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Bark Beetle Attacks Reduce Survival of Wood Ant Nests

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Abstract: Central European coniferous forests are facing the most significant bark beetle outbreak in history. The consequence is the creation of large clearings, which are associated with changes in environmental parameters. We studied how these changes affected the survival of wood ant nests. Specifically, we monitored the relationship between mound occurrence, tree coverage, and the coverage and height of vegetation on ant mounds. We found that wood ant nests were less likely to survive (39% decline) in bark beetle-affected forests than in unaffected forests. The *Formica rufa* species was more affected than *F. polyctena*. The bark beetle attack was significantly positively correlated with increases in understory vegetation cover and height. Several factors may explain the negative effects of bark beetles on wood ants. The removal of trees subsequently increased the amount of light on ground vegetation. The support of understory vegetation growth on ant mounds cast shadows on the nests and disrupted nest thermoregulation. Additionally, the bark beetle attack may have been associated with a loss of food resources for wood ants. Our results showed that early (small-scale) management intervention against the spread of bark beetles is the preferred method for maintaining the ant population in conifer forests prone to bark beetle attacks.

Keywords: bark beetles; clear-cuts; *Formica*; spruce; tree coverage; vegetation

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1. Introduction

Since 2015, Central European spruce and pine forests have faced the most historically significant bark beetle outbreak [1,2]. To control beetle spread, among other activities, forest managers apply sanitation logging (i.e., unplanned clear-cuts) to save undamaged trees [3]. The consequence is the creation of extensive clearings, which reach unusual dimensions. In Czechia, the maximum legal area of planned clear-cuts is 1 ha, and the width of the clearing may not exceed the height of two trees. The average size of a planned clear-cut is about ¾ ha [4]. However, for sanitation cutting, there are no restrictions. Instead, forest managers are obliged to cut all infested trees [5]. In 2021, the total area of clearings in Czechia had increased over three-fold compared to the areas recorded in the years before the bark beetle outbreak [4].

The formation of forest clearings is associated with changes in the microclimate. Clearings cause increases in solar radiation, soil and surface temperatures, and soil moisture [6,7]. Plants and animals have different reactions to these changes. The species diversity of some taxa increases (e.g., bees and wasps, non-saproxylic beetles, lichens, birds); however, for other species, diversity does not change (e.g., moths, Mollusks, Carabids), or it decreases (e.g., wood-inhabiting fungi, some soil taxa) [8–11]. Grass coverage and the appearance of pioneer species increase [12]. Additionally, the diversity and abundance of ant taxa sensitively and ambiguously respond to the clear-cutting of spruce plantations [13,14].

Red wood ants are an important component of forest ecosystems, including plantations. They improve the soil pH and nutrient content [15,16]. Microsites created by wood

ants increase the environmental capacity, the ß diversity of territory, and its vegetation diversity [17]. Nests can become the habitat for many myrmecophilous organisms [18]. The same is true for abandoned nests [19,20]. Moreover, wood ants are beneficial in forest protection; they can reduce the proportion of trees infested by bark beetles [21–24]. These features are useful because soils in coniferous forests are acidic, the species composition of vegetation is poor, and forest plantations are susceptible to pest damage [12,16,17,25,26].

Despite their ecosystem functions, there is evidence that wood ants' current numbers are locally declining [27,28]. Current national and international regulations are insufficient to protect wood ants [28]. Their local decline is due to many factors, including, among others, insufficient forest management (low interest among forest managers) and a lack of knowledge about their habitat requirements [28,29]. Moreover, increased attention should be paid to these ants in view of the likely negative impact of world climate change [30].

The impact of bark beetle clearings on wood ants was studied by [31], who found a declining number of workers towards the center of the clearcut. The survival of ant nests has not been investigated so far, whereas further outbreaks are expected in the future [32]. Consequently, here, we focused on the influence of clearings created by sanitation cutting on the survival of wood ant nests. We hypothesized that bark beetle attacks would negatively affect wood ant nest survival. To test our hypothesis, we compared historical and recent wood ant nest distributions in areas affected and unaffected by bark beetles. Then, we explored relationships between nest survival and recent environmental factors to elucidate potential mechanisms that underlie bark beetle effects on wood ant nest survival. Specifically, we investigated relationships between the coverage and height of vegetation on ant mounds and tree coverage.

2. Materials and Methods

2.1. Data Collection

To quantify the effects of bark beetles, we compared historical and recent distributions of wood ant nests in sites that were either affected or not affected by bark beetle attacks. As a source of historical data, we used maps from the turn of the millennium, hereafter called historical data (i.e., before the bark beetle outbreak), where the areas that wood ants inhabited had been marked. Maps with dots indicating nests' occurrence were available for over a thousand nests in 7 study sites in Czechia. All sites were covered by spruce plantations [33–36]. During September 2021, we conducted area-wide mapping and constructed new maps of nests at all the same sites. This re-survey of sites (hereafter called recent data) included forests that were not affected by bark beetle attacks and sites affected by bark beetle attacks (Supplementary material Figure S1). The nests studied belonged to 3 species: *Formica polyctena* Förster 1850 (4 sites), *F. rufa* Linnaeus, 1761 (2 sites), and *F. aquilonia* Yarrow, 1955 (1 site). For each nest location recorded in the historical data, it was noted whether or not the nest was still present. If the nest was not found at the original location, an area 50 m in diameter was searched around the historical occurrence. Due to the original nest density, we searched mounds on the whole area of their historical occurrence. For all the historical nest locations, we recorded whether the historical position of the nest was in an area affected by bark beetles or not; a bark beetle-affected area was defined as an area where all trees were removed as a consequence of a previous bark beetle attack (see Supplementary Figure S1, for example). In addition, we measured the tree coverage (as a factor that reflected the amount of incident solar radiation and also as an indicator of the presence or absence of trees) and the coverage and height of vegetation growing on the ant mound surface. The height of the vegetation was measured with the folding meter to the nearest 5 cm. Tree and herb coverages were estimated (as the percentage shading of the sky above the nest resp. the percentage of the nest surface covered with vegetation) with an accuracy of 10%. This study was conducted 4–5 years after cutting following bark beetle infestation, as it may take several years for the ant colony to become extinct [37].

2.2. Data Processing and Statistical Evaluation

For all statistical tests performed, the basic unit was an individual nest (specifically the 1070 nests mapped in the historical survey). The study focused only on nest survival, not on nest dynamics. To test whether the bark beetle attack affected wood ant nest survival, we constructed 2 × 2 contingency tables and analyzed them with the Fisher exact test. Contingency tables are widely used for the evaluation of categorical data, typically when one has a control group and treatment group, and to explore whether the experimental subjects (e.g., laboratory animals) in these groups survived or not. This was a case in our contingency tables, where we organized the data into two groups. Treatment groups were nests affected by bark beetles, and unaffected nests represented the control group. Then we compared the historically recorded nests with those recently recorded; this gave us two categories, nests that were there in the past and survived until today and nests that perished (giving a 2 × 2 contingency table with control and treatment groups being whether an experimental subject survived or not) [38]. Alternatively, we used the Pearson rank correlation [38], where for each historical nest, we had two statuses: survived (1) or did not survive (2). Then, survival was correlated with either the presence or the absence of a bark beetle attack, tree coverage, ground vegetation coverage, and ground vegetation height at the current nest site and at the historical nest site. All computations were performed in Statistica 13.0. These comparisons were performed for the pool of all wood ant nests or only for the dominant species: *F. polyctena* and *F. rufa*, separately.

3. Results

Out of the total 1070 historical red wood ant (*Formica s. str.*) nests revisited, 24.9% had disappeared between the years of the historical and recent inventories. In forests that were not subjected to bark beetle attacks, only 16.8% of the nests disappeared; in contrast, in bark beetle-affected forests, about 38.5% of the nests disappeared (Tables 1 and S1). Our analyses with contingency tables and the Fisher exact test showed that this difference was highly significant ($p < 0.0001$). However, survival differed between the two dominant ant species. Out of the 1070 nests, 736 belonged to *F. polyctena*, 186 belonged to *F. aquilonia*, and 148 belonged to *F. rufa*. However, all *F. aquilonia* nests were located in forests unaffected by bark beetles; therefore, the effect of bark beetles on ant species could only be evaluated for *F. polyctena* and *F. rufa*. Among the *F. polyctena*, only 22.9% of the nests disappeared (or only their remains have been found); but among the *F. rufa*, 78.3% of the nests observed around the turn of the century had disappeared in 2021. This difference between species was highly significant ($p < 0.0001$). Nevertheless, in both species, nest loss was more severe in bark beetle-affected forests than in unaffected forests. The lost *F. polyctena* nests represented 16.7% (intact forests) and 31.5% (bark beetle-affected forests) of the nests observed at the turn of the century ($p < 0.0001$). Similarly, the lost *F. rufa* nests represented 67.7% (intact forests) and 86.0% (bark beetle-affected forests) of the nests observed in 2000 ($p = 0.0090$). We could not perform this analysis for *F. aquilonia* because all the available historical maps showed that these nests were in areas that were not affected by bark beetles; however, all but one nest had not disappeared in the 2021 mapping.

Table 1. Numbers of wood ant nests present or absent in forests, compared to historical numbers, in areas affected or not affected by bark beetles.

Forest Status	*Formica s. str.*		*F. polyctena*		*F. rufa*	
	Perished	**Survived**	**Perished**	**Survived**	**Perished**	**Survived**
no bark beetle (control)	113	557	71	354	42	20
bark beetle present (treatment)	154	246	98	213	74	12

Similarly, the Pearson rank correlation analysis showed a highly significant negative relationship between the recent presence (Table 2) and bark beetle infestations. This relationship indicated that wood ant nests were less likely to survive in bark beetle-affected forests than in unaffected forests. This relationship held for all the *Formica s. str*. pooled together

and for both dominant species, *F. polyctena* and *F. rufa*, when they were evaluated separately. Bark beetle attacks were significantly positively correlated with an increase in the coverage and height of the understory vegetation, and they were negatively correlated with tree coverage. Likewise, nest survival over 20 years was significantly negatively correlated with the coverage and height of the understory vegetation and positively correlated with tree coverage. Again, these relationships held for all *Formica s. str.* pooled together and for both dominant species, *F. polyctena* and *F. rufa*, when they were evaluated separately.

Table 2. Pearson rank correlation results show relationships between wood ant nest survival (historical nests which were found in recent sampling were assumed as those which survive, those historical nests which were not found in recent sampling were assumed to have perished) of those that were compared based on the presence or absence of bark beetle infestation, and several continual data recorded during recent sampling, namely the height and coverage of understory vegetation (nest veg.), and tree coverage.

Formica s. str.	Bark Beetle	Nest Veg. Coverage	Nest Veg. Height	Tree Coverage
nest survival	**−0.29**	**−0.77**	**−0.45**	**0.12**
nest veg. coverage	**0.41**		**0.63**	**−0.36**
nest veg. height	**0.42**	**−0.04**		**−0.42**
tree coverage	**−0.79**	**−0.36**	**−0.42**	
F. polyctena				
nest survival	**−0.17**	**−0.71**	**−0.24**	0.03
nest veg. coverage	**0.32**		**0.54**	**−0.32**
nest veg. height	**0.28**	**0.54**		**−0.31**
tree coverage	**−0.77**	**−0.32**	**−0.31**	
F. rufa				
nest survival	**−0.22**	**−0.76**	**−0.51**	0.02
nest veg. coverage	**0.38**		**0.65**	**−0.29**
nest veg. height	**0.70**	**0.65**		**−0.67**
tree coverage	**−0.89**	**−0.67**	**−0.29**	

Bold font indicates significance of $p < 0.05$.

4. Discussion

Our results clearly indicated that bark beetle attacks significantly reduced *Formica s. str*. nest survival. This may be contra intuitive as wood ants are sun-loving species commonly occurring on sun-exposed edges of forest stands [39]. Based on that, one can expect that clear-cuts may form more edges suitable for wood ants. This may hold for small clear-cuts. However, the bark beetle infestation and subsequent logging created very large contiguous areas where the forest was cleared, which appears to have a negative impact on the survival of ant nests. This is consistent with previous data showing that deforestation negatively affects wood ants' survival [40,41]. This result is also consistent with the general claim that the decline in nest numbers is caused by habitat loss because clearings have differential environmental parameters, including radiation, moisture, and temperature changes [6,37,42]. Thus, our results supported our hypothesis (Figure 1). On the other hand, differences in the amount of solar radiation in older stands are lower compared to younger ones, and the mound size has a normal distribution, both of which indicate low dynamics of the nest numbers in mature forest stands [43,44].

We found that the proportion of extinct nests differed between *F. rufa* and *F. polyctena*. The number of abandoned nests was high for *F. polyctena*, where 23% of nests had disappeared in clear-cut areas. For *F. rufa*, more than three-quarters of the nests were abandoned in affected areas. These results were roughly comparable to those reported in a previous study [13], where approximately 50% of *F. aquilonia* nests were abandoned in 4–5-year-old clear-cut areas and with the observation of a low number of workers on clear-cuts no older than three years [31]. The survival of *F. rufa* and *F. polyctena* nests could not be attributed

to their slightly different environmental requirements (*F. rufa* nests are more often found on forest edges, and *F. polyctena* nests are found in connected forests) [45,46] because both types of habitat were lost in the clearings. A more important cause could be the different dispersal and reproduction strategies. *F. rufa* is generally monogynous (or oligogynous), whereas *F. polyctena* is polygynous and can create polydomous colonies [47]. Polydomous ant colonies may move their populations to more favorable habitats through nest budding, and accordingly, they have less chance of extinction [41,47].

Our data showed that 4–5-year-old clearings created by the sanitation of bark beetle-affected trees were associated with increases in the coverage and height of vegetation growing on the ant mounds, and consequently, nest survival was reduced in these areas. All of the study clearings were densely covered by undergrowth vegetation, particularly red grass (*Calamagrostis epigejos*) and blackberries (*Rubus* sp.), which also grew on ant mounds. The dense grass made it difficult for worker ants to hunt, and in particular, it shaded the mounds, which disrupted the nest microclimate [37,45,48]. Nests that are overgrown with vegetation have lower temperatures from summer to late autumn and higher moisture in nest materials [48]. Thermoregulation is necessary for the successful development of the population and for the production of winged ants [49,50]. Moreover, when more radiation falls on the clearings [42], it supports a rise in metabolic rates and, consequently, a loss of winter energy stores [51]. Indeed, similar to a study in Finland [51], in the present study in Czechia, we observed worker ants moving about on sunny mound surfaces of the nest during the winter months when the temperature reached 5 °C (unpublished data).

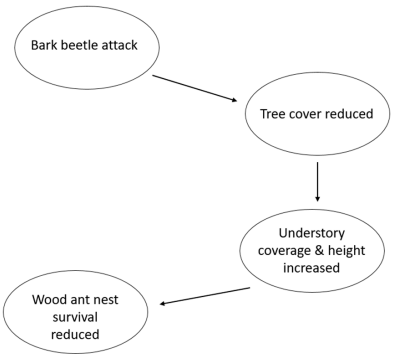


Figure 1. Hypothesized mechanism of how a bark beetle infestation influences wood ant nest survival.

Food resources are mandatory for maintaining stable, optimal nest temperatures and for the production of offspring [52]. Ants obtain most of their food from trees (e.g., honeydew, arthropods); therefore, clear-cutting causes a reduction in the food supply [53]. The abundance of aphids can be considered essential because aphids′ honeydew constitute the main food source for wood ants [54]. Additionally, workers harvest less honeydew mass from clearings compared to the amounts they harvest in middle-aged and mature stands [55,56]. When nests are located in the central parts of clearings, the ants cannot find sufficient food on trees [41]. The surrounding older stands can serve as food resources for wood ants [39], but the average distance of foraging routes is relatively short (16 m). In the event of a lack of resources, the ants will extend routes up to distances of 50–100 m and, exceptionally, up to 164 m [37,57]. However, bringing honeydew from greater distances is not ideal because the amount of honeydew harvested declines with the distance to the trees [58]. Food availability may determine the body size and fat resources of ant workers. The large worker ants may be nest defenders [59,60]. Moreover, factors other than the number of food sources may contribute to nest disappearance. For example, the composition of the honeydew collected from the remaining trees in clearings is lower in quality [56]. These factors also contribute to an increase in the susceptibility of ants to diseases and parasites [61]. In addition, the resin used as protection against pathogens [62] may be in short supply in clearings.

The use of insecticides is widely applied to defend forests against bark beetle infestations. About 10% (or 2046 thousand m^3) of spruce wood was treated with insecticides in 2020 [63]. All approved preparations contain alpha-cypermethrin or deltamethrin, derived from pyrethroids, which act non-selectively and have a significant negative impact on many groups of invertebrates, including ants and their prey [64,65]. Our observations showed that, sometimes, wood was sprayed with insecticides, and Storanet® insecticidal nets were installed in the immediate vicinity of nests. Additionally, parts of nests may have been damaged during logging and transport of wood.

The long-term effect of the clear-cuts can also be positive. These areas could be, after ca. 20 years and their regrowth by trees, spots with a high density of nests [66]. Creating clearings may not be the only cause of nest decline. The distribution of wood nests is also attributed to quasi-invariant factors (tectonics, geochemical composition of the bedrock, geogenic gases) and forest factors and management (stand age, tree species composition, canopy cover) [13,20,27,39,66–69]. Inappropriate or absent protection policies may also be an indirect consequence of their local declines or extinctions [28].

5. Conclusions

Clear-cuts are associated with reduced nest survival caused by lower worker ant survival, lower probability of offspring production, and a skewed sex ratio [41,59,70]. Our results showed that the creation of clear-cuts and the subsequent decline in the abundance of nests might not be solely connected with planned commercial management. On the contrary, it may be a consequence of an uncontrolled outbreak of bark beetles. Wood ants can survive in a relatively wide range of forest conditions (e.g., *F. rufa* nests occupy 40 to 80% of the canopy cover); they only require light areas and nearby food sources [41,45]. Alternatively, ants can move closer to food resources [41]. However, relocation may not be possible due to the presence of other nests in the remaining forest fragments and strong competition between nests [71]. Therefore, large clearings created by bark beetle damage destroy the ant habitat, and often, the nests cannot move. Consequently, bark beetle infestations can have a more significant negative impact than a planned clear-cut because the areas cleared due to bark beetle damage are not legally limited. In addition, clearings can also have indirect and long-term effects because they disturb the connectivity between forests, which negatively influences the presence of *Formica* ants [72]. The typical method of protecting a forest after bark beetle infestations is the timely clearing of infested trees. This clearing can prevent the formation of extensive clearings and, in addition, it contributes to maintaining the mosaic environment. It is necessary to maintain a balance between sunlit forest soils and forage trees and to retain the connectivity between habitat patches without applying insecticides near ant nests to conserve ant populations [37,72]. Large clearings created after a bark beetle outbreak are unsuitable for maintaining ant populations. Moreover, replacing coniferous trees with deciduous seedlings, which are now largely preferred in planting, is unsuitable for the conservation of wood ants [4,57,73].

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f14020199/s1. Figure S1: Example of the revisited site which was not attacked by the bark beetle, Kleť (a) and site which suffer by the bark beetle attack, Třebouň (b); Table S1: Total area of the study site, representation of clearings (%), year of 1st mapping, no. of present and absent nests, and no. of nests, nest and environment characteristics (Mean ± SD) in bark beetles affected and unaffected parts of study sites.

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References

1. Hlásny, T.; Zimová, S.; Merganičová, K.; Štěpánek, P.; Modlinger, R.; Turčáni, M. Devastating outbreak of bark beetles in the Czech Republic: Drivers, impacts, and management implications. *For. Ecol. Manag.* **2021**, *490*, 119075. [CrossRef]
2. Liška, J.; Knížek, M.; Véle, A. Evaluation of insect pest occurrence in areas of calamitous mortality of Scots pine. *Cent. Eur. For. J.* **2021**, *67*, 85–90. [CrossRef]
3. Miścicki, S.; Grodzki, W. Can sanitation cutting contribute to reduced mortality of Norway spruce *Picea abies* (L.) H. Karst., due to infestation by *Ips typographus* (L.)? *Sylwan* **2022**, *165*, 749–762.
4. MZe. *Zpráva o Stavu Lesa a Lesního Hospodářství České Republiky v Roce 2021*, 1st ed.; Ministerstvo Zemědělstí: Prague, Czech Republic, 2022; pp. 5–10.
5. Act of 3 November 1995 No 289/1995 Coll., on forests and amendments to some acts (the Forest Act) 1995.
6. Hais, M.; Kučera, T. Surface temperature change of spruce forest as a result of bark beetle attack: Remote sensing and GIS approach. *Eur. J. For. Res.* **2008**, *127*, 327–336. [CrossRef]
7. Olchev, A.; Radler, K.; Sogachev, A.; Panferov, O.; Gravenhorst, G. Application of a three-dimensional model for assessing effects of small clear-cuttings on radiation and soil temperature. *Ecol. Model.* **2009**, *220*, 3046–3056. [CrossRef]
8. Beudert, B.; Bässler, C.; Thorn, S.; Noss, R.; Schröder, B.; Dieffenbach-Fries, H.; Foullois, N.; Müller, J. bark beetles increase biodiversity while maintaining drinking water quality. *Conserv. Lett.* **2015**, *8*, 272–281. [CrossRef]
9. Jokela, J.; Siitonen, J.; Koivula, M. Short-term effects of selection, gap, patch and clear cutting on the beetle fauna in boreal spruce-dominated forests. *For. Ecol. Manag.* **2019**, *446*, 29–37. [CrossRef]
10. Lóšková, J.; Ľuptáčik, P.; Miklisová, D.; Kováč, Ľ. The Effect of Clear-Cutting and Wildfire on Soil Oribatida (Acari) in Windthrown Stands of the High Tatra Mountains (Slovakia). *Eur. J. Soil Biol.* **2013**, *55*, 131–138. [CrossRef]
11. Przepióra, F.; Loch, J.; Ciach, M. Bark beetle infestation spots as biodiversity hotspots: Canopy gaps resulting from insect outbreaks enhance the species richness, diversity and abundance of birds breeding in coniferous forests. *For. Ecol. Manag.* **2020**, *473*, 118280. [CrossRef]
12. Jonášová, M.; Prach, K. The Influence of bark beetles outbreak vs. salvage logging on ground layer vegetation in Central European mountain spruce forests. *Biol. Conserv.* **2008**, *141*, 1525–1535. [CrossRef]
13. Sorvari, J.; Hakkarainen, H. Wood ants are wood ants: Deforestation causes population declines in the polydomous wood ant *Formica aquilonia*. *Ecol. Entomol.* **2007**, *32*, 707–711. [CrossRef]
14. Véle, A.; Holuša, J.; Frouz, J.; Konvicka, O. Local and landscape drivers of ant and carabid beetle communities during spruce forest succession. *Eur. J. Soil Biol.* **2011**, *47*, 349–356. [CrossRef]
15. Jílková, V.; Matějíček, L.; Frouz, J. Changes in the pH and other soil chemical parameters in soil surrounding wood ant (*Formica polyctena*) Nests. *Eur. J. Soil Biol.* **2011**, *47*, 72–76. [CrossRef]
16. Lavelle, P.; Bignell, D.; Lepage, M.; Wolters, V.; Roger, P.; Ineson, P.; Heal, O.; Dhillion, S.P. Soil function in a changing world: The role of invertebrate ecosystem engineers. *Eur. J. Soil Sci.* **1997**, *33*, 159–193.
17. Rubashko, G.E.; Khanina, L.G.; Smirnov, V.E. The dynamics of vegetation on and around *Formica rufa* Nests. *Entmol. Rev.* **2011**, *91*, 169–176. [CrossRef]
18. Parmentier, T.; Dekoninck, W.; Wenseleers, T. A highly diverse microcosm in a hostile world: A review on the associates of red wood ants (*Formica rufa* group). *Insect. Soc.* **2014**, *61*, 229–237. [CrossRef]
19. Jílková, V.; Frouz, J.; Mudrák, O.; Vohník, M. Effects of nutrient-rich substrate and ectomycorrhizal symbiosis on spruce seedling biomass in abandoned nests of the wood ant (*Formica polyctena*): A laboratory experiment. *Geoderma* **2015**, *259–260*, 56–61. [CrossRef]
20. Sondej, I.; Domisch, T. Abandoned wood ant nests as sites for seedling germination. *Forests* **2022**, *13*, 764. [CrossRef]
21. Maňák, V.; Nordenhem, H.; Björklund, N.; Lenoir, L.; Nordlander, G. Ants protect conifer seedlings from feeding damage by the pine weevil *Hylobius abietis*. *Agric. For. Entomol.* **2013**, *15*, 98–105. [CrossRef]
22. Sorvari, J. Foraging distances and potentiality in forest pest insect control: An example with two candidate ants (Hymenoptera: Formicidae). *Myrmecol. News* **2009**, *12*, 211–215.
23. Trigos-Peral, G.; Juhász, O.; Kiss, P.J.; Módra, G.; Tenyér, A.; Maák, I. Wood ants as biological control of the forest pest beetles *Ips* spp. *Sci. Rep.* **2021**, *11*, 17931. [CrossRef]
24. Véle, A.; Dobrosavljević, J. *Formica rufa* ants have a limited effect on the abundance of the parasitic fly *Ernestia rudis* in Scots pine plantations. *Sociobiology* **2021**, *68*, e7286. [CrossRef]
25. Brady, N.C.; Weil, R.R. *The Nature and Properties of Soils*, 15th ed.; Pearson Education: London, UK, 2016; pp. 135–136.
26. Day, K.R.; Leather, S.R. Threats to Forestry by Insect Pests in Europe. In *Forests and Insects*; Watt, A.D., Ed.; Springer Science & Business Media: London, UK, 1997; pp. 177–205.
27. Risch, A.C.; Ellis, S.; Wiswell, H. Where and why? Wood ant population ecology. In *Wood Ant Ecology and Conservation*; Stockan, J.A., Robinson, E.J.H., Eds.; Cambridge University Press: Cambridge, UK, 2016; pp. 81–105.

28. Balzani, P.; Dekoninck, W.; Feldhaar, H.; Freitag, A.; Frizzi, F.; Frouz, J.; Masoni, A.; Robinson, E.; Sorvari, J.; Santini, G. Challenges and a Call to Action for Protecting European Red Wood Ants. *Conserv. Biol.* **2022**, *36*, e13959. [CrossRef]
29. Robinson, E.J.; Stockan, J.; Iason, G.R. Wood Ants and their interaction with other organisms. In *Wood Ant Ecology and Conservation*; Stockan, J.A., Robinson, E.J.H., Eds.; Cambridge University Press: Cambridge, UK, 2016; pp. 177–206.
30. Fitzpatrick, B.R.; Baltensweiler, A.; Düggelin, C.; Fraefel, M.; Freitag, A.; Vandegehuchte, M.L.; Wermelinger, B.; Risch, A.C. The distribution of a group of keystone species is not associated with anthropogenic habitat disturbance. *Divers. Distrib.* **2021**, *27*, 572–584. [CrossRef]
31. Żmihorski, M. Distribution of red wood ants (Hymenoptera: Formicidae) in the clear-cut areas of a managed forest in Western Poland. *J. For. Res.* **2010**, *15*, 145–148. [CrossRef]
32. Trubin, A.; Mezei, P.; Zabihi, K.; Surový, P.; Jakuš, R. Northernmost European spruce bark beetle *Ips typographus* outbreak: Modelling tree mortality using remote sensing and climate data. *For. Ecol. Manag.* **2022**, *505*, 119829. [CrossRef]
33. Dad'ourek, M. O vybraných lokalitách lesních mravenců na Moravě I. *Formica—Zprav. Pro Apl. Výzkum A Ochr. Lesn. Mravenců* **2001**, *4*, 37–44.
34. Miles, P.; Nešpor, J. Inventarizace a mapování mravenišť v Blanském lese (jižní Čechy). *Formica—Zprav. Pro Apl. Výzkum A Ochr. Lesn. Mravenců* **2003**, *6*, 37–42.
35. Nešporová, M. Inventarizace a výzkum lesních mravenců druhu *Formica polyctena* Förster, 1850 v lokalitě u Babolek. *Formica—Zprav. Pro Apl. Výzkum A Ochr. Lesn. Mravenců* **2003**, *6*, 20–28.
36. Véle, A. *Zpráva z mapování hnízd lesních mravenců na území PP Rohovec*; KÚ Ostravského kraje: Ostrava, Czech Republic, 2005; pp. 2–35.
37. Mabelis, A.A.; Korczyńska, J. Long-term impact of agriculture on the survival of wood ants of the *Formica rufa* group (Formicidae). *J. Insect. Conserv.* **2016**, *20*, 621–628. [CrossRef]
38. Sokal, R.; Rohlf, F. *Biometry: The Principles and Practice of Statistics in Biological Research*, 3rd ed.; Freeman: New York, USA, 2013; pp. 551–801.
39. Kilpeläinen, J.; Punttila, P.; Finér, L.; Niemelä, P.; Domisch, T.; Jurgensen, M.F.; Neuvonen, S.; Ohashi, M.; Risch, A.C.; Sundström, L. Distribution of ant species and mounds (*Formica)* in different-aged managed spruce stands in eastern Finland. *J. Appl. Entomol.* **2008**, *132*, 315–325. [CrossRef]
40. Sorvari, J.; Huhta, E.; Hakkarainen, H. Survival of transplanted nests of the red wood ant *Formica aquilonia* (Hymenoptera: Formicidae): The effects of intraspecific competition and forest clear-cutting. *Insect Sci.* **2013**, *21*, 486–492. [CrossRef]
41. Sorvari, J.; Hakkarainen, H. Deforestation reduces nest mound size and decreases the production of sexual offspring in the wood ant *Formica aquilonia*. *Ann. Zool. Fenn.* **2005**, *42*, 259–267.
42. Radler, K.; Oltchev, A.; Panferov, O.; Klinck, U.; Gravenhorst, G. Radiation and temperature responses to a small clear-cut in a spruce forest. *Open Geogr. J.* **2010**, *3*, 103–114. [CrossRef]
43. Domisch, T.; Finér, L.; Jurgensen, M.F. Red Wood Ant Mound Densities in Managed Boreal Forests. *Ann. Zool. Fenn.* **2005**, *42*, 277–282.
44. Sonohat, G.; Balandier, P.; Ruchaud, F. Predicting Solar Radiation Transmittance in the Understory of Even-Aged Coniferous Stands in Temperate Forests. *Ann. For. Sci.* **2004**, *61*, 629–641. [CrossRef]
45. Antonova, V.; Marinov, M.P. Red wood ants in Bulgaria: Distribution and density related to habitat characteristics. *J. Hymenopt. Res.* **2021**, *85*, 135–159. [CrossRef]
46. Czechowski, W.; Radchenko, A.; Czechowska, W.; Vepsäläinen, K. *The Ants of Poland; with Reference to the Myrmecofauna of Europe*, 1st ed.; PAS: Warszawa, Poland, 2012; pp. 71–74.
47. Mabelis, A.A. Flying as a Survival strategy for wood ants in a fragmented landscape (Hymenoptera, Formicidae). *Memorab. Zool.* **1994**, *48*, 147–170.
48. Véle, A.; Holuša, J. Impact of vegetation removal on the temperature and moisture content of red wood ant nests. *Insectes Soc.* **2008**, *55*, 364–369. [CrossRef]
49. Kadochová, Š.; Frouz, J. Thermoregulation strategies in ants in comparison to other social insects, with a focus on red wood ants (*Formica rufa* group). *F1000Res* **2014**, *2*, 280. [CrossRef]
50. Jones, J.C.; Oldroyd, B.P. Nest Thermoregulation in Social Insects. *Adv. Insect Phys.* **2006**, *33*, 153–191.
51. Sorvari, J. Wood Ants: Threats, Conservation and Habitat Management. In *Wood Ant Ecology and Conservation*; Stockan, J.A., Robinson, E.J.H., Eds.; Cambridge University Press: Cambridge, UK, 2016; pp. 264–286.
52. Rosengren, R.; Fortelius, W.; Lindström, K.; Luther, A. Phenology and causation of nest heating and thermoregulation in red wood ants of the *Formica rufa* group studied in coniferous forest habitats in southern Finland. *Ann. Zool. Fenn.* **1987**, *24*, 147–155.
53. Lenoir, L. Response of the foraging behavior of red wood ants (*Formica rufa* group) to exclusion from trees. *Agric. For. Entomol.* **2003**, *5*, 183–189. [CrossRef]
54. Domisch, T.; Finer, L.; Neuvonen, S.; Niemelä, P.; Risch, A.C.; Kilpeläinen, J.; Ohashi, M.; Jurgensen, M.F. Foraging activity and dietary spectrum of wood ants (*Formica rufa* group) and their role in nutrient fluxes in boreal forests. *Ecol. Entomol.* **2009**, *34*, 369–377. [CrossRef]
55. Gibb, H.; Johansson, T. Forest succession and harvesting of Hemipteran honeydew by boreal ants. *Ann. Zool. Fenn.* **2010**, *47*, 99–110. [CrossRef]

56. Johansson, T.; Gibb, H. Forestry alters foraging efficiency and crop contents of aphid-tending red wood ants, *Formica aquilonia*. *PLoS ONE* **2012**, *7*, e32817. [CrossRef]
57. Juhász, O.; Mikó, Á.; Tenyér, A.; Somogyi, A.; Aguilon, D.J.; Kiss, P.; Bátori, Z.; Elek, M. Consequences of climate change-induced habitat conversions on red wood ants in a Central European mountain: A case study. *Animals* **2020**, *10*, 1677. [CrossRef]
58. Gibb, H.; Andersson, J.; Johansson, T. Foraging loads of red wood ants: *Formica aquilonia* (Hymenoptera: Formicidae) in relation to tree characteristics and stand age. *PeerJ* **2016**, *4*, e2049. [CrossRef]
59. Sorvari, J.; Hakkarainen, H. The role of food and colony size in sexual offspring production in a social insect: An experiment. *Ecol. Entomol.* **2007**, *32*, 11–14. [CrossRef]
60. Véle, A.; Modlinger, R. Body size of wood ant workers affects their work division. *Sociobiology* **2019**, *66*, 614–618. [CrossRef]
61. Sorvari, J.; Hakkarainen, H.; Rantala, M.J. Immune defense of ants is associated with changes in habitat characteristics. *Environ. Entomol.* **2008**, *37*, 51–56. [CrossRef]
62. Brütsch, T.; Chapuisat, M. Wood ants protect their brood with tree resin. *Anim. Behav.* **2014**, *93*, 157–161. [CrossRef]
63. Lubojacký, J.; Knížek, M. Výskyt lesních škodlivých činitelů v roce 2020 a jejich očekávaný stav v roce 2021. *Zprav. Ochr. Lesa. Suppl.* **2021**, *24*, 35–45.
64. Inglesfield, C. Pyrethroids and terrestrial non-target organisms. *Pestic. Sci.* **1989**, *27*, 387–428. [CrossRef]
65. Zahradník, P.; Zahradníková, M. *Metodická Příručka Integrované Ochrany Rostlin Pro Lesní Porosty. Příloha 1. Seznam Povolených Přípravků a Dalších Prostředků na Ochranu Lesa*; Lesnická práce: Kostelec nad Černými lesy, Czech Republic, 2022.
66. Berberich, G.M.; Berberich, M.B.; Gibhardt, M. Red wood ants (*Formica rufa*-group) prefer mature pine forests in Variscan granite environments (Hymenoptera: Formicidae). *Fragm. Entomol.* **2022**, *54*, 1–18.
67. Toro, I.D.; Berberich, G.M.; Ribbons, R.R.; Berberich, M.B.; Sanders, N.J.; Ellison, A.M. Nests of red wood ants (*Formica rufa*-group) are positively associated with tectonic faults: A double-blind test. *PeerJ* **2017**, *5*, e3903. [CrossRef]
68. Berberich, G.; Grumpe, A.; Berberich, M.; Klimetzek, D.; Wöhler, C. Are red wood ants (*Formica rufa*-group) tectonic indicators? A statistical approach. *Ecol. Indic.* **2016**, *61*, 968–979. [CrossRef]
69. Berberich, G.M.; Klimetzek, D.; Paraschiv, M.; Stancioiu, P.T.; Grumpe, A. Biogeostatistics confirm: Even a low total number of red wood ant nests provide new information on tectonics in the East Carpathian Orogen (Romania). *Ecol. Indic.* **2019**, *101*, 486–500. [CrossRef]
70. Sorvari, J.; Haatanen, M.-K.; Vesterlund, S.-R. Combined effects of overwintering temperature and habitat degradation on the survival of boreal wood ant. *J. Insect. Conserv.* **2011**, *15*, 727–731. [CrossRef]
71. Mabelis, A.A. Wood Ant Wars. The relationship between aggression and predation in the red wood ant (*Formica polyctena* Foerst). *Neth. J. Zool.* **1979**, *23*, 451–620.
72. Buggenum, V. Presence after three decades of red wood ants (*Formica rufa* group; Hymenoptera: Formicidae) in forests in an agricultural landscape. *Eur. J. Entomol.* **2022**, *119*, 85–91. [CrossRef]
73. Sondej, I.; Domisch, T.; Finér, L.; Czechowski, W. Wood ants prefer conifers to broadleaved trees in mixed temperate forests. *Agric. For. Entomol.* **2020**, *23*, 287–296. [CrossRef]

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