

Article

A Re-Inventory after 12 Years—Increase in Red Wood Ant Nests and Woodpecker Cavities in Nests in the West Eifel Volcanic Field despite Climatic Changes

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Abstract: We re-inventoried red wood ant nests (RWA) in 12 study sites (≈ 1281 ha) in the tectonically active Westeifel Volcanic Field, Germany, in an area-wide and integrated ecosystem approach after 12 years. Combined with the re-identification of previously mapped nests using a photo database, this approach leads to more accurate nest counts in (re)inventories. A total increase in nests from 1144 (2009) to 1252 (2021), and a dramatic one for the Heidelberg site by 52-fold (2009) and 85-fold (2021) compared to a 1984 inventory was observed, contrasting with earlier postulations of a decline in RWA. Early to medium mature (41–80 years) and mature (≥ 81 –140 years) spruce forests were the preferred habitat. A large increase in small-sized nests suggests an increase in new nest settlements also in clearings, despite climate-induced forest dieback over the past decade. A decline in biodiversity in the herbaceous layer was observed; highly proliferating blackberries had no negative impact on RWA nests. Monitoring of woodpecker cavities in RWA nests is suggested as an indirect indicator tool for evaluating populations in forests. Positive ground movement rates caused by the Eifel plume are suggested as another factor favoring nest settlements, especially in NE-SW and WNW-ESE directions. This study contributes to the urgent need for updating the statistical data required to (a) effectively substantiate the status quo of RWA occurrences, (b) protect RWA as ecosystem engineers, (c) advance understanding of GeoBio-Interactions in the wake of climate change, and (d) contribute to the German government’s Insect Conservation Action Program.

Keywords: red wood ants (*Formica rufa*-group); tree age classes; West Eifel Volcanic Field; herbaceous layer; woodpecker cavities; clearings; re-inventory; climate change



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1. Introduction

Recent studies suggest plate tectonics as a fundamental driver of global biodiversity in marine and terrestrial ecosystems (e.g., [1]). Understanding these processes is critical to ecology and biology. Insects are the world’s most diverse group of animals and are essential to the functioning of terrestrial ecosystems. This is especially true for red wood ants (*Formica rufa*-group; hereafter RWA), a key ecological group of species (e.g., [2]). Their interactions with the environment are most diverse, e.g., contributing to forest habitat biodiversity (e.g., [3]), controlling of undesirable insects (e.g., [4]), and indicating undetected tectonic activity and geogenic gases (“GeoBio-Interactions”) that play a critical role in their settlement (e.g., [5–14]).

Recent works report declines in insect diversity, species, and biomass in Europe due to habitat loss and fragmentation, pollution, climate change, or invasive species (e.g., [15,16]). For RWA, some researchers suggest declines (e.g., [17,18]), while others report population increases (e.g., [19,20]). A decline in RWA populations is also postulated for Germany [21]. Therefore, RWA are considered of conservation concern in Germany and are included in the German government’s Insect Conservation Action Program [22–24].

However, a reliable, statistically valid database for Germany on the distribution of RWA nests and species to substantiate the postulated threats and declines is completely lacking so far, as a standardized and systematic monitoring of RWA has been discontinued since the 1980s.

Therefore, no statements about a much-needed protection status can be made at present. In this re-inventory study, conducted after 12 years in the tectonically active Westeifel Volcanic Field (WEVF), we applied our standardized and integrated mapping approach for RWA which not only counts the number of RWA nests, but records the coordinates of their location and monitors the entire ecosystem around an RWA nest, e.g., tree species, tree age, and herb layer [6]. For a comparative analysis of RWA population dynamics [10], 12 study sites (total ≈ 1281 ha) were selected that had to meet the following criteria: (a) more than 20 nests in 2009 [14], (b) well-defined study site boundaries, and (c) location within and on the edges of the WEVF.

We investigated forest–tectonic interactions by asking five interrelated questions: (1) What are the requirements for reliable, science-based, standardized, and statistically valid re-inventories of RWA nests? (2) Are the number of RWA nests and their physical nest parameters decreasing or increasing in the study sites compared to the 2009 inventory? (3) What influence do variable factors (e.g., forest stand type and composition, tree age, clearings, and herbaceous layer) have on potential changes in nest numbers? (4) Are there other biological influences on RWA nests such as woodpeckers?, and (5) What influence do quasi-invariant factors, such as ground movement or Radon concentrations have on RWA nest distribution (GeoBio-Interactions)? We asked these questions specifically with respect to individual RWA nests. These results will further improve the understanding of the “GeoBio-Interactions”, contribute to better protection of RWA in forest management in the WEVF, and contribute to the German government’s Insect Conservation Action Program.

2. Materials and Methods

2.1. Location and Geologic Setting

The 12 forested study sites, Duppach (01-Dup); Dockweiler Wald (02-Doc), Oberehe (03-Obe), Samersbach (04-Sam), Neunkirchen/Oberstadtfeld (05-Neu), Marschbachtal (06-Mar), Salm (07-Sal), Berndorf (08-Ber), Lissendorf (09-Lis), Heidberg (10-Hei), Vierherrenstein (11-Vie), and Rockeskyll (12-Roc) were located around and within the volcanic center of the Quaternary WEVF (Figure 1), which is part of one of the youngest and most active volcanic regions in Europe [25]. The Paleozoic basement consists of Lower Devonian and Triassic sedimentary rocks and Neogene and Quaternary volcanic rocks. Ongoing geotectonic processes, such as uplift caused by the active magma reservoir (“Eifel plume”) in the lithospheric mantle and the present-day NW–SE-directed compressive stress field influence the regional tectonics and geochemistry of the NW–SE directed volcanic field [14]. The site locations are about ≈ 100 km away from Cologne, North-Rhine-Westphalia (NRW), and ≈ 60 km from Koblenz (Rhineland-Palatinate, RLP), West Germany and were part of the PhD thesis of the first author [14]. The hilly landscape (350–650 m a.s.l.) is characterized by individual ridges, cinder cones, and basalt domes as well as deep valleys, and cut by rivers such as river Kyll. The forest, with an area share of almost 50%, is the economically most important sector, followed by the agricultural sector (42%). The annual average temperatures range from -1.5 °C to 14 °C [26].

2.2. Forest Owners

The study sites are part of five forest districts (FD) in RLP and NRW: FD Prüm, FD Gerolstein, FA Daun, FD Hillesheim, and FD Gemeindeforstamt Dahlem. The State (SF), municipal communities in RLP and NRW (MF), and private persons (PF) hold portions of the forest. In accordance with the five forest districts, the medium tree age class was chosen for all analyses.

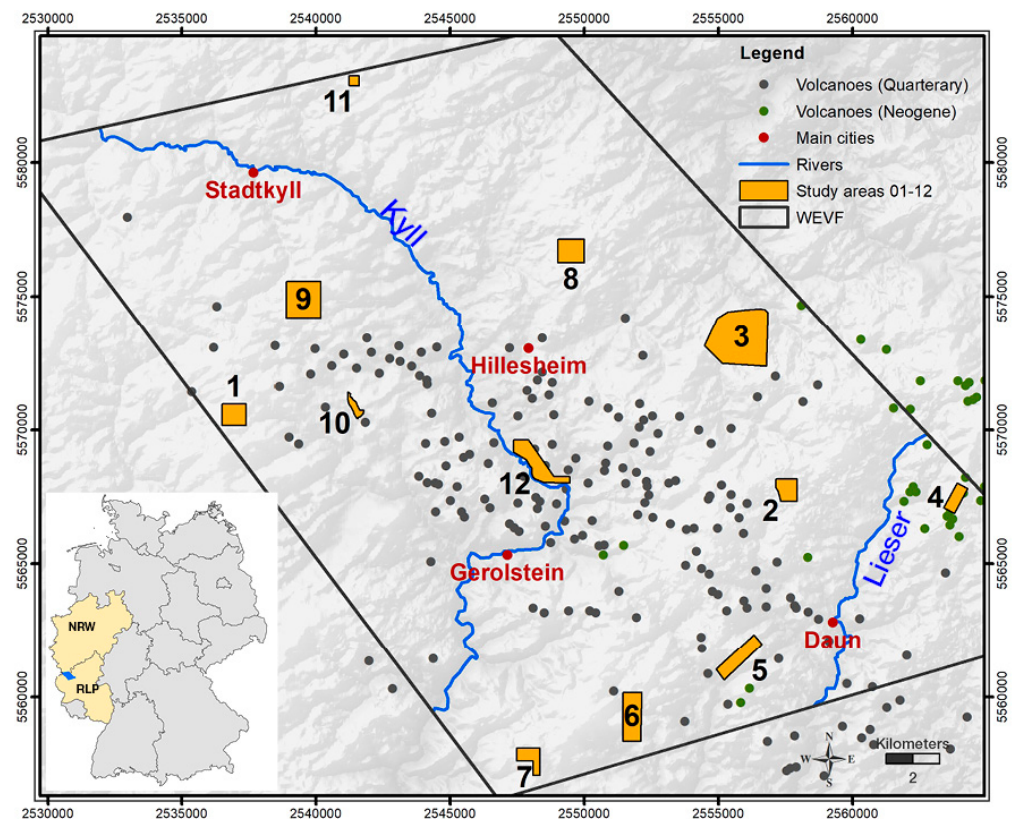


Figure 1. Schematic depiction of the position of the 12 study sites (orange areas) within the West Eifel Volcanic Field (WEVF; black border), main rivers (blue lines), Quaternary (gray dots), and Neogene volcanoes (green dots) underlain by a digital surface model (DSM). Inlet shows location of the WEVF within Germany in Rhineland-Palatinate (RLP) and North-Rhine-Westphalia (NRW; [14,27]).

2.3. Standardized, Integrated Mapping Approach and Data Collection

Mapping of RWA nests followed the area-wide, systematic, reproducible, and integrated approach developed by Berberich et al. [6,14]. A total of ≈ 1281 ha were mapped in two inventory campaigns, in 2009 and 2021. The total number of RWA nests (n_{tot}) was mapped in all 12 study sites using GPS receivers (Garmin 60CSx and 62S). Random sampling of RWA species in the field revealed that mainly *F. polycтена* and *F. pratensis* were identified, because *F. rufa* and *F. polycтена* are not easily distinguished without binoculars. Six nest height classes (NH; 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, extra tall: >2.01 m), five diameter classes (ND; small: 0.01–0.50 m, medium: 0.51–1.00 m, large: 1.01–1.50 m, very large: 1.51–2.00 m, extra-large >2.01 m), inactive (n_{inact} ; nest structures were still present but no ant activity was observed during the inventory; therefore, the nest was considered dead) and active nests (n_{act}), and the nest location (e.g., within the forest, forest roads, forest edges, open areas), were classified in the field. In addition, qualitative information on tree species (e.g., spruce, pine) and herbaceous layer (e.g., nettles, grass, blackberry) on and around the RWA nest was recorded. Furthermore, cavities created by woodpeckers in each nest (WpC) were counted in the field. Finally, at least two photographs (landscape and normal format) were taken of each nest. These photographs were used to compare and (re)-identify (a) nests, (b) forest composition, and (c) herbaceous layer mapped in 2009 and 2021.

2.4. Definition of Variable Site Factors

In this study, we applied similar variable factors as in a previous study [6] that are influenced in a short time frame: (1) total number of nests (n_{tot}), (2) number of active nests (n_{act}), (3) number of inactive nests (n_{inact}), (4) NH, (5) ND, (6) nest location, (7) primary tree species (TS_{prime}), (8) secondary tree species (TS_{sec}), (9) medium tree age classes, (10) herba-

ceous layer, (11) spatial distribution of RWA nests, (12) woodpecker cavities (WpC), and (13) clearing plots. Forest information on ownership type (SF; MF; PF) and medium tree age (mTA) was taken from the most recent forest inventories and management plans of the different forest offices, which contain five general tree age classes: newly planted (<20 years), young (21–40 years), early mature (41–60 years), medium mature (61–80 years), mature (≥ 81 –140 years).

2.5. Data Analysis

MATLAB R2019b and the geographic information system ArcGIS 10.8.2 were used for analyses. To investigate whether RWA nests were evenly or randomly distributed or clustered, point distribution statistics (X^2 -test) was applied. Patterns of multiple dependent variable factors were investigated by applying one-way ANOVA, Kruskal–Wallis Test and Multivariate ANalysis Of VAriance (MANOVA). To identify differences in the qualitative text-based data set of the herbaceous layer and to visualize the results, word frequency analysis and font colors were applied. The bigger and more pronounced or bolder a word is, the more significant it is in the word cloud.

3. Results

In both inventories, RWA nests were spatially clustered, as indicated by a nearest neighbor ratio < 1 (2009: 0.4; 2021: 0.3) and Z-statistic -1.96 (2009: -11.03 ; 2021: -20.12) at the 95% significance level. The returned value of p indicates that Kruskal–Wallis and multiple comparison results for both inventories for physical nest parameters (NH, ND) of active nests, medium tree age (mTA) for TS_{prime} , and woodpecker cavities (WpC) in nests confirmed the null hypothesis that the data for NH-ND, NH-mTA, ND-WpC, ND-mTA, and WpC-mTA come from the same distribution at the 1% significance level and that there is no significant difference between these groups in both inventories (Table 1a). A difference is indicated by a slightly elevated p -value for NH-WpC in the 2021 inventory, suggesting a change in continuous distribution (Table 1b). Results of the MANOVA differ from 2009 to 2021 (Figure 2a) and showed in combination with the grouped scatter plots of the first two canonical variables more separation between groups as well as (a) a shift to smaller NH and ND sizes, (b) a strong increase in WpC, and (c) a shift of mTA to more mature forests in 2021 (Figure 2b).

Table 1. Results of (a) Kruskal–Wallis ANOVA test and (b) multiple comparison results for the 2009 and 2021 inventory for physical nest parameters (NH, ND) of active nests and medium tree age (mTA) for TS_{prime} and woodpecker cavities (WpC) at the 1% significance level.

(a) 2009						(a) 2021					
Source	SS	df	MS	Chi-sq	Prob > Chi-sq	Source	SS	df	MS	Chi-sq	Prob > Chi-sq
Groups	4503029613	3	1501009871	2974.7	0.00	Groups	3916176557	3	1305392186	2418.48	0.00
Error	2003097694	4295	466,379.0			Error	3287961357	4446	739,532.47		
Total	6506127307	4298				Total	7204137914	4449			
(b) 2009						(b) 2021					
Group A	Group B	Lower Limit	A-B	Upper Limit	p -Value	Group A	Group B	Lower Limit	A-B	Upper Limit	p -Value
NH	ND	−525.5	−390.7	−255.8	0.0000	NH	ND	−711.1	−575.5	−440.0	0.0000
NH	WpC	758.8	893.6	1028.5	0.0000	NH	WpC	−362.1	−226.6	−91.1	0.0001
NH	mTA	−2119.8	−1981.8	−1843.7	0.0000	NH	mTA	−2634.6	−2492.0	−2349.4	0.0000
ND	WpC	1149.5	1284.3	1419.1	0.0000	ND	WpC	213.4	348.9	484.5	0.0000
ND	mTA	−1729.2	−1591.1	−1453.1	0.0000	ND	mTA	−2059.1	−1916.5	−1773.9	0.0000
WpC	mTA	−3013.5	−2875.4	−2737.4	0.0000	WpC	mTA	−2408.0	−2265.4	−2122.8	0.0000

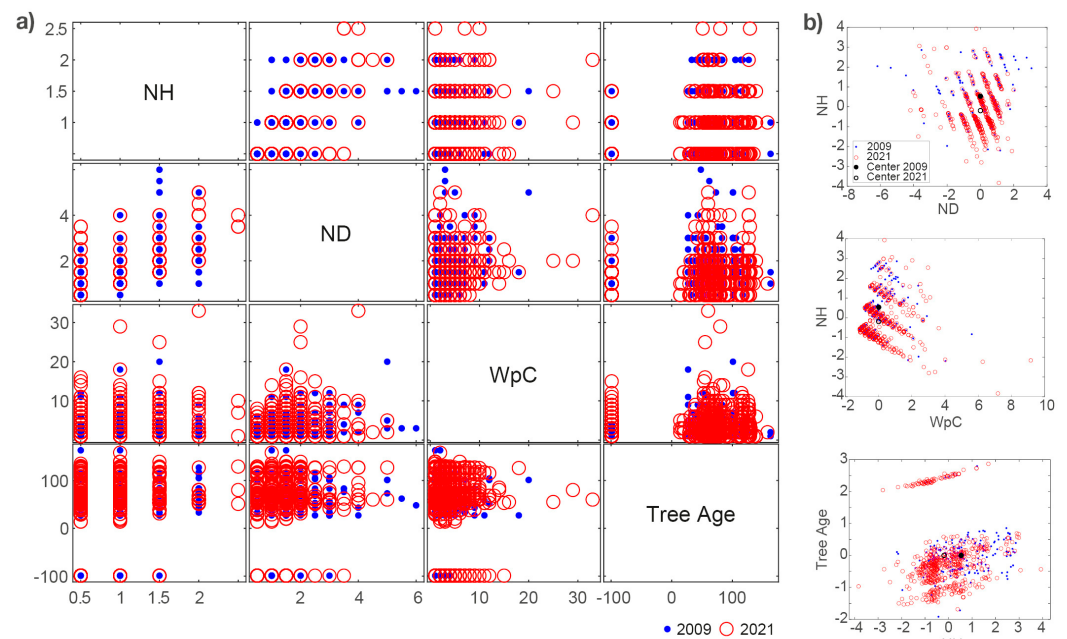


Figure 2. Results of MANOVA for NH, ND, medium tree age (TS_{prime}), and woodpecker cavities (WpC) showing (a) a grouped plot matrix and (b) grouped scatter plots of the first two canonical variables and their centers for the 2009 and 2021 inventories. Tree age with a -100 signature represents no trees or clearings in the study sites.

3.1. Physical Nest Parameters

In both inventories, nest counts differed between active nests (n_{act}) and inactive nests (n_{inact}). In 2009, a total of 1144 nests (n_{tot}) were mapped ($n_{\text{act}} = 1099$; $n_{\text{inact}} = 45$; Figure 3a); in 2021, this number increased to 1252 nests ($n_{\text{act}} = 1164$; $n_{\text{inact}} = 88$; Figure 3b). This is an overall increase of 108 RWA nests ($\approx 10\%$) in all sites and an increase in active nests of $\approx 6\%$ in 2021. Eight of 12 study sites showed a significant increase in nest numbers compared to 2009, of which four sites, 05-Neu (98%), 01-Dup and 10-Hei (both 46%), and 12-Roc (45%) had the highest increase; four study sites (02-Doc, 03-Obe, 07-Sal, 09-Lis) showed a decrease (Figure 3; Table 2). The re-inventory in study site 07-Sal could only be carried out incompletely, because due to the hazard situation (snow breakage) in winter 2020/2021, entry to central areas was not allowed. Therefore, it cannot be excluded that the total number of nests was higher, so the decrease in nests in this area must be interpreted with caution.

In total, 342 RWA nests (n_{totR}) and their forest habitat were re-identified and re-mapped ($n_{\text{actR}} = 296$ nests) using the GPS records and the 2009 photo data base. The number of re-mapped nests varied across the 12 study sites (Figure 3b; Table 2): The highest re-mapped nest numbers ($\approx 40\%$ on average) were found in study sites 11-Vie, 02-Doc, 03-Obe, and 10-Hei. Sites 08-Ber, 04-Sam, 07-Sal, and 05-Neu had the highest increase ($\approx 83\%$ on average) in new nests. On the other hand, the highest nest losses ($\approx 80\%$ on average) were recorded in 07-Sal, 08-Ber and 04-Sam, and 02-Doc. Only active nests (2009: 1099 n_{act} ; 2021: 1164 n_{act}) are discussed below.

In 2021, a strong overall shift toward smaller nests was observed, e.g., start-ups and short nests, as $\approx 65\%$ of nests were recorded in these two height classes (2009: $\approx 47\%$), suggesting a surge in new nest foundations. In particular, short nests nearly doubled from $\approx 34\%$ (2009) to $\approx 55\%$ (2021). A quarter of the nests were medium-sized in 2021 (2009: $\approx 30\%$). In 2021, $\approx 11\%$ (2009: $\approx 23\%$) could be classified as tall and very tall nests (Table 2). The same trend was observed for nest diameters. In 2021, $\approx 61\%$ could be classified as small and medium diameters (2009: $\approx 54\%$). One fifth of all nests showed large diameters in both inventories. In 2021, the largest diameters (≥ 1.51 m) were also declining ($\approx 17\%$; 2009: $\approx 25\%$).

Table 2. Descriptive statistics of total nest numbers (n_{tot}), active nest numbers (n_{act}), nest height (NH), and diameter classes (ND) of RWA nests in the 12 study sites for the 2009 and 2021 inventories. Increases in active nest numbers (n_{act}) and percentages are set in bold. – = not present.

2009										2021								2009–2021	
Nest Height (NH) Classes of Active Nests (n _{act})																			
No	Study Site	Numbers		n						Numbers		n						n _{act}	%
		n _{tot}	n _{act}	Start-Ups	Short	Medium	Tall	Very Tall	Extra Tall	n _{tot}	n _{act}	Start-Ups	Short	Medium	Tall	Very Tall	Extra Tall		
				0.01–0.10	0.11–0.50	0.51–1.00	1.01–1.50	1.51–2.00	>2.01			0.01–0.10	0.11–0.50	0.51–1.00	1.01–1.50	1.51–2.00	>2.01		
01	Dup	102	97	1	26	26	18	26	–	153	142	14	44	40	32	12	–	45	46
02	Doc	147	142	10	40	74	5	13	–	81	57	10	24	16	5	1	1	–85	–60
03	Obe	216	210	44	74	37	3	52	–	170	163	23	77	46	14	2	1	–47	–22
04	Sam	96	93	7	31	42	9	4	–	109	103	2	59	30	11	1	–	10	11
05	Neu	66	64	10	19	27	7	1	–	135	127	11	74	37	5	–	–	63	98
06	Mar	76	71	18	17	17	19	–	–	94	93	4	56	22	11	–	–	22	31
07	Sal	117	108	17	57	21	13	–	–	80	78	2	53	22	1	–	–	–30	–28
08	Ber	103	100	22	56	22	–	–	–	150	142	31	96	15	–	–	–	42	42
09	Lis	92	85	9	34	24	18	–	–	85	78	5	54	11	8	–	–	–7	–8
10	Hei	52	52	5	5	28	14	–	–	85	76	3	62	10	1	–	–	24	46
11	Vie	48	48	–	11	–	14	23	–	66	63	2	17	21	12	10	1	15	31
12	Roc	29	29	–	3	10	16	–	–	44	42	1	29	9	2	1	–	13	45
	Total	1144	1099	143	373	328	136	119	0	1252	1164	108	645	279	102	27	3	65	6
Nest Diameter (ND) Classes of Active Nests (n _{act})																			
No	Study Site	Numbers		n						Numbers		n						n _{act}	%
		n _{tot}	n _{act}	Small	Medium	Large	Very Large	Extra-Large	–	n _{tot}	n _{act}	Small	Medium	Large	Very Large	Extra-Large	–		
				0.01–0.50	0.51–1.00	1.01–1.50	1.51–2.00	>2.01	–			0.01–0.50	0.51–1.00	1.01–1.50	1.51–2.00	>2.01	–		
01	Dup	102	97	28	19	16	16	18	–	153	142	28	29	29	22	34	–	45	46
02	Doc	147	142	16	44	49	24	9	–	81	57	15	16	12	6	8	–	–85	–60
03	Obe	216	210	76	58	35	19	22	–	170	163	62	45	32	16	8	–	–47	–22
04	Sam	96	93	8	21	28	14	22	–	109	103	17	32	37	13	4	–	10	11
05	Neu	66	64	15	12	13	15	9	–	135	127	38	44	31	13	1	–	63	98
06	Mar	76	71	25	13	10	6	17	–	94	93	33	31	26	3	–	–	22	31
07	Sal	117	108	50	23	15	7	13	–	80	78	28	32	12	3	3	–	–30	–28
08	Ber	103	100	36	39	19	4	2	–	150	142	81	33	17	7	4	–	42	42
09	Lis	92	85	29	20	15	10	11	–	85	78	22	32	15	6	3	–	–7	–8
10	Hei	52	52	14	18	13	3	4	–	85	76	16	32	15	8	5	–	24	46
11	Vie	48	48	3	12	9	11	13	–	66	63	7	11	23	10	12	–	15	31
12	Roc	29	29	5	2	12	5	5	–	44	42	5	18	11	8	–	–	13	45
	Total	1144	1099	305	281	234	134	145	–	1252	1164	352	355	260	115	82	–	65	6

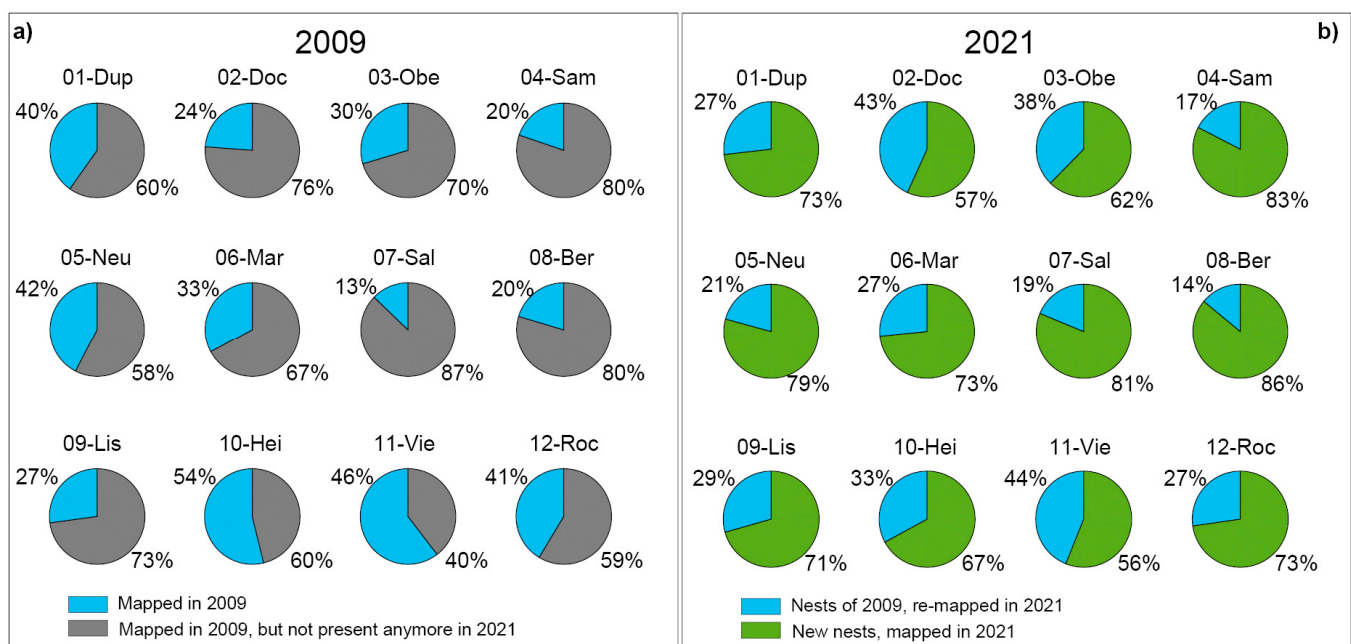


Figure 3. Gain and loss of RWA nests (total) in 12 study sites for the (a) 2009 and (b) 2021 inventory.

3.2. Type and Composition of Forest Stands, Tree Age, and Clearing Plots

In 2009, coniferous forest was strongly dominated by spruce (*Picea abies*; $\approx 79\%$) as the primary tree species (TS_{prime}). Mixed conifer stands were characterized by spruce (TS_{prime}) and larch (*Larix decidua*; $\approx 5\%$), Douglas-fir (*Pseudotsuga menziesii*; $\approx 4\%$), and pine (*Pinus sylvestris*; $\approx 1\%$). Deciduous trees such as sessile oak (*Quercus petraea*) and beech (*Fagus sylvatica*) accounted for $\approx 2\%$ as TS_{prime} , whereas beech (*Fagus sylvatica*) accounted for $\approx 15\%$ as secondary tree species (TS_{sec}). In 2021, forest compositions changed as the proportion of spruce ($\approx 76\%$ TS_{prime}) and larch ($\approx 3\%$ TS_{prime}) decreased. The proportion of sessile oak and beech as TS_{sec} ($\approx 2\%$) was also reduced.

In absolute numbers, early mature (41–60 years) spruce-dominated forests (TS_{prime}) were the preferred location for RWA nests (41%) in all study areas. Here, $\approx 13\%$ of short and $\approx 14\%$ of medium-sized nests were mapped in 2009. A quarter of all nests were mapped in mature (≥ 81 –140 years) spruce-dominated forests (TS_{prime}), of which $\approx 9\%$ were short and $\approx 7\%$ medium nests. In 2021, $\approx 45\%$ of the RWA nests ($\approx 25\%$ short nests) were mapped in early-to-medium mature spruce forests (41–80 years) and one third in mature forests ($\approx 14\%$ short nests). Deciduous trees, e.g., beech, were not relevant TS_{primes} as given by the low RWA nest counts. In 2009, percentages of ND classes in early mature forest were similar ($\approx 11\%$) for small and large diameters. In mature forests, small and medium diameters accounted for $\approx 13\%$ (2009) and $\approx 17\%$ (2021), respectively. Forest composition observed in the field differed from forest records, showing a shift from conifer stands such as pure spruce stands (2009: $\approx 53\%$; 2021: $\approx 34\%$) and spruce–larch stands (2009: $\approx 3.2\%$; 2021: $\approx 1.5\%$) to naturally regenerated mixed stands consisting of, e.g., spruce–beech (2009: $\approx 21\%$; 2021: $\approx 30\%$), spruce–oak (2009: $\approx 2\%$; 2021: $\approx 5\%$).

Overall, clearing activities increased at each site between the two inventories, e.g., due to bark beetle infestation or snow breakage. The size of clearing plots with active RWA nests doubled from 5 ha (2009) to ≈ 11 ha (2021), but the total number of active nests on these clearing plots quadrupled in 2021 ($n_{\text{actC}} = 205$; 2009: $n_{\text{actC}} = 51$; Table 3), especially for start-ups ($\approx 14\%$) and short ($\approx 64\%$) nests, but also for medium nests ($\approx 18\%$). The greatest clearing activity occurred at four study sites that showed large increases in nest numbers in the clearing plots: 03-Obe (2021: 61; 2009: 26), 04-Sam (2021: 58; 2009: 16), 08-Ber (2021: 29; 2009: 4), and 07-Sal (2021: 17; 2009: 0). Surprisingly, 41 active RWA nests from 2009 were re-identified on current clearing plots: 01-Dup (3), 03-Obe (18), 04-Sam (11); 05-Neu (1),

07-Sal (2), 08-Ber (2), and 09-Lis (4) in 2021. About one third of these nests ($n_{act} = 13$) were previously mapped in 2009 (03-Obe: 9), 04-Sam (2), and 08-Ber (2) on clearing plots.

Table 3. Descriptive statistics of mapped area (ha), forest owners (SF, MF, PF) that hold share of the mapped area, numbers of active nests (n_{act}), size of clearing plots with active RWA nests for the 2009 and 2021 inventory; – = not present.

No	Study Site	Mapped Area	State Forest (SF)		Municipal Forest (MF)		Private Forest (PF)		Number of Nests (n_{act}) 2009			Number of Nests (n_{act}) 2021			Clearing Plots with RWA Nests			
			ha	ha	%	ha	%	ha	%	SF	MF	PF	SF	MF	PF	2009	2021	2021
01	Dup	72.4	38.2	52.8	4.9	6.8	29.3	40.5	66	–	31	104	–	38	2.13	2	0.38	16
02	Doc	59.3	–	–	59.3	100.0	–	–	–	142	–	–	57	–	–	–	0.28	–
03	Obe	408.5	–	35.9	261.7	64.1	–	–	118	92	–	108	55	–	1.38	26	2.69	61
04	Sam	46.7	–	–	33.9	72.6	12.8	27.4	–	85	8	–	98	5	0.87	16	3.4	58
05	Neu	92.9	–	–	60.6	65.2	32.3	34.8	–	34	30	–	95	32	–	–	0.03	1
06	Mar	124.7	0.8	0.6	82.8	66.4	41.1	33.0	–	63	8	–	77	16	–	–	0.38	1
07	Sal	56.5	50.7	89.7	–	–	5.8	10.3	108	–	–	78	–	–	–	–	1.36	17
08	Ber	85.2	–	–	–	100.0	–	–	–	100	–	–	142	–	0.25	4	1.24	29
09	Lis	176.6	–	–	171.2	96.9	–	3.1	–	77	8	–	73	5	–	–	0.64	10
10	Hei	21.4	–	–	3.7	17.3	17.7	82.7	–	28	24	–	37	39	–	–	0.43	12
11	Vie	14.1	–	–	6.3	44.7	7.8	55.3	–	25	23	–	33	30	0.15	3	–	–
12	Roc	122.9	–	–	105.1	85.5	17.8	14.5	–	29	–	–	42	–	–	–	–	–
Total		1281.2	236.5	18.5	874.7	68.3	170.0	13.3	292	675	132	290	709	165	4.78	51	10.83	205

* ha sizes estimated from satellite imagery (Google Earth) for 2009 and 2020/2021.

The percentages of nest numbers in SF, MF, and PF were almost the same for the three different forest owners in both inventories: SF ($\approx 26\%$), MF ($\approx 61\%$), and PF ($\approx 13\%$; Table 3). In 2009, one third of tall and very tall nests (≥ 1.01 m) were observed in PF, one-fourth in SF, and one fifth in MF. In 2021, the numbers were lower (PF $\approx 21\%$, SF $\approx 12\%$, and MF $\approx 8\%$). In exchange, the number of nests doubled for short nests in SF, MF, and PF, with the highest increase in MF ($\approx 57\%$), followed by PF ($\approx 54\%$) and SF ($\approx 52\%$; Table 3). At study sites 02-Doc and 09-Lis, losses were highest primarily for short, medium, and tall to very tall nests in MF.

In 2021, $\approx 71\%$ (2009: $\approx 76\%$) of active nests were within forest stands (including forest roads and skid trails), approximately one fifth (2009: $\approx 8\%$) were in open space areas (e.g., clearing plots), and $\approx 11\%$ (2009: $\approx 15\%$) were at forest edges.

3.3. Herbaceous Layer

In both inventories, single occurrences of grasses (*Poaceae*) and mosses (*Bryophyta*) or a combination of both herbs were highly abundant as visualized by word clouds in Figure 4a (2009: $\approx 54\%$; 2021: $\approx 45\%$). The combination of grasses (*Poaceae*) and blackberries (*Rubus*) increased from $\approx 9\%$ (2009) to $\approx 14\%$ (2021). In addition, the proportion of blackberries in combination with moss, broom (*Genista*), and other plants, e.g., common thistle (*Cirsium vulgare*), stinging nettle (*Urtica*) increased from $\approx 20\%$ (2009) to $\approx 31\%$ (2021), indicating a greater distribution of blackberries at and on RWA nests in 2021. In 2009, 196 nests of almost all nest heights (29 start-ups, 68 short, 70 medium sized, 18 tall, and 11 very tall nests) were affected by the proliferating blackberry or blackberry in combination with other herbs. In 2021, the number of these nests doubled (380 nests: 31 start-ups, 208 short, 108 medium-sized, 31 tall, and 2 very tall nests). Other typical plants of the herb layer, such as burdock (*Arctium*; 2009: $\approx 8\%$; 2021: 0%), European blueberry (*Vaccinium myrtillus*; 2009: $\approx 6\%$; 2021: $\approx 1\%$), eagle fern (*Pteridium aquilinum*; 2009: $\approx 7\%$; 2021: $\approx 3\%$); foxglove (*Digitalis purpurea*; 2009: $\approx 6\%$; 2021: $\approx 1\%$) mostly occurred in combination with grasses and mosses; other plants only played a minor role in 2021 due to seasonal influence at some sites (Figure 4a). In 2009, other herbs such as buttercup (*Ranunculus*), clover (*Trifolium*),

dandelion (*Taraxacum*), bellflower (*Campanula*), red dead nettle (*Lamium purpureum*), wild garlic (*Allium ursinum*), gooseberries (*Ribes*), pilewort (*Ficaria verna*), rushes (*Juncus*), wood avens (*Geum urbanum*), wild strawberry (*Fragaria vesca*), or yarrow (*Achillea*) could be observed but played a minor role.



Figure 4. Visual representation of the qualitative composition of main herbs around and on (a) active RWA nests (n_{act}), (b) re-identified nests (n_{actR}), and (c) nests on clearings (n_{actC}) for the 2009 and 2021 inventory. The larger and bolder a term for a herb, the more frequently it appears and the more important are the herbs: Dominant herbs are shown in red, bold, and large letters. Herbs that hold the same share are listed in the order of occurrence and are separated by commas.

The herb layer around and on the 296 re-identified RWA nests showed a similar picture (Figure 4b). Single occurrences of grasses (*Poaceae*) and mosses (*Bryophyta*) or a combination of both herbs were highly abundant (2009: $\approx 46\%$; 2021: $\approx 49\%$). The combination of grass, moss, and blackberry increased from $\approx 8\%$ (2009) to $\approx 18\%$ (2021), and the combination of grass, moss, and broom doubled from $\approx 6\%$ (2009) to $\approx 11\%$ (2021). In 2021, more than one third of the re-identified nests (84 nests) were affected by the proliferating blackberry as single plant or in combination with grass, moss, or broom (6 start-ups, 41 short, 25 medium sized, 11 tall, and 1 very tall nests). Half of the 84 nests were already infested by blackberry in 2009. Other typical plants of the herb layer still observed in 2009 played a minor to no role. The proportion of herb-free plots was $\approx 11\%$ in 2021 (2009: 0%).

Even in cleared areas (Figure 4c), the proportion of the most dominant herbs (grass, moss, blackberry) increased from $\approx 60\%$ (2009) to $\approx 79\%$ (2021). Combinations of these dominant plants with fern and broom accounted for $\approx 12\%$ in 2021.

3.4. Woodpecker Cavities

Woodpecker cavities (WpC) were observed throughout the nest surface in both inventories. Nest counts (2009: 224 n_{act} ; 2021: 634 n_{act}) with WpC and counts of WpC in nest (2009: 699; 2021: 2362) tripled in 2021 compared to 2009 (Table 4). In 2021, less than half of active nests ($\approx 46\%$) had no woodpecker cavities (2009: $\approx 80\%$), and $\approx 39\%$ (2009: $\approx 17\%$) had cavity counts between 1–4. The WpC to nest ratio nearly tripled from 0.6 in 2009 to 2.0 in 2021. In 2021, one fifth (2009: $\approx 4\%$) of short nests and $\approx 12\%$ (2009: $\approx 7\%$) of medium-sized nests had one–four cavities. In both inventories, larger nests (tall–extra tall) had fewer cavities than smaller nests (Table 5). In 2009, seven short–medium-sized nests had >10 woodpecker cavities (04-Sam = 3; 06-Mar = 2; 07-Sal = 2); in 2021, there were 21 short–extra tall nests (01-Dup = 1; 03-Obe = 4; 04-Sam = 5; 05-Neu = 6; 11-Vie = 5) with >10 woodpecker cavities.

Table 4. Descriptive statistics of total number (n_{tot}) of woodpecker cavities (WpC) in active nests (n_{act}), number of active nests and WpC/nest ratio per study site, numbers of nest with woodpecker classes and percentage numbers of nest with woodpecker classes for the 12 study sites for the (a) 2009 and (b) 2021 inventory.

No	Study Site	Mapped Nests (n_{act})	Numbers of WpC (n) in n_{act}	Ratio WpC/Nest	Nests (n) with WPC Classes				Nests (n) with WPC Classes (%)			
					0	1–4	5–10	>10	0	1–4	5–10	>10
(a) 2009: 224 Nests with WpC												
01	Dup	97	33	0.3	84	13	0	0	86.6	13.4	0.0	0.0
02	Doc	142	159	1.1	80	52	10	0	56.3	36.6	7.0	0.0
03	Obe	210	34	0.2	195	13	2	0	92.9	6.2	1.0	0.0
04	Sam	93	128	1.4	62	25	3	3	66.7	26.9	3.2	3.2
05	Neu	64	55	0.8	46	15	3	0	71.9	23.4	4.7	0.0
06	Mar	71	116	1.6	47	14	8	2	66.2	19.7	11.3	2.8
07	Sal	108	113	0.9	79	24	3	2	72.2	22.2	3.7	1.9
08	Ber	100	0	0.0	100	0	0	0	100.0	0.0	0.0	0.0
09	Lis	85	43	0.5	69	14	2	0	81.2	16.5	2.4	0.0
10	Hei	52	14	0.3	48	4	0	0	92.3	7.7	0.0	0.0
11	Vie	48	12	0.3	42	5	1	0	87.5	10.4	2.1	0.0
12	Roc	29	12	0.4	23	5	1	0	79.3	17.2	3.4	0.0
Sum		1099	699	0.6	875	184	33	7	79.6	16.7	3.0	0.6

Table 4. Cont.

No	Study Site	Mapped Nests (n_{act})	Numbers of WpC (n) in n_{act}	Ratio WpC/Nest	Nests (n) with WPC Classes				Nests (n) with WPC Classes (%)			
					0	1–4	5–10	>10	0	1–4	5–10	>10
(b) 2021: 624 nests with WpC												
01	Dup	142	313	2.2	60	57	24	1	42.3	40.1	16.9	0.7
02	Doc	57	50	0.9	39	15	3	0	68.4	26.3	5.3	0.0
03	Obe	163	339	2.1	73	64	22	4	44.8	39.3	13.5	2.5
04	Sam	103	343	3.3	26	49	23	5	25.2	47.6	22.3	4.9
05	Neu	127	429	3.4	43	49	29	6	33.9	38.6	22.8	4.7
06	Mar	93	150	1.6	38	48	7	0	40.9	51.6	7.5	0.0
07	Sal	78	121	1.6	38	32	8	0	48.7	41.0	10.3	0.0
08	Ber	142	75	0.5	114	24	4	0	80.3	16.9	2.8	0.0
09	Lis	78	156	2.0	32	35	11	0	41.0	44.9	14.1	0.0
10	Hei	76	85	1.1	41	33	2	0	53.9	43.4	2.6	0.0
11	Vie	63	203	3.2	21	27	10	5	33.3	42.9	15.9	7.9
12	Roc	42	98	2.3	15	18	9	0	35.7	42.9	21.4	0.0
Sum		1164	2362	2.0	540	451	152	21	46.4	38.7	13.1	1.8

Table 5. Descriptive statistics of nest height (NH) classes versus woodpecker cavities (WpC) for the (a) 2009 and (b) 2021 inventory.

Nest Height (NH) Classes (m)	Woodpecker Cavities (WpC) in Nests							
	n				%			
	0	1–4	5–10	>10	0	1–4	5–10	>10
(a) 2009								
0.01–0.10	143	0	0	0	13.0	0.0	0.0	0.0
0.11–0.50	322	45	2	2	29.2	4.1	0.2	0.2
0.51–1.00	246	79	15	2	22.4	7.2	1.4	0.2
1.01–1.50	64	31	11	3	5.8	2.8	1.0	0.3
1.51–2.00	100	29	5	0	9.1	2.6	0.5	0.0
>2.00	143	0	0	0	0.0	0.0	0.0	0.0
Sum	875	184	33	7	79.6	16.7	3.0	0.6
(b) 2021								
0.01–0.10	108	0	0	0	9.3	0.0	0.0	0.0
0.11–0.50	333	253	54	5	28.6	21.7	4.6	0.4
0.51–1.00	73	137	62	6	6.3	11.8	5.3	0.5
1.01–1.50	21	47	29	6	1.8	4.0	2.5	0.5
1.51–2.00	5	14	7	4	0.4	1.2	0.6	0.3
>2.00	0	0	0	0	0.0	0.0	0.0	0.0
Sum	540	451	152	21	46.4	38.7	13.1	1.8

An increase in woodpecker cavities was observed in SF (2021: $\approx 32\%$; 2009: $\approx 25\%$) and PF (2021: 13% ; 2009: $\approx 8\%$). In MF, the cavities decreased from $\approx 67\%$ (2009) to $\approx 56\%$ (2021). In 2021, the cavity-to-NH class ratio was highest for short (0.4), medium (0.3), and

tall (0.1) nests in SF; in PF, the highest ratio was observed for extra tall nests (0.1). In 2009, ratios were much lower for all NH classes and forest owners.

4. Discussion

Quantifying species distribution and abundance is essential for ecology and conservation [28]. A recent study showed the poor data situation for the different sessile RWA, a keystone species abundant in Northern Hemisphere forests and their occurrence in most European countries including Germany [29]. Our statistical analyses confirmed our hypothesis: It is absolutely necessary that approaches to RWA monitoring and conservation have to rely on timely, science-based, standardized, and integrated information and data providing scientific evidence of the status quo of RWA occurrences, and their increase or decrease.

4.1. Pre-Requisites for (Re-)inventories of RWA Nests

For effective protection of RWA, six factors are important: (1) A scientifically reliable data base of RWA occurrences based on a standardized and comparable mapping approach: The area-wide, standardized, systematic, and integrated mapping approach for (re)inventories that we have developed, which also includes a photo database in which each RWA nest and its habitat is documented with at least two photos (e.g., [6,14]), has shown that a general statement about an RWA decline in Germany, as suggested, e.g., by [21], is not tenable for the WEVF. The opposite is the case: The total number of RWA nests increased by 10% and at one site (05-Neu) by up to 98%. (2) Observers experience documenting all nest sizes from start-ups to very tall nests: Working with lay observers protecting RWA in Germany revealed that lay people overlooked not only small nests but even medium-sized nests in the field [10,30]. This might explain the large differences among studies on RWA population dynamics [10]. However, it is these small nests that are important for understanding population dynamics in a study area and for evaluating spatial distribution and tectonic patterns [5–7,10,12]. (3) Inappropriate selection of a mapping method: Our approach provides more accurate results in contrast to imperfect detection and under-detection of small NH classes by using random sampling, transects (at 20–50 m intervals), or using satellite imagery with a 30 m threshold spacing, without the ability to identify start-ups and short nests (e.g., [30–33]). (4) Incorrect documentation of mapping results: Our own field experience with lay observers revealed that they rarely record nests digitally with GPS and record data collected from memory only vaguely on analog maps rather than with geographic information systems (GIS). Published results based on such unusable data are not comparable and lead to misinterpretations. (5) Statistically inadequate sampling sizes: Re-inventories by, e.g., members of the “Ameisenschutzwerke” who postulate general declines in RWA occurrences, draw their conclusions sometimes of, e.g., no more than one nest [34] or 14 nests for the entire study [30]. Drawing conclusions from such an insignificant database lead to misinterpretations. The authors’ experience has shown that a minimum number of 1000+ nests per study to be mapped will provide a more complete and statistically adequate database [6,12,13]. (6) Short time intervals for re-inventories: This is the most critical aspect. Recent studies conducted after several decades show a mixed picture: stable RWA nest counts in England and Romania (two decades), a pressure situation in Belgium (three decades), and both decreases and increases in RWA nest counts in The Netherlands (six decades [32,35–38]). The results of re-inventories after several decades should be viewed critically because a time interval of more than 20 years seems much too long to document population dynamics [39]. Compared to previous inventories conducted 18, 16, and 7 years ago at the 12 sites studied (Figure 5; [14]), the 2009 and 2021 inventories already showed an increase in RWA nest counts at all sites, with a maximum increase, e.g., for 10-Hei by 52-fold (2009) and 85-fold (2021), as compared to the inventory in 1984. In addition, the photo database of RWA nests and habitats was found to be a very useful tool for re identifying ≈340 RWA nests and their forest habitat. Therefore, it is suggested that re-inventories should be conducted earlier than after 20 years because

climate change leading to hot summers and a lack of precipitation is affecting forest vitality in Germany much faster than expected and could also have an impact on RWA population dynamics [40].

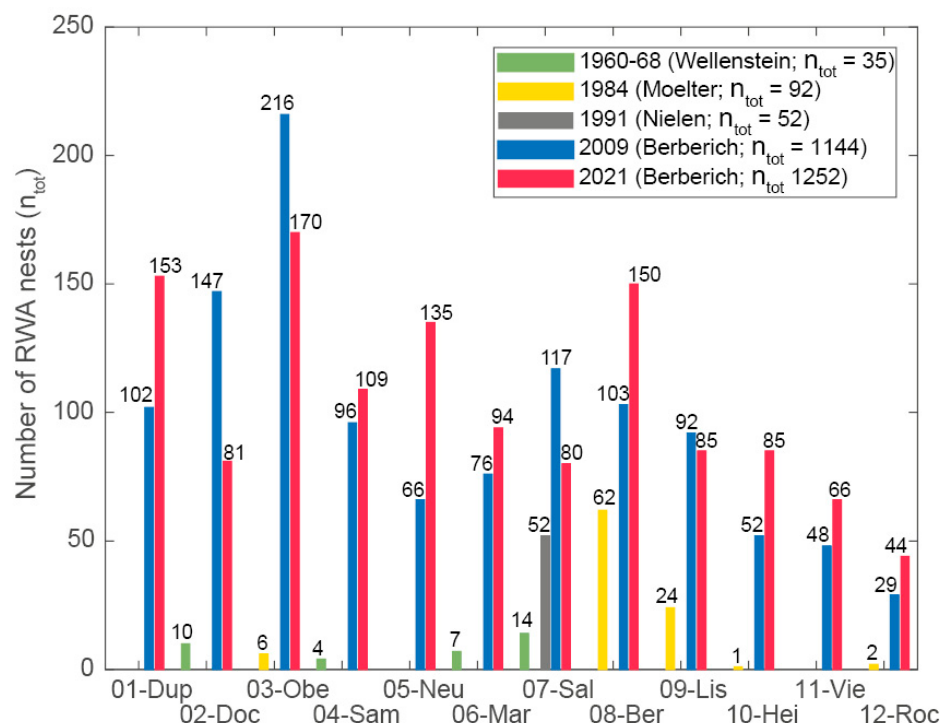


Figure 5. Comparison of total RWA nest numbers (n_{tot}) in different mapping campaigns conducted by Wellenstein (1960 and 1968), Moelter (1984), Nielen (1991) with the 2009 and 2021 inventories. Data 1960–2009 taken from [14].

4.2. Interconnection of Forest Composition, Physical RWA Nest Parameters, and Clearings

4.2.1. Tree Species and Age

The age structure of the German forest is characterized by the large-scale reforestation after World War II, with trees now between 40 and 60 years old and an average forest age of 77 years [40]. In the WEVF, the preferred tree age classes by RWA nests correspond to the reforested and averaged tree age: early to medium mature (41–80 years) and mature (≥ 81 –140 years) spruce forests, confirming our findings in the Oberpfalz region that *F. polyclena* are more abundant in mature forests (Figure 2; [6]). The distribution of nest heights was also consistent with the findings in the Oberpfalz region [6]: One-fifth (2009) and one third (2021) of start-ups to short nests and $\approx 10\%$ (2009; 2021: $\approx 6\%$) of tall–very tall nests were observed in medium mature (61–80 years) and mature spruce-dominated stands. Young (21–40 years) spruce-dominated stands comprised only $\approx 9\%$ (2009; 2021: $\approx 4\%$) of all NH classes in the WEVF. This finding contrasts with the results by Sondej et al. [31], who found that very young open canopy forests (<20 years) promote preferred habitats for nest settlements, and Domisch et al. [41], who found no RWA occurrences in 20-year-old Scots pine stands. Positive effects on species and habitat diversity are also expected from further development toward deciduous and mixed forests. Natural beech regeneration is increasingly gaining dominance in RLP forests [42]. This could be confirmed by our findings. The forest composition observed shows a shift from coniferous to naturally regenerated mixed stands, consisting of, e.g., spruce–beech and spruce–oak at RWA nest sites (Section 3.2). This is a positive development for beech and oak, as their vitality was affected by drought stress, oak powdery mildew (*Microsphaera alphitoides*), and insect infestation from 2018 to 2020 [43].

4.2.2. Clearings

German forests are currently facing outbreaks of bark beetles, the most devastating tree-killers in coniferous forests, especially in spruce stands. European spruce bark beetle species (*Ips typographus*, *Pitogenes chalcographus*) benefit from climate change and higher temperatures by developing more generations per year, resulting in bark beetle-induced tree mortality [43,44]. Bark beetles introduce wood-decay fungi that lead to enzymatic degradation of lignin and significantly alter the physical and mechanical properties of wood [45]. Rapid salvage clearing of infested standing spruce trees is a preferred combat measure. RWA live in trophobiosis with many plant-sucking insects (*Aphidae*, *Coccidae*, *Psyllidae*), especially on spruce. They protect these insects from predators and parasites [46]. Degradation of lignin or holocellulose is hypothesized to have negative effects on plant-sucking insects that feed RWA. The overall large shift toward smaller nests in all tree age classes (Figure 2) suggests that (a) there is an increase in new nest settlements, which is contrary to the general statement of a nest decline [21,30], (b) there is increasing pressure on RWA food resources due to a change in nutrient cycling in spruce stands as a result of a substantial reduction in wood quality [45], and (c) smaller colonies in smaller RWA nests could be an advantage for the survival of the whole colony after clearing bark beetle-infested trees and creating clearing areas. This could be confirmed by our results: Although clearing plots doubled in size due to bark beetle infestations in 2021, the total number of active nests on these plots quadrupled in 2021. This result contrasts with those of [33], which suggest that bark beetle outbreaks reduce RWA nest survival, particularly in clearings. Clearings are thought to favor the spatial distribution of species that are more xerothermophilic, such as the black-backed meadow ant (*F. pratensis*) which is adapted to higher temperatures and prefers more xerothermic, dry habitats [47].

4.2.3. Herbaceous Layer

The herbaceous layer with its high species diversity has an important role in maintaining biodiversity in the forest. This is because the herbaceous layer community is sensitive to spatial and temporal disturbances. Changes and increasing loss of species diversity provide important information about forest site characteristics [48]. In general, the composition of the herbaceous layer around a nest site and on RWA nests changed dramatically from 2009 to 2021, even though both surveys were conducted in the same months. Compared to 2009, typical herb layer plants observed in 2009 played little to no role in 2021, indicating lower species diversity. The most important herbs were grass, moss, or a combination of both, and broom. However, it is noticeable that the highly proliferating blackberry as a single plant or in combination with, e.g., grasses or mosses is becoming more dominant on the study sites (Figure 4). Blackberries are considered pests and competitors for trees and are controlled by foresters to prevent re-emergence (oral comm. from forester managers). Extreme weather events such as extreme drought and prolonged heat waves from 2018 to 2020 have affected forest vitality in RLP and contributed to the emergence of blackberry [43,49]. However, this study does not confirm that RWA nests are affected by blackberries as claimed by Vélé and Frouz [33]. In 2009, a quarter of the nests that were re-inventoried in 2021 were affected by blackberries. In 2021, the proportion increased to $\approx 26\%$. Although this plant is highly sprawling and sometimes covers the entire nest area, RWAs do not appear to be disturbed in their daily routine.

4.3. Interconnection of RWA Nests and Woodpeckers

Old forests with several development phases are an important factor for biodiversity. They provide a rich supply of deadwood and biotope trees, which offer special microhabitats such as coarse bark, crown deadwood, or woodpecker cavities [40]. Deadwood is part of the natural cycle in the forest and has reached a share of 6% of the living wood stock in Germany. Many species are specialized in this which serves, e.g., as a food source, shelter, breeding ground, and drumming ground for various species, such as woodpeckers, bats, insects, fungi, and lichens [40,50]. Woodpecker species are considered indicators of

forest biodiversity because they have adapted to old-growth forest habitat structures, use large breeding territories, and are active year-round [50,51]. The observation of a tripling of woodpecker cavities in RWA nests in 2021, especially in short and medium-sized nests (Table 5), may indicate a substantial increase in the number of foraging woodpeckers. This is especially true for the Black (*Dryocopus martius*), Green (*Picus viridis*), and the Gray woodpecker (*Picus canus*) in the study areas, as these three species feed on ants and forage not only on tree trunks, but mostly on the ground in RWA nests. Foraging in smaller nests could be more effective and beneficial because prey is captured more quickly. Woodpeckers that forage in large nests must dig small tunnels into the nest and remain for up to 12 min, such as the Green woodpecker (*Picus viridis*; AntCam data by Berberich and Berberich, unpublished). Our findings of an increase in WpC in nests are consistent with up to fivefold population increases of various woodpecker species, e.g., the black (*Dryocopus martius*), middle (*Dendrocopos medius*), and lesser spotted woodpecker (*Dryobates minor*), in the largest contiguous riparian woodland area of Rhineland-Palatinate [52]. Furthermore, our results showed that woodpeckers were more abundant in SF and PF, suggesting a different forest managing than in MF. Although biotope trees and deadwood are actively preserved, especially in SF, for insect conservation reasons [49], these key structures are ephemeral and require permanent replenishment [50]. Therefore, it is also conceivable that at the time of the two inventories, the number of these habitats had decreased and woodpeckers were therefore focusing more on RWA nests. In this case, woodpecker populations in the study areas would not increase, but habitat trees would decrease. Integrated monitoring woodpecker cavities in RWA nests is therefore another valuable, albeit indirect, indicator tool for monitoring sustainable forest management and assessing woodpecker populations and their habitats in the forest. Our monitoring contributes to the findings by Wübbenhorst and Südbeck [51] that other indicator species besides woodpeckers are needed as part of a monitoring system for sustainability in forests.

4.4. GeoBio-Interactions

As already shown in recent studies, e.g., for the Black Forest, Lake of Constance, Oberpfalz, and Romania [6,7,12], tectonic-volcanic processes and geochemical composition of bedrock are additional factors promoting spatial distribution of RWA nests and their high nest numbers [6,53]. In the WEVF, the active magma reservoir (Eifel plume) leads to a maximum uplift of ≈ 1 mm/year combined with a significant horizontal extension [25,54]. Such positive ground movement rates [55], as observed at nearly all study sites, open pathways for geogenic gases (e.g., Radon (Rn)). Radon emanation has a significant influence on the spatial distribution of nests [5,8,9,11]. At all study sites, medium to high soil Radon concentrations, were measured during the 2009 inventory [14] and taken from the literature for the re-inventory [56]. Weathered rocks show good adsorption properties of clay minerals and accumulation of U-bearing minerals [57]. In the WEVF, RWA nests were in direct contact with the natural Rn potential of the bedrock (Lower Devonian Klerfer and Gladbach Schichten and Triassic Buntsandstein), their structural dispersal pathways (e.g., Rn degassing faults) and the high U-content in the small grain fractions (<0.125 mm) of the soils [57]. Study sites with maximum concentration of 114 kBq/m^3 (11-Vie) and 101 kBq/m^3 (12-Roc) showed an increase in RWA nests of $\approx 31\%$ (11-Vie) and $\approx 45\%$ (12-Roc). Here, especially start-up and short nests that were mostly located in NE-SW direction, indicated new settlements in the present-day stress-field direction [14], confirming recent findings in other tectonically active study areas [5,7,12,13]. This is thought to be caused by micro-fracturing due to a high stress induced by the uplift forces of the Eifel plume, leading to the formation of new emanation surfaces and significant increase in the radon signal, although the applied stress remains constant over time [57]. Since local negative displacement rates in 09-Lis are almost equal to the positive ascending rates, this could explain the only small loss of RWA nests in this area [55]. Local negative displacement rates are thought to slowly close pathways for geogenic gases, resulting in lower Radon concentration (90 kBq/m^3) and a decrease in RWA nest numbers, as observed at, e.g., the

03-Obe site (Table 2; [8,55,56]). This hypothesis was already established in previous studies and has now been further confirmed [5,6,8,12].

5. Conclusions

Our standardized, area-wide, reproducible, and integrated (re-)inventory approach not only monitors the entire habitat at a RWA nest, but is also able to detect and identify particularly small nests. When combined with presence/absence data and by re-identifying previously mapped nests, the use of such a comprehensive approach results in more accurate and realistic RWA nest counts in (re-)inventories, providing scientific evidence of the status quo of RWA occurrence. In addition, the photo database of RWA nests and habitats proved to be a very useful tool for re-identifying RWA nests and their habitats. Woodpecker cavities in nests are suggested as an indirect tool for assessing woodpecker populations. GeoBio-Interactions, e.g., positive ground movement rates, open pathways for geogenic gases are suggested as an additional positive factor for nest settlements. Two planned inventories in two other study sites, after 8 and 4 years, will show whether the trends observed here in terms of RWA nests and WpC are confirmed in these areas as well.

Author Contributions: G.M.B. conceived the idea, designed the study, performed the field work, carried out the statistical analysis, and wrote the manuscript. M.B.B. performed the field work, analyzed the data, and contributed to the manuscript. Both authors edited the manuscript and approved the final version. All authors have read and agreed to the published version of the manuscript.

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