

Red Wood Ants

Subjects: Animal Sciences & Zoology

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Definition

The consequences of anthropogenic climate change are one of the major concerns of conservation biology. A cascade of negative effects is expected to affect various ecosystems, one of which is Central European coniferous forests and their unique biota. These coniferous forests are the primary habitat of many forest specialist species such as red wood ants. Climate change-induced rising of temperature allows trees to skip winter hibernation, making them more vulnerable to storms that cause wind felling, and in turn, promotes bark beetle infestations that results in unscheduled clear-cuttings. Red wood ants can also be exposed to such habitat changes. We investigated the effects of bark beetle-induced clear-cutting and the absence of coniferous trees on colonies of *Formica polyctena*, including a mixed-coniferous forest as a reference. Our aim was to investigate how these habitat features affect the nest characteristics and nesting habits of *F. polyctena*. Our results indicate that, in the absence of conifers, *F. polyctena* tend to use different alternatives for nest material, colony structure, and food sources. However, the vitality of *F. polyctena* colonies significantly decreased (smaller nest mound volumes). Our study highlights the ecological flexibility of this forest specialist and its potential to survive under extreme conditions.

1. Introduction

Global climate change is one of the major threats facing humanity in the 21st century because it contributes to various environmental problems, such as extreme weather conditions (e.g., strong storms and frequent temperature changes) and pest outbreaks ^{[1][2][3]}. A cascade of negative effects on various habitats and their biota is expected. For instance, rising temperature allows the trees to skip winter hibernation which makes them more sensitive to unforeseen frost, or snow ^[3]. Frost-damaged trees are more vulnerable to storms that can cause wind felling, leading to a higher amount of dead wood, which increases the probability of bark beetle (*Ips typographus*) infestations ^{[1][3]}. Between 1950 and 2000, half of the biotic damages (e.g., tree decay caused by insect or fungi infection) were caused by bark beetle infestations in European forests ^[1]. In addition, bark beetle infestations are expected to increase in the 21st century ^[2], making bark beetles one of the most dangerous pests of coniferous forests in Europe ^{[4][5]}.

An increase in bark beetle infestations has led forest managers to introduce “unscheduled salvage” cutting (i.e., immediate clear-cut before the forest reaches its cutting age) to save the undamaged timber ^[2]. In Hungary, the cutting age for trees in coniferous forests is normally between 50 and 70 years (Decree No. 96/2011. (X. 17.) of the Minister of Rural Development). This has a harmful effect on coniferous forest ecosystems, particularly when most of the trees are removed ^[6]. Likewise, frequent clear-cutting can inhibit the survival or recolonization of coniferous forest specialists. In addition, deciduous tree species are often planted to prevent further bark beetle infestations, however, this method decreases the proportion of older coniferous forests. Deciduous plantations do not have the same environmental conditions as coniferous forests. Therefore, these management practices do not favor the maintenance of coniferous forest specialists ^[7]. As a result, many plantation forests are becoming more susceptible to the adverse impact of climate change (e.g., monocultures with trees in lines and in even distances are more vulnerable to heavy storms) and increases in other pest infestations ^{[1][3]}.

Members of the *Formica rufa* group (commonly called red wood ants) are very important keystone species and ecosystem engineers of coniferous forests but decades are usually needed to develop large colonies and fulfil this role ^{[8][9][10]}. Investigations in Northern Europe have shown that clear-cuttings hinder the

colony development of red wood ants and have a profoundly negative effect on their population survival [11][12][13][14]. Clear-cutting makes the habitat for red wood ants unsuitable and also causes or results in habitat fragmentation. The cleared area is often impenetrable for gynes and workers [7][15][16] and isolation can lead to inbreeding [17]. In addition, clear-cutting negatively influence the strategies of ants to properly exploit food sources (tended aphids) [18]. As a result, aphids on remaining trees produce less and lower quality honeydew which finally leads to starvation and suppressed immune response of ant workers [6][10][18][19]. Ultimately, these effects cause a high mortality rate among the nests in the clear-cut areas [10].

According to our personal observations in Central Europe (e.g., Hungary, Slovakia, and Poland), red wood ants mainly occur in coniferous or mixed coniferous/deciduous forests and are rarely found in deciduous forests, see also [20]. This is the main reason why we have only a limited understanding in terms of the characteristics of the colony structure of red wood ants occurring in deciduous forests [21][22]. It is also unclear whether deciduous plantations can support viable red wood ant colonies for a long term (for many decades).

2. Study Sites

Our investigation was performed in the Mátra Mountains (Northern Hungary, 47°49'36.50" N, 19°58'10.84" E), at an altitude of 429 m a.s.l., in July of 2017 and 2018. The exposure of the study sites was west to southwest with slopes of 10–15°. We compared the red wood ant nests in three different sites. The first study site was the reference site (RS), a recreational forest covered by a mixed coniferous/deciduous forest with *Pinus nigra*, *Quercus cerris*, and *Q. petraea*, where the age of the trees varied between 2 and 105 years. The second study site was a clear-cut area (Cc), which was once part of a large recreation forest (alongside with our RS) composed of *P. nigra*, *Q. cerris*, and *Q. petraea*. Clear-cutting was done in 2016, because of a bark beetle infestation. The retention trees were mostly *Q. cerris* and *Q. petraea* with a few *P. nigra* (5–10 trees/ha according to the current forestry management practices). Lastly, the third site (Qu hereafter) was a deciduous forest further from the other sites (ca. 6 km by air, Figure 1C) dominated by *Q. petraea*, *Q. cerris*, and *Carpinus betulus*. The trees were between 11 and 116 years old. During the frost period in April 2017, many trees were damaged or uprooted, and serious crown damages were commonly observed on *C. betulus*.



Figure 1. Different nest mound structures in the Mátra Mountains and the sampling sites. (A) Half ellipsoid nest shape; (B) Changed nest structure in the deciduous site; (C) Location of the sampling sites.

3. Results

F. polyctena formed polydomous colonies with interconnected nests in the study area. Different nest abandonment ratios were found in the sites: 45% in the RS, 22% in the Cc, and 11% in the Qu. The nest

abandonment ratio in the RS was significantly higher than in the Qu (GLM, $t = 2.54$ and $p < 0.05$). In the other two cases, we did not find any significant difference ($t < 1.9$ and $p > 0.05$).

In 2017, we found the largest variance in nest mound volumes in the Cc, with the smallest and largest nest mound volumes present in this site (Table 1, Figure 2 and Figure 3). Nest mound volumes were significantly larger in the RS than in the Qu (GLM, $t = 3.39$ and $p < 0.05$) and only marginally larger than in the Cc ($t = 2.11$ and $p = 0.059$). A similar situation was also found in 2018, as the nest mound volumes were significantly larger in the RS (GLM, $t = 3.12$ and $p < 0.001$) and the Cc ($t = 2.18$ and $p < 0.05$, Figure 3) than in the Qu. However, there were no significant differences in the nest mound volumes between the Cc and Qu during either of the years (2017, $t = -1.77$ and $p > 0.05$ or 2018, $t = -1.38$ and $p = 0.17$, Figure 2 and Figure 3). In this year, several nests disappeared in the disturbed habitats (in Cc = 10 and in Qu = 11 nests). A significant decrease in living nest mound volumes was observed in the study area between 2017 and 2018 (Wilcoxon coefficient = 874, $p = 0.05$, Figure 3). Although nest mound volumes decreased in each plot, these changes were significant only in the Cc (Wilcoxon coefficient = 161, $p = 0.05$).

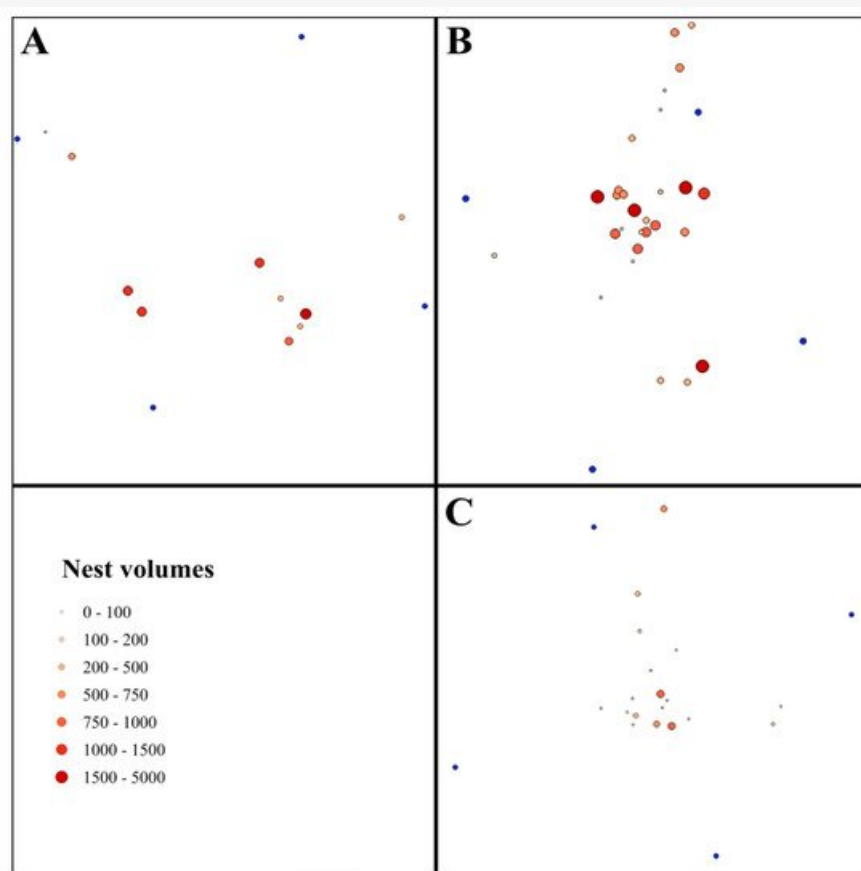


Figure 2. The nest volumes in the studied sites of the Mátra Mountains. (A) The reference site; (B) The clear-cut site; (C) The deciduous site.

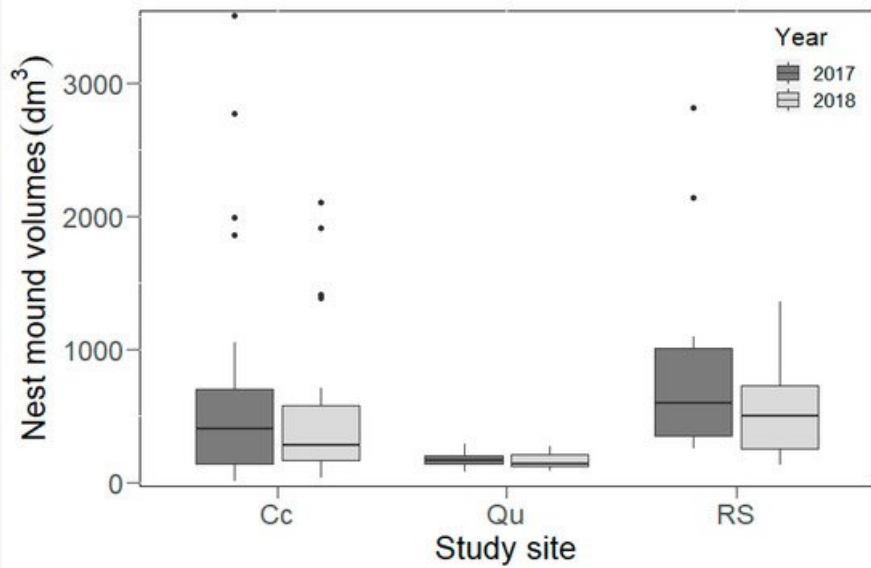


Figure 3. The nest mound volumes (medians, quartiles, range, and outliers) in the studied sites of the Mátra Mountains measured in two consecutive years (2017 and 2018). Cc: clear-cut site; Qu: deciduous site dominated by *Quercus* species; RS: reference site.

Table 1. Nest mound characteristics of *F. polyclctena* colonies in the Mátra Mountains.

	RS	Cc	Qu	Study Area
Number of nests	22	41	27	90
Number of living nests 2017	12	32	24	68
Number of living nests 2018	12	22	13	47
Min. nests mound volumes 2017	250 dm ³	7.9 dm ³	82 dm ³	7.9 dm ³
Max. nests mound volumes 2017	2812 dm ³	3506 dm ³	288 dm ³	3506 dm ³
Average nests mound volumes 2017	895 dm ³	638 dm ³	167 dm ³	542 dm ³
Average nests mound volumes 2018	562 dm ³	538 dm ³	163 dm ³	440 dm ³

We found the highest nest density in the Cc (21.3 nests/ha) and the lowest in the RS (8 nests/ha). In the Qu, an intermediate nest density (16 nests/ha, Figure 2) was found. According to the nearest neighbor analysis, the nests in each plot showed a more random distribution (RS, NNI = 1.03 and Z-score = 0.16; Cc, NNI = 0.89 and Z-score = -1.18; Qu, NNI = 0.96 and Z-score = -0.31) (Figure 2 and Figure 3).

We found 590 foraging routes within the study area with an average length of 16 m. The lowest number of foraging routes was in the Qu (124 routes, Table S1 and Figure 4A) but the shortest average length was in the Cc (12 m, Table S1 and Figure 4B). However, the greatest variance in foraging route length was found in the RS, because the shortest (0.62 m) and longest (164 m) foraging routes were present in this plot (Table S1 and Figure 4B). In general, the average foraging route length per nest was positively influenced by the number of foraging routes (LMM, $t = 7.65$ and $p < 0.001$), but not by the nest volume ($t = 0.41$ and $p = 0.68$). The length of the foraging routes was significantly shorter in the Qu compared with the Cc ($t = -2.91$ and $p = 0.01$, Figure 4B). The other comparisons gave no significant differences ($t < 0.71$ and $p > 0.05$, Figure 4B). Taken separately for each plot, we found a positive correlation between the length and the number of foraging routes (GLM, RS: $t = 6.24$ and $p < 0.01$; Cc: $t = 7.93$ and $p < 0.001$; and Qu: $t = 4.71$ and $p < 0.001$). The mound volume did not have a significant effect on the average length of the foraging routes ($t = 1.76$ and $p > 0.05$).

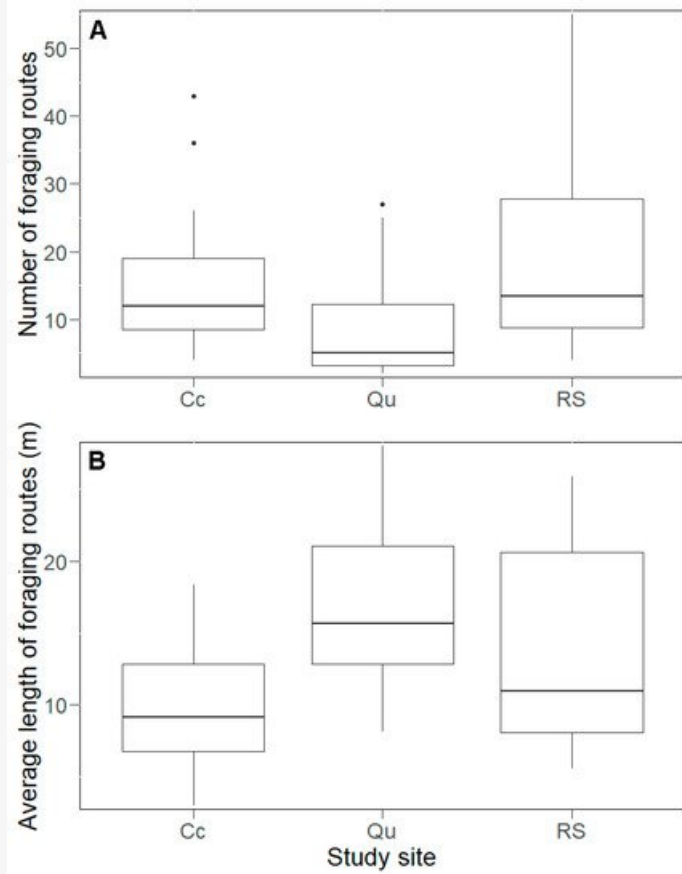


Figure 4. The number (A) and average length (B) of the foraging routes (medians, quartiles, range, and outliers) found in the study sites of the Mátra Mountains. CC: clear-cut site; Qu: deciduous site dominated by *Quercus* species; RS: reference site.

The characteristics of the nest locations of the different sites are presented in Table S2 and Figure S1. In general, the girth of trees had a positive effect (GLMM, $z = 5.64$ and $p < 0.01$), whereas the distance of trees from the nests had a negative effect ($z = -3.93$ and $p < 0.01$) on the presence of aphid tending ants. On the one hand, the distance of the nearest trees from the nests was positively influenced by the girth of trees (LMM, $t = 3.62$ and $p < 0.001$), however, there were no differences among the different sites in this respect ($t < 0.92$ and $p > 0.05$). On the other hand, the girth of trees was significantly larger in the Qu than in the other two sites (RS, $t = -7.05$ and $p < 0.001$; CC, $t = -8.321$ and $p < 0.001$). The difference was only marginally significant ($t = 2.39$ and $p = 0.06$) between the RS and Cc. In the Qu, both the girth of trees (GLM, $t = 2.93$ and $p = 0.01$) and the distance of nearest trees ($t = 2.8$ and $p < 0.05$) had positive effects on the nest mound volume, and the interaction of these two variables had a negative effect on the nest volume ($t = -2.69$ and $p < 0.05$). In the other two sites, neither of the variables had a significant effect ($t < 1.24$ and $p > 0.05$).

4. Discussion

Our results are consistent with the expected effects of clear-cutting and the absence of coniferous trees on nest mound volumes and foraging habits of the polydomous red wood ant colony systems. Findings from our study indicated a larger variance in nest mound volumes in the clear-cut area which were characterized by slightly smaller nests as compared with the nests found in the reference site (i.e., mixed coniferous/deciduous forest). Ants in the clear-cut areas used the shortest foraging routes. However, the deciduous forest patch resulted in a very different nest structure and foraging habits, having the smallest sized nests and longest foraging routes. This supports our second hypothesis about the effects of the deciduous forest environment which stated that availability and location of suitable nesting sites could be a stronger determining factor for red wood ants than the distance from food sources that led to longer foraging routes. Altogether, we found polydomous systems with random nest distribution in each plot that could be the result of the spreading strategy of *F. polyctena*. Polydomous colonies are spread by nest splitting which can lead to the uniform coverage of the territory [23] and are also influenced by the location of

appropriate nesting sites. This distribution is in accordance with the findings of Tsikas et al. [24] for *F. lugubris* in the Rhodope Mountains (Greece). However, since we investigated only one repetition per treatment, the possibilities for generalization of the results should be handled cautiously.

We found a high nest abandonment ratio (45%) in the reference site, which was similar to that found 4–5 years after clear-cutting in Finland [11][12][13]. However, in our case, this pattern could be related to the lack of appropriate insolation and disturbance regimes [25][26][27][28][29]. Our results showed that the nests were situated away from trees with larger girth which could be due to the shading of the large trees. Thus, there may be a correlation between the distance of foraging routes and the girth of trees. New nests can be established in areas with a sufficient amount of sunlight [25][27][28].

In our reference site, appropriate light conditions were found only at the edge of pathways that were kept clear for the tourists, but smaller nests did not tolerate larger disturbances (e.g., high trampling intensity) [26][29]. As a result, new nests could be established only in less visited and trampled areas. In addition, rapid shrub encroachment can also lead to high nest turnover. Nonetheless, old and large colonies can persist under these disturbances, close to the most visited tourist sites, or in overgrown and shaded areas [25][27][28][29]. Abandoned nests were usually close to larger nests, possibly as the result of nest relocations over time (i.e., finding better conditions for the growing colonies). The abandoned nests were still recognizable, presumably due to the slower degradation rate of the pine needles in the nest material.

Although the reference site had the smallest number of nests, it showed considerable variation in nest size distribution and foraging route length. The main reason for this was that the food availability and quality in this plot were close to a preferred habitat of red wood ants with many coniferous trees.

The presence of larger and closer conifer trees support ant populations by providing proper food sources and allow them to visit aphids. In general, the nest volumes did not change significantly between the years, and all the nests were present in both years of the study.

Nest abandonment ratio was 22% in the clear-cut plot, which was lower than that found in 4–5 years old cuttings in Finland [11][12][13]. It is important to note that our clear-cut plot was sampled one year after the disturbance, whereas ant colonies in Finland had more time to react [11][12][13][30]. However, the nest mound volumes decreased between the years, indicating that clear-cutting had a significant effect on red wood ants, even after two years of clear-cutting. Presumably, the rate of abandonment should increase in the future as many nests disappeared from 2017 to 2018. The clear-cut area provided habitat for the largest number of nests, and it showed the largest variation in nest mound volumes (from the smallest to the largest in the study area), which reflected the age of colonies [31]. This large variation indicated that very young and old nests were present in this area. This was presumably due to the fact that many large and old colonies survived under the protection of remaining shrubs and deciduous trees and whereas more exposed larger nests were split into several small ones in order to reach the nearest forest edge [10][11][12][13][30][32]. The newly established small nests were mostly found in quite exposed areas, on the trunks of recently cut trees. This could lead to the desiccation of the small nests [33] resulting in a higher mortality rate, which is already elevated due to a reduced capacity to efficiently defend against competitors, predators, and parasites, as well as lowered thermoregulation capability [10]. Some small nests still occurred in “unoccupied” and less exposed sites under shrubs or scattered trees. Ants using this strategy could stay closer to the remaining aphid colonies, allowing them to compensate for the lack of enough food sources, which can be one of the main problems of the nests in clear-cut areas [6][11][12][13]. Ants also visited larger trees that could support a larger number of aphid colonies. As predicted, our findings are in accordance with previous studies which have shown that clear-cutting had a strong effect on the colony size of redwood ants, resulting in smaller nest mound volumes compared to a reference plot [10][11][12][13]. We also found the highest number of foraging routes and the shortest average length in the clear-cut plot. The increased number of connections among the newly established nests and mother nests increased the number of foraging routes and decreased their distances, as also shown in former studies [10][11][12][13][30]. After clear-cutting, the quality and quantity of aphid honeydew decreased [6]. This could lead to colony

starvation and to a decrease in the size of workers [11][12][13]. The nest abandonment ratio was the lowest (11%) in the deciduous plot, similar to the ratio (10%) found for the managed part of the Białowieża Primaver Forest (Poland) [20]. We also found the smallest nest size in the deciduous plot (tree size had a negative effect on the nest size). This is in contrast with other studies, which have shown that nest size grows with increasing shade [20][34]. As a replacement for the absence of conifer needles, the ants use fallen trees to strengthen their nest. Without the needles the nests are lower but longer alongside the fallen tree trunks. This is in agreement with other studies which indicated that the complete absence of conifers caused abnormalities in wood ant colonies such as changed nest size structure and distribution [21][22]. For instance, Kristiansen and Amelung [21] found that *F. polyctena* built below-ground nests in an oak forest. In addition, Dolek et al. [22] found that *F. polyctena* associated with semi-open forest stands if the forest was primarily composed of oak species. The fewest but longest foraging routes were found in the deciduous plot with a preference for *Q. cerris* trees (ca. 90%). This is in contrast with the findings in *Formica lugubris* which does not show a preference for any tree species in mixed coniferous/deciduous forests where both *Pinus sylvestris* and *Quercus* spp. are available [35]. However, other studies have found that *F. lugubris* used *Quercus* trees as the main food resource [36]. Our findings suggest that *Q. cerris* has great potential to be a sufficient substitute to replace conifers for red wood ants. However, ants try to find the best aphid-infested trees, and therefore establish longer routes to find them. We found a negative correlation between the number of foraging routes and their length. This was the consequence of the nests' cost-efficiency optimization [37]. The limited number of workers cannot maintain unlimited foraging routes. Therefore, the workers have to optimize their choice between the number of routes and the quality of the honeydew of the visited trees. Food searching behavior of the red wood ants is primarily related to the distribution of aphids on conifers [6][25][38][39]. In the absence of enough coniferous trees, ants used *Q. cerris* trees (42% of the searching trees) to fulfil their needs. We strongly suspect that the decreased nest mound volumes in the deciduous forest are in relation to the insufficient food sources provided by aphids on deciduous trees because this forest is slightly older than the others, and older forests can support larger red wood ant colonies [6]. In addition, many nests disappeared between the years. Robinson et al. [36] showed that deciduous trees could also provide important resources for *Formica lugubris*, but the use of such resources was lower than their abundance predicted. In addition, if conifers are also present, ants use them in a disproportionately large amount [36]. This is in line with the findings of Sondej et al. [20], who reported that deciduous forests in Poland usually did not provide a suitable habitat for red wood ants. Another possible explanation for these patterns is the lack of conifer resin in the deciduous plot. Red wood ants collect and use the pine resin actively to disinfect the nest material [40], and therefore the lack of conifer resin can lead to the decline of populations. In this case study, we have taken the first step to understand how clear-cutting and the absence of conifers could affect nest size and foraging strategies of red wood ants in Central European managed forests. These disturbances will become more common in the future because the frequency of bark beetle infestation and wind felling will increase due to the effects of anthropogenic climate change [3]. Although the sample size was small, our results indicate that different disturbances cause different responses within red wood ant colonies such as nest splitting in clear-cuts and the use of fallen trees for nesting in a deciduous forest. Their foraging behavior can also change in response to a changing environment, from pine-feeding aphids to oak-feeding aphids. It is also possible that they use tannin from *Q. cerris* trees to replace the missing antimicrobial potential of pine resin. Although we cannot rule out other mechanisms (such as the effect of site differences) due to the small sample size, this work provides the first step to understand the consequences of conifer loss on this ecologically important species group, and we encourage myrmecologists to conduct further investigations with larger sample sizes to clarify these aspects. The smaller nest mound volumes observed in the studied sites without coniferous trees could lead to decreased surviving chances of red wood ants in the changed habitats. Although they seem to be ecologically flexible and also can survive under extreme conditions [30][41][42][43][44], the disappearance of many nests in the disturbed habitats gives concern and calls for action from conservation managers. However, further investigations on a larger scale and with a larger sample size are needed to answer the still unresolved question, "How long can red wood ants (e.g., *F. polyctena*) survive in a rapidly changing environment?" The results of our case study indicate that nest relocation would be advantageous before clear-cuttings and it would be important to plant mixed forest

stands instead of monocultures in areas where the climate is suitable for native coniferous tree species. These activities could help to maintain viable populations of this ecologically significant forest specialist species in the long term.

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Keywords

clear-cut;oak forest;coniferous forest;colony size;foraging activity;*Formica polyctena*

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