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Article

Space, Habitat and Isolation are the Key Determinants of Tree Colonization by the Carpenter Ant in Plantation Forests

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Abstract: Forest plantations are still often considered the antithesis of real nature. However, plantations can host many organisms. The problem is that some of the hosted species are regarded ad hoc as pests. The main aim of our paper was to study the carpenter ant (*Camponotus ligniperdus*) in windstorm habitats. We studied forests in East Bohemia, Czech Republic, and focused on the spatial distribution of snapped trees and the influence of selected forest characteristics on the incidence of ant nests. We found that the nests in the study area mainly occurred in Norway spruce, which is the most commercially important tree in the majority of Central Europe. More than one quarter of the snapped trees were inhabited by the ants. We found that nests exhibited a spatially autocorrelated pattern that differed on spatial scales. The most important characteristic of the host tree for determining carpenter ant nests was the presence of brown rot, and the majority of tree nests were isolated from forest openings. The presence of carpenter ants in forest plantations is, therefore, not harmful. Their presence could be used by forest managers as an indication of unsuitable stand conditions for the successful growth of the Norway spruce and other coniferous plantation trees.

Keywords: *Camponotus ligniperdus*; Norway spruce; rot type; sanitation cuttings; wind disturbance

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1. Introduction

Forest plantations are often grown as monocultures, with clear cut harvest as the dominant management type. In addition to the composition of one dominant, often non-indigenous tree species, this forest land use type can negatively influence soil chemistry, moisture, and physical attributes, together with vegetation. It can also influence other abiotic factors such as solar radiation, air, and soil temperatures [1–3]. The response of insects, as the most abundant and biodiverse group of organisms, to the management of plantation forests can be highly varied. For example, saproxylic insects, in general, often have lower diversity, but, more particularly, bark beetle populations can reach outbreak levels [4,5]. The dominant tree species in plantation forests in Central Europe is the Norway spruce (*Picea abies* (L.) Karst.). This tree is highly susceptible to the attack of spruce bark beetles, drought, and wind. Plantation forests, as monocultures, are therefore often less resilient to disturbances caused by insect pests [6]. Current research has indicated that the protection of forests against such pests is a complex issue.

Plantation forests are not only a place for timber products, but also provide ecological functions such as water retention, soil conservation, and biodiversity maintenance [7–10]. Many forests with high commercial importance for the timber industry are located in areas with specific biodiversity [11].

Research has indicated that such land use is important for the survival of many different species, including some threatened species [7,12,13]. A high population density of species that are beneficial for forestry is also important. For example, parasitoids are used in biocontrol and fungi help with the decay process of wood residuals [14,15].

Several insect species have two opposing functions, and are often considered, at least potentially, pests. However, evidence of their damage is often lacking, or the damage they cause is negligible. For example, aphids tended by red wood ants can reduce tree growth, but they protect trees against herbivorous pests [16]. Woodpeckers can reduce the population of bark beetles, but they sometimes damage trees while hunting and nesting [17]. Another example of a taxon often referred to as a pest is the carpenter ants of the genus *Camponotus*. The two ant species that are most typical in forests dominated by Norway spruce in Europe are *C. herculeanus* and *C. ligniperdus* [18,19]. Both species build nests in the lower part of tree trunks. Their nests form a typical lamellar structure, with summer wood being almost untouched [20,21]. Whereas *C. herculeanus* is often part of the insect communities of indigenous spruce forests at higher elevations, *C. ligniperdus* is most common in lowland spruce plantations. The literature indicates that *C. ligniperdus* is a forest species. Besides coniferous stands, this species often occurs in mixed and deciduous forests or in habitats sparsely overgrown with woody plants. Typical places of its occurrence include stone banks and sunlit forest edges [20,22]. Carpenter ant nests are built in stumps and rarely in living trees; regardless, this species is often regarded as a pest that is damaging the wood of the most commercially important part of the tree (i.e., the lower part of the stem). The average population of a nest is approximately 3000 individuals. Ants collect food on bushes and trees, and less often in deeper soil layers or from vegetation [22]. They partly feed on honeydew, but they are also effective predators of insects [23]. This is one of the contrasting indications of the situation of this neglected big insect species—is it a pest or a beneficial predator? Highly unstable spruce plantations need beneficial species that can help combat insect outbreaks. Thus, information about the requirements of carpenter ants in plantation forests has a high potential to help foresters with successful protection.

In this study, we focused on the characteristics of plantation forest that influence the distribution of the carpenter ant, *Camponotus ligniperdus* (Latreille, 1802). Namely, we were interested in the spatial distribution of their tree nests, and the influence of the habitat, patch, stand, and isolation forest characteristics.

2. Materials and Methods

2.1. Study Area

We studied plantation forests in East Bohemia, Czech Republic, with a total area of more than 800 ha. The elevation was from approximately 300 to 350 meters above sea level. The dominant tree species in the area was Scots pine (*Pinus sylvestris* L.). Some stands were dominated by the Norway spruce (*Picea abies*) and sessile oak (*Quercus petraea* (Matt.) Liebl.)), with the occasional dominance of introduced European larch (*Larix decidua* Mill.) and white pine (*Pinus strobus* L.).

The study was conducted during the winter of 2017–2018 and early spring 2018. This area was affected by the windstorm caused by cyclone Xavier in early October 2017. The windstorm reached a peak speed of 202 km/h at Sněžka, the highest point in the Czech Republic. The effect of the windstorm was not the same as that of previous windstorms caused by Kyrill (2007) and Emma (2008). This means that the wind disturbance did not cause large areas of damaged trees with a clumped distribution, but rather individual (in the case of spruce) or small group disturbances (in pine) scattered throughout the whole study area.

2.2. Data Collection

Carpenter ants more often inhabit weakened trees, which are less resistant to wind. For this reason, we searched for all snapped trees in our study area. We carefully investigated all stands older than 40 years old. This is the approximate age at which trees start being damaged by windstorms in the study area. We observed no damage in the younger stands. This means that all stands were walked along their entire length in 50 m distant transects (i.e., two transects in stands that were wider than 100 m). In cases of the presence of natural regeneration, we performed individual visits to places that could not be observed from transects.

The sanitation cuttings by forest mechanization started immediately after the end of the climate conditions that caused the poor accessibility to the stands. This means that in the late spring, there were nearly no residual snapped trees (except for stumps), and only a few of them stayed in roundwood timber stocks until the late spring. The main reason for snapped tree removal was sanitation, mainly for the suppression of potential bark beetle outbreaks. This led to the relatively short period of the study (early October–early April).

2.3. Studied Variables

Our dependent variable was the presence of carpenter ant, *Camponotus ligniperdus* (Latreille, 1802) nests where trees had snapped (Figure 1). The presence of the studied species is easily recognized due to its galleries through the spring annual rings and the summer rings left nearly untouched (Figure 2). Other species of the genus *Camponotus* that can create their nests in trees have not been observed in the study area in the past during spring. Therefore, we confirmed that the nests were of *Camponotus ligniperdus* origin without the observation of adults. Furthermore, adults are not present in galleries outside the vegetation period.

Figure 1. Distribution of all snapped trees (**left**) and the presence of nests of carpenter ant, *Camponotus ligniperdus* (Latreille, 1802), (**right**) in our study area in the Czech Republic.

Figure 2. Snapped Norway spruce (*Picea abies* (L.) Karst.) tree (**a**). Structure of wood affected by the carpenter ant (*Camponotus ligniperdus*) in the snapped stem of the Norway spruce (**b**). Worker of the carpenter ant with its prey, observed in the late spring (**c**). Cut snag of the Norway spruce infested with a large nest of carpenter ant (**d**) in the East Bohemian woodlands, Czech Republic.

1. The first two independent variables collected were regarding the spatial distribution of nests. Each snapped tree was localized using a geographical positioning system (GPS) using geographical coordinates of (a) northing and (b) easting in WGS84 format (center: 50.0058; 16.1780).
2. We searched for four habitat characteristics. We identified (a) the tree species of the snapped tree, and five tree species were snapped. All were coniferous: the Norway spruce (N = 102), Scots pine (N = 17), larch (N = 9), white pine (N = 1), and silver fir (*Abies alba*; N = 1). We also searched for (b) the presence of rot in the place of the snap. We divided the type of rot into two commonly used categories: white (N = 8) and brown (N = 69) rot. The white rot was most probably caused by *Armillaria* and brown by *Heterobasidion* [24]. The rest of the trees were without any indication of the presence of rot. We also checked for (c) the presence of resin on the stem, but this was highly correlated with the presence of rot ($R_s = 0.37$; $p < 0.001$). This has been confirmed by current research [25], and we thus did not use resin indication for further analyses. We measured (d) the height of the breakage on the stem (mean = 246.57 ± 1.63 cm SE), and the height of snapped of trees inhabited by carpenter ant nests was 93.71 ± 12.20 SE (5–230) cm.
3. We also collected two patch-based characteristics. We estimated (a) the canopy closure as a percentage (80.04% ± 1.63%). (b) The composition of the same tree species as the snapped tree was also investigated (57.81% ± 2.66%).
4. The stand-based characteristic was the age of the stand (73.83 ± 1.93 years).
5. Two characteristics that reflected isolation were measured. The first was (a) the distance to the forest track (67.36 ± 5.31 m) as a permanently open area. (b) The second variable was the distance

to clear-cut or non-forest land (93.65 ± 12.57 m)—the gaps created by actual windstorm were not measured.

2.4. Statistics

The spatial distribution of the nests was analyzed using Moran's I, which is the measure of spatial autocorrelation in SAM v4.0 [26]. Regarding this analysis, we used coordinates (northing and easting) of the snapped trees. The number of geographic distance classes in SAM was manually set to six. Class size in SAM was set to an equal number of pairs and symmetric distances. The test for significance had 199 permutations.

Multicollinearity of independent variables was reflected by variance inflation factor (VIF) and computed using package HH in R 3.5.1. Tree species were removed from the generalized linear model (GLM) with forest characteristics due to multicollinearity (VIF > 2).

We computed a GLM with a binomial distribution of the dependent variable (presence and absence of the studied species) for analysis of the influence of the space and the forest environment. The global test for spatial autocorrelation was not significant ($I = -0.01$; $p = 0.08$). However, due to the significant influence of space on more particular distances, we used the autocovariate of the dependent variable as the control of the influence of spatial autocorrelation [27]. It was computed using package spdep in R. The differences among types of rot were analyzed by GLM and visualized by observed weighted means with 95% confidence intervals.

As the tree species was removed from GLM due to multicollinearity, we independently analyzed the possible relationship of the carpenter ant to tree species by Kruskal–Wallis ANOVA in R.

3. Results

We found 34 snapped trees that were inhabited by the carpenter ant, representing 26.15% of all snapped trees found.

Positive values on short distances (up to 1.5 km) between nests indicated their statistically significantly positive autocorrelation; thus, they had a clustered distribution and nests were attracted. Negative values for longer distances indicated that the nests were significantly negatively autocorrelated; this means that they switched to uniform distribution and were repulsed. Finally, there was no significant autocorrelation at the longest distance (over five kilometers) and the distribution of nests started to be random. This means that space had, in this case, no effect (Figure 3).

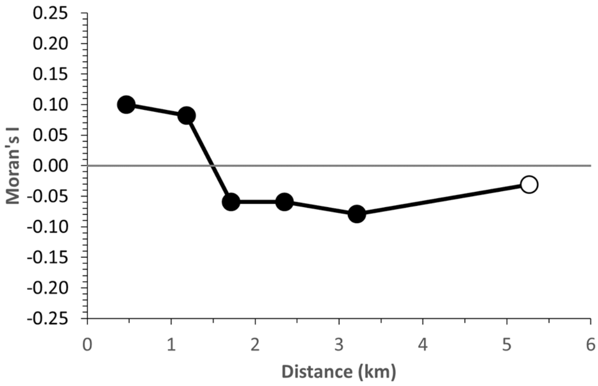

Figure 3. The influence of geographic distances in kilometers using the computed Moran's I from the observed incidence of the carpenter ant in the Czech Republic. Full circles represent $p < 0.05$, empty denote non-significant values.

The number of snapped trees inhabited by the carpenter ant significantly increased toward the east. The number of nests was the highest in the north-eastern part of the studied area (Figure 4).

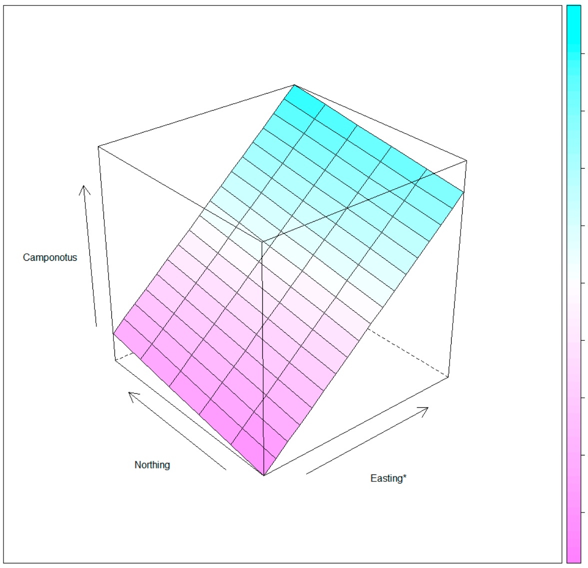

Figure 4. Influence of distribution of snapped trees on the incidence of the carpenter ant in the Czech Republic. * denotes $p < 0.05$.

The incidence of carpenter ant was statistically significantly positively related to the presence of rotten wood in snapped trees. The second significant positive relationship was with the increasing distance from clear-cut and non-forest land. The other studied characteristics showed no significant influences (Figure 5).

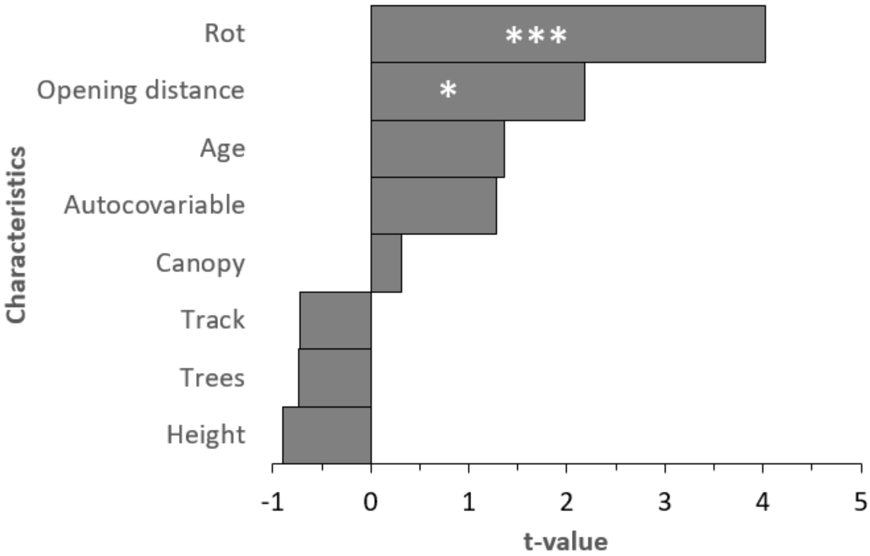

Figure 5. Influence of forest characteristics on the incidence of the carpenter ant in the Czech Republic. * denotes $p < 0.05$ and *** denotes $p < 0.001$.

Five tree species were found to be snapped in the study area. Only two were inhabited by the carpenter ant (Figure 6). We did not observe a significant difference in the incidence of the carpenter ant regarding the tree species ($H = 8.18$; $p = 0.085$).

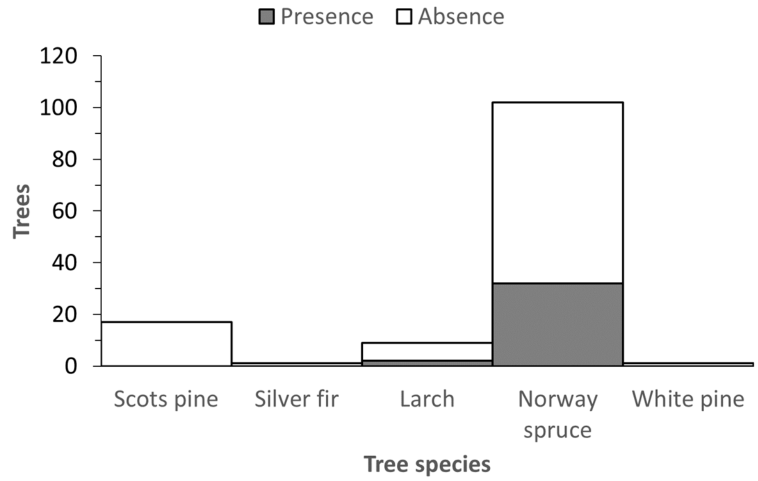

Figure 6. Incidence of carpenter ant nests with respect to tree species in the Czech Republic.

The trees preferred by the carpenter ant were rotten (Figure 5). The presence of brown rot had a positive effect on incidence of the nests ($t = 4.22$; $p < 0.001$), whereas the absence of rot had a significantly opposite effect ($t = -4.44$; $p < 0.001$). White rot had no effect ($t = 0.35$; $p = 0.725$; Figure 7).

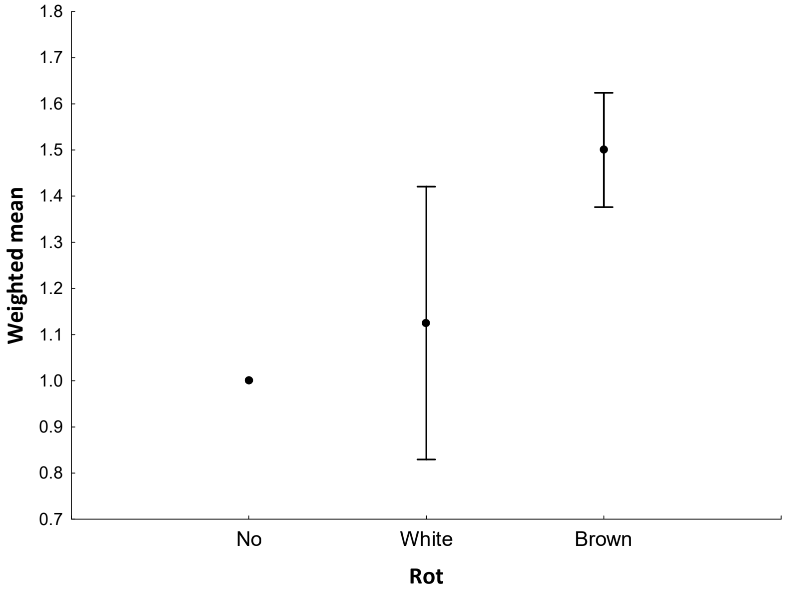

Figure 7. Influence of rot type on incidence of the carpenter ant in the Czech Republic.

4. Discussion

We observed that the nest distribution in the study area was most influenced by space, habitat, and isolation characteristics. More than one quarter of the trees broken by the windstorm were inhabited by carpenter ants. We found that the nests exhibited a clumped distribution on small scales, but had the opposite spatial pattern across larger distances. Nests were more frequent in the eastern part, although the forest structure was nearly the same in the whole study area. The most important tree parameter for the ants' nests being present was the presence of brown rot of the core wood. Ant nests were less frequent close to the forest openings.

Focusing on nest distribution, one of the main causes for the pattern could be the carpenter ant manner of breeding. After the mating flight, fertile queens build new nests. New queens sometimes occupy existing nests, and rarely the maternal nests [28,29]. The distances found between nests indicate that nests close to each other are related. The queen's dispersal ability after swarming is limited [30,31]. The observed distance between the nests, 1.5 km, mainly corresponds to the flying distance of wood ants. Their queens are able to fly a few kilometers. However, in 80% of flight incidences, the distance is less than 2 km [30,31]. This distance mainly corresponds to our results. Larger queens are able to disperse greater distances. Several morphological differences (such as a large and heavy abdomen) may limit dispersal [32]. One of the important aspects of our information about the aggregated distribution of nests over short distances is that the nest of one *C. ligniperdus* colony can be placed in several trees [33]. Some nests may have up to three queens, but they do not tolerate one another, and maintain territories within the diffused nests [28]. This also appears to be the cause of our finding of aggregation of inhabited trees, as closely inhabited trees could be inhabited by one ant colony. As the nest aggregation decreased with increasing geographical distance between them, a mosaic structure of transition from aggregated to segregated spatial structure was created. A similar pattern of ant nest distribution was noted by [34], who attributed it to several species-specific factors, as well as stochastic processes. Competition is an example of a relationship with a strong effect on nest distribution [35]. It is possible that only kinship nests exist in one clump. The subterranean species *Camponotus cruentatus* establishes new colonies near maternal ones, and the foraging areas of colonies overlap [36]. *Formica exsecta* nests that produce new queens supply nearby nests as well [37]. *Formica truncorum* ants hibernate in shared winter nests, which causes homogenizing of the population from several nests [38]. Conversely, strong interspecies animosity exists among unrelated ant colonies [39].

Our finding of a north-eastern aggregated distribution of snapped trees with nests could be caused by the prevailing direction of the wind. The wind direction in the Czech Republic is generally from the west. However, Reference [40] stated that the direction of the wind does not affect the direction of spread of the queens. However, a relatively high altitude of adult flight, which reaches up to 40 m, indicates that they could use the wind to obtain sufficient altitude [40]. The spread of ants with the help of wind corresponds to ant queens sometimes trying to establish new nests in unsuitable locations, which confirms their low active dispersion ability [22]. This fact could explain the observations of non-forest nest habitats mentioned in the literature.

The significant relationships of carpenter ant colonies with increasing distance from clear-cut and non-forest land were relatively surprising, considering the information known from the majority of entomological and forestry literature. The majority of ant species in spruce forests occur in or close to clearings. Their numbers in these habitats are also higher [41]. One possible reasons for the carpenter ants' distance from more sunny places is the reduction of competition with other ant species. One of the indications that can explain our results is that carpenter ants encounter species that do not defend their territory [42] and avoid forests with wood ants with large territories [43]. It is possible that carpenter ants can compensate for poorer temperature conditions due to their endosymbiosis with the *Blochmannia* bacteria, which improves colony growth and immune defense [44,45]. They have a good ability to heat their nests using metabolic heat [46]. One possible support for open habitats is that *C. ligniperdus* apparently prefers standing dead wood with a large perimeter [47]. Large-diameter dead wood is scarce in dense forest plantations. Thus, this situation mainly occurs in old or conservation forests [48]. Due to the type of damage, we were unable to measure the tree diameter, though the majority of trees were of average diameter in comparison to the surrounding trees in the stands. Information about ant preferences for clearings may be based on observations of nest remainders in stumps, because the discovery of nests is easier in open areas. However, the prime nests were located in tree trunks in the forest. Therefore, we cannot support that *C. ligniperdus* is associated with sunlit forest conditions and stumps.

Closed forests, the prevailing habitat in our case, have a more balanced microclimate than clearings [49,50]. This is an advantage for brown rot occurrence [51], as the probability of trees being inhabited by fungi is greater in darker forests than in gaps. For example, the mycelium of *H. annosum* does not grow if the temperature exceeds 35 °C, and fungi are destroyed at temperatures exceeding 45 °C [51,52]. We found that *C. ligniperdus* only built nests in trees that were inhabited by brown rot. Brown rot fungi preferentially decompose wood cellulose and hemicellulose, whereas white rot fungi are able to use lignin as well as cellulose and hemicellulose [53]. The presence of brown rot causes softer wood [54], but the remaining lignin ensures the maintenance of the wood structure [55]. This means that nest creation is easier in trees which are inhabited by rot, but only the wood with brown rot was suitable for nesting. Nests were mainly found in spruce trees. Spruce is an economically advantageous, highly productive species [56]. However, in Central Europe, it is often grown under unsuitable climatic conditions, which is reflected in its susceptibility to abiotic and biotic damage. Therefore, considerable attention has been paid to its damage [57–59] and the fungi associated with the species [25]. As *C. ligniperdus* inhabits fungus-infected trees, it can be seen as an indicator of weakened trees. Its numerous occurrences in the forest may indicate the unsuitability of growing spruce at lower altitudes. The number of nests in the study area was probably not so high due to the Scots pine dominance. Pines find more favorable conditions here, and they are therefore more resistant to fungal infections. Nevertheless, we observed a 1.5 km distance between the nests, which shows that not all suitable trees could be used for nest building.

Another important fact is that herbivorous insects are the diet of carpenter ants. For example, Reference [60] described successful hunting of *Malacosoma* larvae. During laboratory studies, it was found that workers attacked and killed 98% of the submitted arthropods, and they were able to catch a large number of taxa [23]. Although we have no specific data, we assume that their predation pressure is unlikely to be as strong as that of wood ants. These ants intensively hunt up to 30 m away from the nest [16]. The size of the *Camponotus* population is about 1/100th of the nest population of forest ants [22], which approximately corresponds to the ability to protect one tree. However, due to nest distribution, carpenter ants can protect entire forest patches against insect pests. Therefore, considering *C. ligniperdus* a pest species could be a serious mistake.

5. Conclusions

Carpenter ants are large and conspicuous ants, but they live a relatively hidden life. We found that carpenter ants are often found in coniferous trees, namely the Norway spruce. Regarding our results, ant presence in forest plantations appears not to be harmful, because the possible damage to the wood of stems occurs, in the majority of cases, to already rotten wood. As they often prey on insects that are potential pests, we concluded that the populations of carpenter ants in plantation forests are beneficial. Even when their nests indicated a clustered distribution pattern, we did not observe their damage to many neighboring trees, which would be typical for a bark beetle outbreak. Observation of aggregated incidences of the carpenter ants in trees would indicate to forest managers the unsuitable climatic stand conditions for the Norway spruce, due to the high possibility of damage by pathogens.

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Conflicts of Interest: The authors declare no conflict of interest.

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