly planted spruce trees ( $\leq 20$  years) in  $FB_{BSF}$  (Figures 5 and 6).



**Figure 6.** Visual representation of the forest composition (log-normed) observed in the field at active RWA nests ( $n_{act}$ ): deciduous only (DT), coniferous only (CT), combined deciduous and coniferous (DT & CT), and no trees (none) for the 2016, 2019, and 2023 inventories for (a) MG and (b) FB. Legend—CT included the following: pine (*Pinus sylvestris*), spruce (*Picea abies*), larch (*Larix decidua*), fir (*Abies alba*), and Douglas fir (*Pseudotsuga menziesii*). DT included the following: alder (*Alnus glutinosa*), beech (*Fagus sylvatica*), birch (*Betula pendula*), bloody dogwood (*Cornus sanguinea*), common hazel (*Corylus avellana*), common hornbeam (*Carpinus betulus*), red elder (*Sambucus racemosa*), rowan (*Sorbus aucuparia*), oak (*Quercus robur*), and willow (*Salix*).

Forest composition observed in the field differed from records, with a slight shift from pure spruce stands (2016:  $\approx 62\%$ ; 2023:  $\approx 52\%$ ) to more mixed spruce–pine stands (2016:  $\approx 12\%$ ; 2023:  $\approx 18\%$ ) in MG due to naturally grown trees. In FB, the proportion of pure spruce ( $\approx 53\%$ ) and mixed spruce–pine stands ( $\approx 37\%$ ) remained the same in both inventories. In both study areas, the proportion of naturally grown deciduous trees such as birch (*Betula pendula*), beech (*Fagus sylvatica*), oak (*Quercus robur*), red elder (*Sambucus racemosa*), alder (*Alnus glutinosa*), or a combination of two deciduous species increased in 2023 (Figure 6), as well as a combination of coniferous and deciduous trees in FB (Figure 6b).

Nest numbers of all NH classes multiplied in areas of natural restocking in MG, and short nests especially increased sevenfold; in FB, especially short nests and medium-sized nests predominated. Spruce- and pine-dominated restocking or combinations with, e.g., larch (*Larix*) characterized one third of the flora around nests in MG and FB. Pure deciduous species or combinations of these, e.g., beech (*Fagus sylvatica*), oak (*Quercus robur*), red elder (*Sambucus racemosa*), and rowan (*Sorbus aucuparia*), remained robust with low proportions of  $\approx 4\%$  in both inventories.

A total of 7.7 ha of the MG study site was designated as Natura 2000–Fauna-Flora-Habitat (FFH; “Waldnaabtal between Tirschenreuth and Windisch-Eschenbach”; DE6139371) site (Figure 1b). In 2023, nest numbers increased from 89 (in 2016) to 105. Robust nest numbers were recorded for short nests ( $\approx 61\%$ ) and an increase in medium-sized nests (from  $\approx 22\%$  to  $\approx 29\%$ ).

Overall, there was an increase in partial logging activity at each site between the two inventories, e.g., due to bark beetle infestation, windthrow, and snow break. The number of active nests on clearcuts and partially cleared plots tripled by 2023 (Table 2). In MG, the numbers of short nests almost quadrupled (from 73 to 260) and the number of medium-sized nests almost tripled (from 21 to 57). In FB, start-ups (from 10 to 39) and short nests (from 32 to 122) quadrupled.

### 3.2.2. Herbaceous Layer

In the 2016, 2019, and 2023 inventories, single occurrences of European blueberry (*Vaccinium myrtillus*; Blb), moss (*Bryophyta*; Mo), grass (*Poaceae*; Gr), reed grass (*Calamagrostis*; RGr), cranberry (*Vaccinium vitis-idaea*; CrB), eagle fern (*Pteridium aquilinum*; Fer), and foxglove (*Digitalis purpurea*; FoG) were highly abundant on, at, or around RWA nests (Figure 7a,b). Variable combinations of these main herbs with a large number of other different herbs (difH) increased in 2023 (MG: from  $\approx 42\%$  to  $\approx 76\%$ ; FB: from  $\approx 50\%$  to  $\approx 66\%$ ). Both studies showed small differences in difH. Although these herbs played a minor role, herb biodiversity increased in 2023 at both sites, e.g., May lily (*Maianthemum bifolium*), lady’s fern (*Athyrium filix-femina*), mullein (*Verbascum*), or yarrow (*Achillea filipendulina*) as single plants or in combination with other herbs were not observed in previous inventories.

The herb layer on and around the re-identified RWA nests (MG: 1336; FB: 1712) showed a similar pattern (Figure 7a,b). Blackberry proliferation was not a major factor. The proportion of ant nests that were free of herbs was very low ( $<1\%$ ) in both inventories.



**Figure 7.** Visual representation of the qualitative composition of main herbs (log-normed) around and on active RWA nests ( $n_{act}$ ) for the 2016, 2019 and 2023 inventories for (a) MG and (b) FB. Legend—Highly abundant herbs included Blb: European blueberry (*Vaccinium myrtillus*), CrB: cranberry (*Vaccinium vitis-idaea*), Fer: eagle fern (*Pteridium aquilinum*), FoG: foxglove (*Digitalis purpurea*), Gr: grass (*Poaceae*), Mo: moss (*Bryophyta*), and RGr: reed grass (*Calamagrostis*). Herbs categorized as difH: bellflowers (*Campanula*), blackberry (*Rubus*), broom (*Genista*), cattail (*Typha*), chickweed (*Stellaria media*), cleavers (*Gallium aparine*), coltsfoot (*Tussilago farfara*), cranesbills (*Geranium pratense*), dandelions (*Taraxacum officinale*), dead-nettles (*Lamium*), field pansy (*Viola tricolor*), field pennycress (*Thlaspi arvense*), flatweed (*Hypochaeris radicata*), ground elder (*Aegopodium podagraria*), groundsel (*Senecio vulgaris*), hairy bittercress (*Cardamine hirsuta*), horsetail (*Equisetum*), lady's fern (*Athyrium filix-femina*), lupin (*Lupinus*), May lily (*Maianthemum bifolium*), melde (*Chenopodium album*), mullein (*Verbascum*), nettles (*Urtica*), red dead nettle (*Lamium purpureum*), red sorrel (*Rumex acetosella*), rushes (*Juncus acutus*), St John's wort (*Hypericum perforatum*), thale cress (*Arabidopsis thaliana*), thistle (*Cirsium vulgare*), wild strawberry (*Fragaria vesca*), wood sorrel (*Oxalis acetosella*), and yarrows (*Achillea filipendulina*) and (*Achillea millefolium*).

### 3.3. Dead Wood

At MG<sub>BSF</sub>, dead wood was observed in nearly half of all active nests ( $\approx 44\%$ ) in both inventories (Table 5). Approximately  $\approx 3\%$  of the nests were on or near standing dead wood (dying, decaying, or biotope trees; DW-1), and  $\approx 43\%$  of RWA nests were covered by downed DW (class 2 and 3; Figure 2). Re-identified nests ( $n_{\text{actR}}$ ) in MG<sub>BSF</sub>, MG<sub>MF</sub>, and MG<sub>PF</sub> showed similar proportions. In 2023, nine trees could be reassigned to DW-1 (standing DW) and 96 trees to DW-3 (downed trees) in MG<sub>BSF</sub>.

Similar proportions were found for active nests in FB<sub>BSF</sub>. Dead wood was observed at  $\approx 55\%$  of active nests in both inventories. In FB<sub>BSF</sub>, the proportion of DW-1 ( $\approx 2\%$ ) and DW-2 and 3 ( $\approx 27\%$ ) was slightly lower. Re-identified nests in FB<sub>BSF</sub> ( $\approx 50\%$ ) and active nests in FB<sub>PF</sub> ( $\approx 41\%$ ) have a similar proportion of DW-2 and 3 ( $\approx 50\%$ ) compared to MG<sub>BSF</sub>. In 2023, two trees could be newly assigned to DW-1 (standing DW) and 43 trees to DW-3 (downed trees) in FB<sub>BSF</sub>.

The  $n_{\text{actDW}}/\text{ha}$  ratio for both inventories was the same for active and re-identified nests in MG<sub>BSF</sub> and FB<sub>BSF</sub>. This ratio doubled in MG<sub>MF</sub> and MG<sub>PF</sub> and remained robust in FB<sub>PF</sub>. Re-identified nests in MG<sub>BSF</sub> and FB<sub>BSF</sub> showed twice the rate of MG<sub>MF</sub> and MG<sub>PF</sub> (Table 5).

At both sites, approximately 13.5% of re-identified active nests showed no DW in the 2023 re-inventory. Most nests were located in BSF (MG<sub>BSF</sub>: 732; FB<sub>BSF</sub>: 732; MG<sub>MF</sub>: 54; MG<sub>PF</sub>: 29; FB<sub>PF</sub>: 157). In MG<sub>BSF</sub>, dead wood of mostly class 2 and 3 was no longer observed at short ( $\approx 46\%$ ), medium ( $\approx 25\%$ ), and tall ( $\approx 10\%$ ) nests. In FB<sub>BSF</sub>, the proportions are similar (short:  $\approx 53\%$ , medium:  $\approx 23\%$ , tall:  $\approx 3\%$  nests).

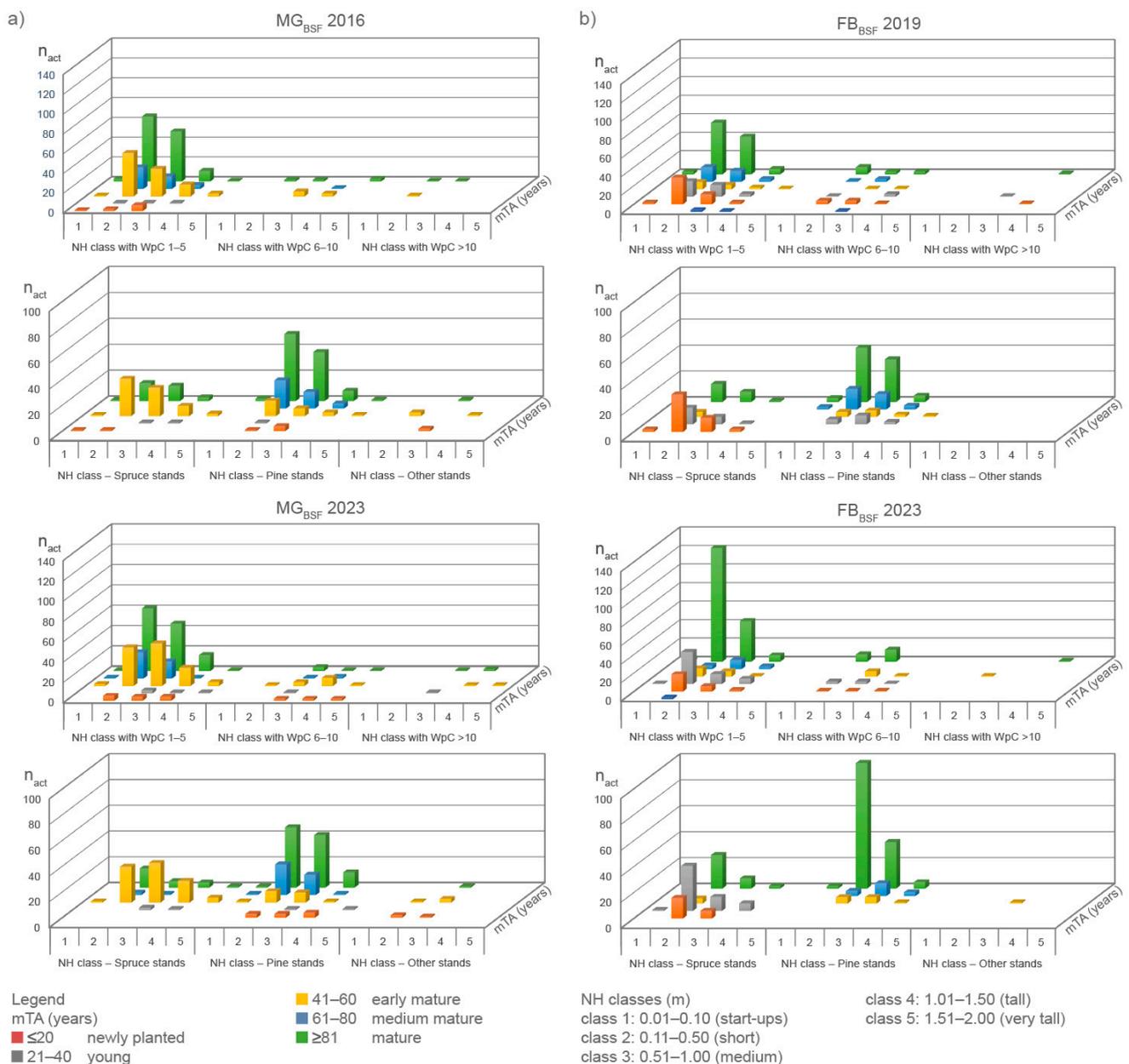
### 3.4. Woodpecker Cavities in RWA Nests

In all inventories in MG and FB, woodpecker cavities (WpC) due to predation were observed throughout the nest surface. In 2023, the number of nests with WpC and the number of WpC in the nest increased in BSF, MF, and PF compared to the 2016/2019 inventories. In MG<sub>BSF</sub>, nest numbers with WpC increased by  $\approx 22\%$  (FB<sub>BSF</sub>:  $\approx 16\%$ ); in FB<sub>PF</sub>, nest numbers with WpC and WpC counts doubled. In MG, nest numbers doubled in 2023 for nests with 6–10 woodpecker cavities; in FB, nest numbers also increased 1.5-fold (Table 6, Figure 8).

**Table 6.** Descriptive statistics of number of active nests ( $n_{\text{act}}$ ) with WpC and number ( $n$ ) of woodpecker cavities (WpC) in active nests for the MG and FB study site for the 2016/2019 inventories and the 2023 re-inventory. – = not present.

Year	Study Site	Mapped Nests ( $n_{\text{act}}$ )	Nests ( $n_{\text{act}}$ ) with WpC (n)			Sum $n_{\text{act}}$	Numbers of WpC (n) in $n_{\text{act}}$			Sum WpC (n)
			BSF	MF	PF		BSF	MF	PF	
2016	MG	2292	291	16	14	321	743	32	36	811
2023	MG	2513	338	31	24	393	921	37	55	1049
2019	FB	2607	272	–	36	308	849	–	120	969
2023	FB	2763	331	–	68	399	908	–	246	1154

Short, medium, and tall nests had the highest proportions of 1–5 cavities at both sites. In MG<sub>BSF</sub>, one third of the nests were observed in early mature and mature spruce forests and two-thirds in medium mature and mature pine forests in both inventories. In 2019, newly planted and mature spruce forests ( $\approx 40\%$ ) and mature pine forests (two-thirds) were the preferred locations in FB<sub>BSF</sub>. In 2023, mTA changed to newly planted, young, and mature spruce forest ( $\approx 40\%$ ) and medium mature and mature pine forests ( $\approx 60\%$ ; Figure 8). Deciduous trees played a minor role.

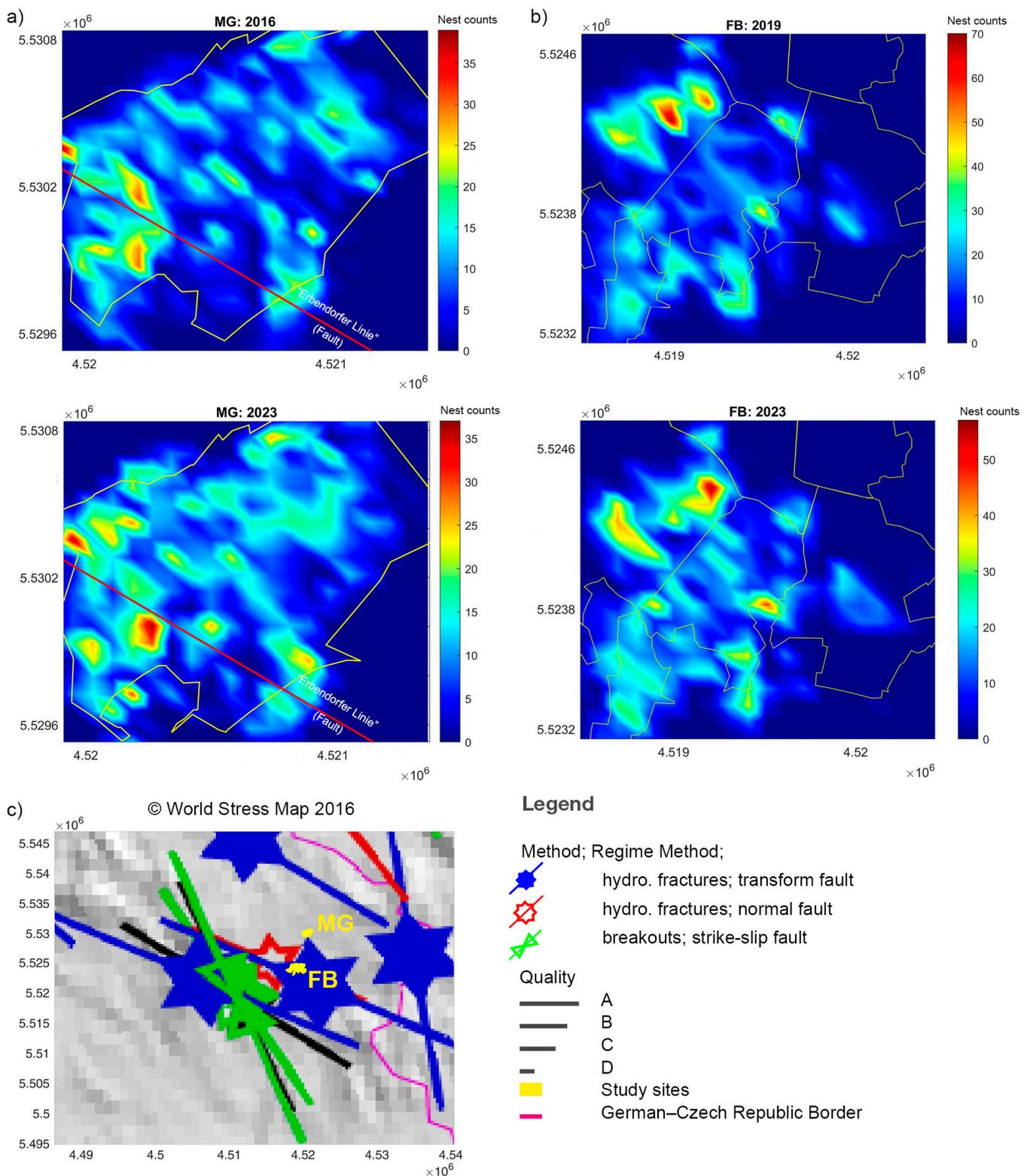


**Figure 8.** Visual representation of nest height (NH) classes 1–5, woodpecker classes (WpC 1–5, WpC 6–10, WpC >10), tree species, and medium tree age (mTA) versus numbers of active nests ( $n_{act}$ ) for (a)  $MG_{BSF}$  and (b)  $FB_{BSF}$  for the 2016/2019 inventories and the 2023 re-inventory.

Medium-sized nests with large diameters had an average of 2.7 WpC ( $MG_{BSF}$ ) in mature and 2.8 WpC in medium mature forests ( $FB_{BSF}$ ). In both inventories, larger nests (tall–extra tall) had fewer cavities than smaller nests. Tall nests with large diameters had 1.9 WpC in  $MG_{MF}$ . Medium-sized nests with large diameters had an average of 1.4 WpC ( $MG_{PF}$ ) and 3.5 WpC ( $FB_{PF}$ ; Table 6).

### 3.5. GeoBio-Interactions

A predominantly NW–SE spatial distribution pattern of RWA nests (Figure 9), parallel to the current main stress direction in the area, is evident from the density plots. In addition, there appears to be a shift of nest hotspots from the NE section towards the “Erbendorfer Line” (fault line) in the SW section of MG (Figure 9a).



**Figure 9.** Density plots of active RWA nests ( $n_{act}$ ) in (a) MG and (b) FB study area, and (c) tectonic stress directions at both sites (yellow; © World Stress Map 2016 [47]). Data for 2016 (MG) and 2019 (FB) were taken from [14].

### 3.6. Time Intervals for Re-Inventories

The time intervals for re-inventories were different at the two study sites: MG at seven years; FB at four years.

## 4. Discussion

Information on abundance and distribution of species is essential for ecology and conservation [48]. The protection of RWA as keystone species that shapes ecosystems and controls pests in an integrally and sustainably managed forest (SFM) is only possible if sufficient scientifically based information on their occurrence and spatial distribution is available. This requires not only censuses, e.g., of individual RWA nests, but also multi-disciplinary integration of knowledge across forest ecosystem sciences, biological, spatial, temporal, behavioral, and geo-tectonic scales [14–23,49]. In most European countries, including Germany, the data situation for the different sessile RWA and their occurrence in forests is poor [50]. The re-inventories in this study are based on our area-wide and integrated approach [14,18,30,31], as suggested by [49]. This approach provides scientifically reliable and very extensive records and documentation of not only the presence/absence data of RWA nests but also of the forest ecosystem and the underlying geo-tectonic processes at short intervals at and around the nests. In addition, each RWA nest and its habitat is documented in a photo database with at least two photos to facilitate comparisons of nests and forest ecosystems of different inventories.

### 4.1. Increase in Number of Active Nests

The outstanding occurrence of RWA nest numbers (*F. polycтена*) in the MG and FB study areas was confirmed by the 2023 re-inventory after seven (MG) and four years (FB). This study clearly showed that the total number of active RWA nests increased ( $\approx 8\%$ ) at both sites, but also for BSF ( $\approx 5\%$ ), MF ( $\approx 36\%$ ), and PF ( $\approx 93\%$ ; Table 1; Table 2). This strong increase in RWA nests in PF was observed on large clearing plots, which are thought to promote nest settlements. These results are confirmed by a comparable 12-year re-inventory in the West Eifel Volcanic Field (WEVF), which also showed an increase in RWA nests ( $n_{tot} \approx 10\%$ ;  $n_{act} \approx 6\%$ ) and a quadrupling of nest numbers on clearing plots [30].

Our results do not support the claim that the number of RWA nests in the Oberpfalz is in sharp decline [51]. These differences may be due to the data collection methods (e.g., analogue instead of digital mapping, simple counting of nests without comparing whether nests were recorded in the previous mapping or not, vague data handling from memory), small sample size, and the conclusions based on this [52,53]. In addition, a study on the detection probability of RWA showed that beginners and laypersons had a very low detection probability of RWA nests, in contrast to our high detection probability when mapping RWA nests. High detection of RWA nests is essential for more realistic RWA nest counts [31].

Furthermore, the IUCN Red List is inconsistent with regard to *F. polycтена*, which is listed as ‘not threatened’ by the Red List Centre [54] but as ‘near threatened’ by the IUCN Red List. This IUCN category based on data collected almost 30 years ago and has not been updated or corrected since [55]. Such outdated and contradictory database is neither helpful nor applicable to RWA conservation.

The Sustainability and Regional Conservation Concept of the Waldsassen Forestry Division from 2010, updated in 2019, describes a wide range of conservation measures as an integral part of near-natural forest management. The primary objectives are to maintain and promote biodiversity, to effectively apply conservation measures for RWA species, and to create site-appropriate, near-natural, climate-resilient, productive, and species-rich mixed forests [33]. To protect RWA nests in the BSF, no logging or processing is allowed near neon-colored logs in the vicinity of a nest. The GPS-based (re-)inventory database of RWA nests from the 2016/2019 and 2023 studies will enable the BSF to achieve its overall goal of further protecting RWA nests by prioritizing conservation over timber harvesting [14].

### 4.2. Interconnection of Forest Composition and RWA Nests

#### 4.2.1. Medium-Mature and Mature Pine-Dominated Forests Preferred

Forests in Germany are predominantly commercial forests [56]. At both study areas, human intervention in the forest communities dates back to the Middle Ages and continued

until after the Second World War [33]. Where previously mixed forests of pine, spruce, fir, beech, oak, and lime were dominant, the forest composition was changed by wood-(over)consuming industries and livestock farming with intensive use of litter to conifer-dominated forest stands that characterize the landscape.

In the study areas, the tree age classes preferred by RWA nests are medium mature (61–80 years) and mature ( $\geq 81$ –140 years) pine-dominated forests, corresponding to the average tree age of 77 years of German forests ([57]; Figure 5), confirming our findings from previous inventories [14] in both the Oberpfalz and the WEVF [30] that *F. polyctena* and all nest heights are more abundant in mature forests. Mature spruce-dominated forests are habitats for start-ups, short nests and medium-sized nests, but with lower proportions compared to pine forests. This confirms findings in the WEVF [30], but contrasts with findings that newly planted forests ( $\leq 20$  years) with an open canopy promote nest settlements [58]. The fourfold increase in nest numbers in young (21–40 years; FB<sub>BSF</sub>) and newly planted spruce-dominated areas (MG<sub>BSF</sub>) also contradicts the findings of [59], who did not witness nests in 20-year-old Scots pine stands.

The best methods to manage forests to mitigate climate change and provide multiple ecosystem services for present and future generations is vehemently debated [60]. As a natural change in tree composition is likely to occur very slowly due to low speed of seed dispersal, an active conversion to deciduous and structurally rich mixed forests is suggested to have stabilizing effects on tree composition, species, and habitat diversity [56,60,61]. Therefore, one of the main objectives of the Bavarian Forest Policy and the Sustainability and Regional Conservation Concept of the Waldsassen Forestry Division is to create site-appropriate, near-natural, climate-tolerant, productive, and species-rich mixed forests and to protect valuable forest structures and important habitats through SFM. To support this goal, site-appropriate tree species are planted according to soil variability and conditions [33]: (a) fir (*Abies alba*), oak (*Quercus robur*), and beech (*Fagus sylvatica*) are planted on sandy, silty, or clayey parent material that results in periodically wet soils (MG, [62]), and (b) beech (*Fagus sylvatica*), birch (*Betula pendula*), Douglas fir (*Pseudotsuga menziesii*), fir (*Abies alba*), Russian elm (*Ulmus laevis*), sycamore (*Acer pseudoplatanus*), and walnut (*Juglans regia*) are the preferred tree species on bedrock (granite, granodiorite), resulting in more acidic soil conditions [62–64]. The forest composition observed in the field at and around RWA nest sites suggests (a) a shift from pure coniferous forests to a combination of coniferous and naturally grown deciduous trees and (b) naturally regenerated mixed stands, e.g., spruce–beech–oak, spruce–birch, pine–oak at nest sites. Furthermore, the proportion of deciduous trees such as birch (*Betula pendula*), beech (*Fagus sylvatica*), oak (*Quercus robur*), red elder (*Sambucus racemosa*), alder (*Alnus glutinosa*), or a combination of two deciduous species increased in 2023 (Figure 6). In addition, areas of natural restocking showed pure deciduous species or combinations of these in both inventories, but at lower levels. This also confirms findings that  $\approx 86\%$  of young stocking with trees up to 4 m in height are naturally regenerated [56].

The Fauna-Flora-Habitat (FFH) Directive [65] serves to conserve, maintain, and restore and enable the long-term recovery of protected species and habitat types of common European interest. Natural disturbances can increase tree species diversity, as well as the diversity of biotope trees and deadwood, but can also decrease it, often exacerbated by pest infestations and the removal of damaged timber. The response of value-determining animal species to this particular conservation area has been little studied [66]. The Natura 2000–Fauna-Flora-Habitat area in MG is characterized as a large wetland complex with traditional ponds and pond farming, wet meadows, bog and open habitats, siltation zones, and open water areas [67]. The increased number of nests (especially short nests and medium-sized nests) of RWA, as a key ecological group of forest species, confirm favorable nest locations in these protected areas. In addition, the threefold increase in WpC in nests indirectly indicates a suitable habitat for various woodpecker species in this particular protected area [68].

Finding suggests that climate change-related natural disturbances in forests create early successional forest stages that provide high deadwood availability, light, and habitat heterogeneity. Such stages increase the diversity of many forest species, in particular promoting threatened red-listed species [60,66]. Although the number of cleared plots and partly cleared plots increased between the inventories due to bark beetle (*Ips typographus*, *Pitogenes chalcographus*) infestations, windthrow, and snow break, the number of active nests on these plots tripled by 2023 (Table 2). This result confirms the results of the recent WEVF study [30] and contrasts with the results of [69], suggesting that bark beetle-induced degradation of lignin or holocellulose may negatively affect plant-sucking insects (*Aphidae*, *Coccidae*, *Psyllidae*) living in trophobiosis with RWA [70,71]. To control bark beetle infestations, rapid salvage logging of the infested tree is performed, which has been suggested to reduce the survival of RWA nests [63]. The fourfold increase in the number of new nests, especially of start-ups to medium-sized nests, contradicts the general statement of nest decline [72] on such plots. The spatial distribution of xerothermophilic species, such as the black-backed meadow ant (*F. pratensis*), has been suggested to be promoted by such dry habitats [71,73]. In addition, it has been suggested that the reduction in wood quality in bark beetle-infested spruce stands alters nutrient cycling [70], and therefore smaller colonies in smaller RWA nests may be more likely to survive in cleared or partially cleared areas [30].

#### 4.2.2. Increasing Herbaceous Biodiversity at and around RWA Nests

Important information on forest site characteristics can be obtained from spatial and temporal disturbances in forests that influence and change the diversity of species in the herb layer [74]. In general, the observed composition of the herb layer at, on, and around a nest can be addressed in relation to the specific tree species such as cranberry–spruce–fir–pine forests (*Vaccinio vitis-idaeae-Abietetum*) in MG and FB, and spruce, rowan, and birch (*Betula pubescens-Sorbus aucuparia*) on skeleton-rich soils (silicate blocks) with an acidic humus layer in sections of FB [33]. This study confirms the findings of the previous inventories at and around RWA nests at both sites [14]. In addition to the known main herbs that characterize the forest communities, an increase in herb biodiversity was observed in 2023, although all surveys were conducted in the same months to allow for comparison (Figure 7). This contrasts findings of the WEVF survey, where the herb layer composition decreased dramatically [30]. Reasons for this increase in diversity may reflect inertia due to past environmental changes [75]. Results from Great Britain showed that in addition to bird and butterfly communities, plant communities increased overall in species richness over short (20 years) time scales, associated with increasing temperatures and precipitation. These results cannot be fully confirmed because (a) the time scale of the re-inventory might be too short (four and seven years) and (b) little difference was found in the averaged weather data (e.g., temperature, humidity) for the inventory months in 2016, 2019, and 2023 [76]. A more plausible explanation is a shift in forest composition due to logging, which created open spaces and allowed pioneer plants such as foxglove or mullein to colonize.

#### 4.3. No Negative Impact from Dead Wood

Every forest ecosystem has dead wood, a dynamic resource that is produced and controlled by factors such as tree productivity, forest type and age, disturbances such as harvesting, windthrow, and snow break, and decomposition rates [10,77]. Dead wood plays a key role in forest ecosystems by providing a habitat for a variety of species, contributing to the complexity of forest structure, and influencing fire behavior [78]. In commercially managed forests, standing and coarse woody debris are severely depleted and need to be enriched to combat depletion biodiversity loss [79]. This is the case in the Bavarian state forests, where dead wood is enriched in all stands, but especially in near-natural-forests ( $\geq 140$  and  $\geq 100$  years) with natural tree species composition during harvesting. The enrichment targets are 40 m<sup>2</sup>/ha and 20 m<sup>2</sup>/ha, respectively [80]. In addition, special forest

structures of particular ecological importance are created: (a) coarse DW, (b) biotope trees, and c) tree torsos up to 6 m high, which provide valuable habitats for insects, birds, bats, and small mammals as standing dead wood until their natural decay ([34,80], Figure 2).

The qualitative DW analyses of this study showed that there is a high proportion of DW around RWA nests and identical  $n_{\text{actDW}}/\text{ha}$  ratios at both sites (Table 5). The average amount of  $\approx 44\%$  ( $\text{MG}_{\text{BSF}}$ ) and  $\approx 55\%$  ( $\text{FB}_{\text{BSF}}$ ) for both inventories showed that BSF foresters at both study sites contribute to the overall objective of the Bavarian state forests and to the “2020 Nature Conservation Concept for the Waldsassen Forestry Division” of enriching DW in forests [33].

Private forest owners hold average forest sizes just under 2 ha. The large number of small forests results in a wide range of management options for these owners: from intensively managed “tidy” forests without any DW to extensively managed forests with whole islands of deadwood or irregularly managed forest in intermittent operation with DW there for decades. Most forest owners are open to the issue of dead wood, as evidenced by their willingness to have their forest certified according to the PEFC criteria (74% in Bavaria;). This means that forest owners voluntarily commit to leave an appropriate amount of dead wood and hollow trees [81]. This could be confirmed by the results of this study, which show almost similar proportions of DW at and around RWA nests for both inventories ( $\text{MG}_{\text{PF}}$ :  $\approx 51\%$ ;  $\approx 46\%$   $\text{FB}_{\text{PF}}$ ), which are well comparable to those of the BSF. This development of DW at both sites confirms findings of the federal forest inventories of 2002 and 2012, which showed an increase in DW from 11.6 to 20.6 m<sup>3</sup> per ha [79].

Overall, visual inspection and comparison of more than 12,000 photographs of the newly inventoried nests taken during the fieldwork for this study with those from the previous inventories showed that RWA nests are not negatively affected by downed DW (class 2 and 3), as confirmed by robust nest numbers in all differently owned forests and increased nest sizes (Table 5). The photo comparison showed that RWA simply enlarge their nests and incorporate fallen trees into their nest structure. This is corroborated by the findings of [82] that an artificial “highway” of dead logs in the vicinity of ant nests can promote nest growth, increase survival rates, and increase speed of movement on branches and logs [83]. This contrasts to the findings of Zakharov [84], who observed that dead wood may contribute to the extinction of RWA nests in Ukraine.

Also, the  $n_{\text{actDW}}$ -ha ratio for the different forest owners remained robust in both inventories, with the DW proportion decreasing by  $\approx 12\%$  at and around nests in  $\text{FB}_{\text{BSF}}$  in 2023. Reasons for this may be that (a) DW observed in previous inventories is obscured by growth in nest height (NH) and diameter (ND) between inventories. Comparison and analysis of photographs of re-identified nests taken during the 2016/2019 and 2023 inventories confirmed that RWA incorporated branches and tree stems into the nest structure, eventually obscuring them with nest building material. In addition, standing DW that became downed trees is incorporated by RWA nests. (b) More logs were produced prior to the 1st inventory in 2019, the accumulated DW of which has already decomposed during the current inventory. (c) There has been no scheduled logging since 2018. As a result, less timber and processing volume was produced.

#### 4.4. Increase in WpC in Nests and Cavities

Structured forests with several developmental stages, biotope trees, and a large supply of DW with a variety of (micro)habitats, e.g., bark pockets or woodpecker holes, are important for biodiversity. DW provides food, shelter, breeding, and drumming grounds for various specialists such as woodpeckers [57,68,85].

An indicator of forest biodiversity is the year-round active woodpecker, which uses large breeding territories and is adapted to forest habitat structures of old forests [86]. The observed increase in  $\text{WpC}_{\text{BSF}}$  ( $\approx 22\%$ ) at both sites, especially in short nests and medium-sized nests (Table 6; Figure 8), confirms the findings of [30] for the WEVF, although the increase is smaller compared to the WEVF. The monitoring of abandoned food cavities, which can accumulate over time, can be excluded because woodpecker cavities in nests are

immediately maintained by ants within days and nights. Abandoned cavities negatively affect the temperature and humidity inside the nest and provide access to the nest and food for other predators, such as the European robin (*Erithacus rubecula*), common blackbird (*Turdus merula*), Eurasian jay (*Garrulus glandarius*), and common redstart (*Phoenicurus phoenicurus*), as shown by our year-long 24/7 on-site monitoring of various RWA species (>50,000 h of video; AntCam data by Berberich and Berberich, unpublished). The increase in WpC in nests is also consistent with population increases in several woodpecker species (up to 20%) in Bavaria, such as the Three-toed (*Picoides trydactylus*), Green (*Picus viridis*), and Middle Spotted (*Dendrocopos medius*) Woodpecker [68]. A large selection of DW is a prerequisite for their habitat and was observed at both sites in this study.

Our findings could also indicate a significant increase in the number of woodpeckers at both sites, which has also been observed by the responsible foresters. In particular, Black (*Dryocopus martius*), Green (*Picus viridis*), and Gray (*Picus canus*) woodpeckers forage not only on tree trunks but also in RWA nests and feed on ants [87]. It would be more effective and advantageous for woodpeckers to forage in smaller nests, where prey can be captured more quickly. Foraging in large nests, as seen in the Green Woodpecker (*Picus viridis*), requires digging small tunnels into the nest and a longer stay [30]. The higher cavity-to-NH class ratio in larger nests suggest that such nests contain a large number of queens and their brood. It might be more nutritious to forage in a larger supply of prey compared to smaller nests.

Furthermore, our results suggest that woodpeckers were more abundant in the BSF, suggesting a different forest managing than in the MF and PF (Table 6), e.g., in terms of preservation, enrichment, and replenishment of biotope trees and dead wood.

It is also possible that at the time of the two inventories at both sites, the number of habitat trees was decreasing and a stable woodpecker population was therefore more concentrated in RWA nests, as already suggested for the WEVF [30]. Woodpecker cavities in RWA nests have been suggested to be a valuable, albeit indirect, indicator for assessing woodpecker populations and their forest habitats [30,86].

#### 4.5. GeoBio-Interactions: Shift of Nest Hotspots from NE to SW

Dense forest, agriculture, and sediment cover limit the knowledge of the overall tectonic regime in both study areas. Recent studies in European countries, e.g., Denmark, Romania, and Germany, as well as the 2016/2019 inventories in the Oberpfalz with a focus on GeoBio-Interactions, have shown that tectonic-volcanic processes and geochemical composition of the bedrock, e.g., high soil radon concentrations, promote nest settlement, their high nest numbers, and the spatial distribution of RWA nests [14–23].

During the period between the inventories (four to seven years), seismic activity has increased, creating faults and providing degassing pathways in this region [88,89]. Such structures are the most important prerequisite for nest settlements [14–23,30,31]. The ≈9% increase in the total number of small nests (ND < 0.5 m; Table 1), the survival of more than ≈50% of start-ups and short nests since the last inventories, and the positive growth of nest size from start-ups and short nests to larger nests ( $n_{\text{actR}}$ ) are considered to indicate favorable settlement conditions due to active tectonics and confirm that RWA nests are bioindicators of such tectonic structures [14–23,30,31]. In addition, the long persistence of large nests is suggested to indicate that the underlying fault structure and degassing over time are stable, providing a suitable location for RWA, e.g., the continuous, moderately warm granites [90] support the survival of small nests during winter in the study areas [14,91] and their growth into larger nests [14]. This is also consistent with evidence from the tectonically active WEVF [30].

The highly clustered nests, especially in NW–SE direction, suggests a strong interaction between RWA nests distributions and tectonic structures in all inventories, namely (1) the NW–SE present-day stress field, (2) the fault line “Erbendorfer Linie” [36,47], and (3) the NW–SE to NNW–SSE-trending intrusion direction of the Falkenberger Granite Complex [90], confirming the GeoBio-Interaction findings in this area (Figures 1a and 9; [14]). This is in

contrast with entomological studies, which suggest that the spatial distribution pattern of RWA nests and their local occurrence are controlled by, e.g., foraging and food supply, e.g., [92].

Furthermore, a shift of the nest hot spots towards the NW–SE-trending fault line “Erbendorfer Linie” in MG (Figure 9) is suggested to be caused by stronger degassing of the tectonically and structurally controlled “Erbendorfer Linie”, which promotes RWA nest settlements [16,19] due to an increase in regional seismicity as an important driving force causing micro-fracturing (Figure 1a). These new fractures provide pathways for juvenile fluids with mantle-derived CO<sub>2</sub> and Helium to migrate over long distances, indicating hidden volcanic structures in the vicinity of these degassing sites [42,43,88,89]. In addition, seismic events lead to the formation of new emanation surfaces and pathways and a significant increase in the radon signal, even though the applied stress remains constant over time [93]. At the same time, RWA nest hot spots are decreasing in the NE section of the MG study area. These areas are hypothesized to have a reduced degassing output or even closure of degassing structures due to the regional seismicity [19,42,43]. The spatial distribution of RWA nests complements and clarifies the tectonic regime, as information on small-scale fault systems in MG and FB study area is obscured by vegetation cover. This hypothesis, already established in previous studies, has now been further confirmed [14,19].

#### 4.6. Seven to Eight Year Re-Inventory Interval

A suitable and adequate time interval for re-inventories is a critical aspect for long-term monitoring of RWA nests. Re-inventories after different decades show different results: (a) constant nest numbers after two decades (England and Romania), (b) RWA being “under intense pressure” after three decades (Belgium), and (c) decreases and increases in nest counts after six decades (The Netherlands; [94–97]). Re-inventories with a time interval of  $\geq 20$  years are not suitable for documenting the dynamics of RWA populations and the associated forests compositions because (a) the dynamic systems of forests change rapidly, e.g., human intervention (e.g., logging) or natural effects (e.g., windthrow, snow break; [14,30]) and (b) the vitality of German forests is affected by climate change (hot summers, lack of precipitation) much faster than expected and might affect RWA population dynamics [57].

Our multiple experiences and findings from re-inventories of RWA nests carried out in the WEVF after 50, 25, 18, and 12 years [18,30] have already shown an increase in the number of RWA nests, with maximum increases up to 85-fold (2021) compared to the 1984 inventory [30]. An increase in active RWA nests ( $n_{act}$ ) of  $\approx 10\%$  for MG and  $\approx 6\%$  for FB was also confirmed in this study, which was conducted after seven years (MG) and four years (FB). Due to the longer timeframe of the re-inventory, growth and changes in RWA nest distribution are more apparent in MG than in FB. Based on our extensive experience with re-inventories of RWA nests and because the spatial distribution patterns of RWA nests can change rapidly over time, a time interval for re-inventories of seven to eight years seems appropriate for quantifying changes. This interval would also allow changes in forest ecology to be documented prior to updating the 10-year forest inventory and management plan at both sites. In order to compare the inventory methods, it is recommended that the inventory approach we have described be used and supplemented with the extensive photo database. This approach can be used to document not only the effects of climate change on forest vitality but also the potential effects on RWA population dynamics and to identify interactions between species and the BioGeo-Ecosystem [18,30,75].

## 5. Conclusions

In a first systematic, large-scale, area-wide re-inventory in two sustainably managed forests, we recorded presence/absence data of red wood ant (RWA; *Formica rufa*-group) nests in two study areas in the Oberpfalz, NE Bavaria, Germany. Results are as follows: (1) RWA nest numbers: We inventoried outstanding nest occurrences (5393 nests including 5276 active nests) and an increase of  $\approx 8\%$  over 4–7 years. (2) Forest composition: RWA

nests preferred mature ( $\geq 81$  years) and medium mature (61–80 years) pine-dominated forests. The increased biodiversity of the herb layer at and around nests is thought to be related to a shift in forest composition due to logging, which created open spaces and allowed pioneer plants such as foxglove or mullein to colonize. (3) Dead wood: High proportions of standing and downed dead wood, which are enriched in the course of SFM at both study sites, do not negatively affect nests, as confirmed by robust nest numbers and increased nest sizes in all differently owned forests. (4) Woodpecker cavities: The observed increase in woodpecker cavities and the number of nests with woodpecker cavities is an indirect indicator for the assessment of woodpecker populations and their forest habitats. (5) GeoBio-Interactions: The highly clustered nests, especially in NW–SE direction, suggests a strong interaction between the distribution of RWA nests and their tectonic environment at both sites and in all three inventories. (6) Time intervals: We suggest seven to eight years as an appropriate time interval for re-inventories to quantify changes in nest numbers, forest composition, dead wood, woodpecker cavities, and the herb layer.

In addition, we were able to show that (1) the near-natural sustainable forest management not only maintains and promotes biodiversity and species-rich mixed forests, but also effectively protects RWA species, and (2) in order to protect RWA, it is not enough to simply monitor their presence/absence, but it is also important to identify interactions between species and the BioGeo-Ecosystem.

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