

Wood Ants: Important Components of the Forest "Immunity System"

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Abstract

Climate change is one of the major threats to biodiversity, but its impact varies among the species. Bark beetles (*Ips* spp.), as well as other wood-boring pests of European forests, show escalating numbers in response to the changes driven by climate change and seriously affect the survival of the forests through the massive killing of trees. Many methods were developed to control these wood-boring beetles, however, their implementation can be detrimental for other forest specialists. Ants are widely used for biological pest-control, so in our study, we aimed to test the effect of *F. polyctena* on the control of the wood-boring beetles. The results show that the proportion of infested trees is significantly reduced by the increase of the number of *F. polyctena* nests, with a strong effect on *Ips* species. We also show that the boring beetle community is shaped by different biotic and abiotic factors, including the presence of *F. polyctena* nests. However, the boring beetle infestation was not related to the latitude, altitude and age of the forests. Based on our results, we assert the effectiveness of the red wood ants as biological pest control and the importance of their conservation to keep the health of the forests.

Introduction

Beetles are the most diverse group of insects on Earth with about 400,000 described species (88). This large group is distributed worldwide and their species are present in all the ecosystems (84, 87), being involved in many different types of interactions. Some species belonging to the group of wood-boring beetles destroy the wood either to obtain food (xylophagous) or to protect their eggs, larvae, and pupae (14). Wood-boring beetles play an important role in forests due to their contribution to dead wood degradation, involvement in the nutrient cycle, and facilitation of the arrival and establishment of other rare insect species (8, 54, 95). However, some of the xylophagous beetle species are known to cause serious damages in fruit plantations and forests (17, 22, 23, 27, 58).

Wood-boring beetle species belong mainly to the families Cerambycidae, Buprestidae, and Curculionidae, which altogether encompass a vast list of the species considered main forest pests (13). Wood-boring beetles complete their life cycle by establishing a parasitic interaction with the tree (75, 13). Some of the longhorn beetles (Cerambycidae), jewel beetles (Buprestidae), and bark beetles (Curculionidae, Scolitynae) are monophagous or oligophagous, meaning that they are dependent on one or a few tree species of the same genera (32). Wood-boring beetles are very important components of the nutrient cycle in forests as they decompose the decaying wood, contribute to the regeneration of soil nutrients and facilitate the establishment of other insects (62). Usually, they infest living but weakened trees or untreated lumber, in which females (attracted by volatiles produced by dying or recently dead trees) place their eggs in crevices of trees affected by water stress or roots damaged by biotic or abiotic factors (9, 13, 22). Moreover, they can also kill conifer seedlings by feeding on their stem bark (41, 55, 56). In temperate coniferous forests, since infestations can potentially kill the trees, these wood-boring species constitute serious pests (8) and can cause enormous ecological (37, 5) and economic losses (22, 30, 45, 66, 91).

The most harmful wood-boring beetle species throughout the world belong to the subfamily Scolytinae (Latreille, 1804), which are considered the most destructive forest pests (2, 26, 27). In Europe, the bark beetle *Ips typographus*, known as European spruce bark beetle, is the cause of many major economic losses in the forest industry (1, 75) and forest degradation (11, 44, 50). The massive loss of trees is caused by the bark beetle attack in the middle and lower parts of the trees but also by the indirect negative effect of fungi, bacteria, and mites associated with bark beetles (78). Moreover, in European spruce forests, the large-scale windthrow is usually connected with outbreaks of *I. typographus* and results in extensive loss of trees (95). Such outbreaks of the pest species are caused mostly by the changes in the natural or semi-natural environment that can be linked to anthropogenic activities, having a strong impact also on the insect communities (42, 25, 80, 92, 97).

Human activities lead to changes in many environmental factors, such as the increase of the global temperature linked to the climate change that threatens the survival of many insect species (5, 6, 10). The short generation time and the close relation between temperatures and life-history traits (5) make them especially sensitive to temperature changes, in particular, the specialist species like those belonging to the *Formica rufa* group. Besides the changes in temperatures, it also induces habitat loss and other changes in the natural environment, such as alterations in the precipitation regimes, that affect the forest growth and production (81, 83, 85). However, climate change can have an opposite effect in some invasive and pest species (74), like the bark beetles, and influence positively their populations as it can shorten their generation time and facilitate their spread that leads to the outbreak of their native populations (11, 49, 50, 59). In this concern, different management techniques have been developed in order to facilitate an early detection to minimize the damage caused by different pests (1, 11). However, these techniques are designed to overcome the current situation, many times not considering the long term effects and the well-being of many other forest-dwelling species, like birds (as woodpeckers; 24, 39, 40), parasitoids (31, 38) or other arthropods (as the clerid beetle *Thanasimus dubius*; 69) including wood ants (36, 85).

The natural ecosystems tend to find the balance among all the levels by keeping a trade-off between preys and predators (18), a concept that has become the basis of biological pest control. Under such circumstances, the biological control of wood-boring pest species can be more efficient with the use of native enemies together with the current management practices. Ants are known as natural enemies of insect pests worldwide (15, 28, 48, 58, 73, 76, 86, 94). In European mixed forests, red wood ants shape the invertebrate communities through different interactions at multi-trophic levels (73, 86). Considering this concept, in our study, we investigated whether the presence of the red wood ant *Formica polyctena* contributes to the forest ecosystem balance by indirectly reducing the death of trees through decreasing the parasite infestation of trees. We hypothesized that due to its predatory activity, the presence of *F. polyctena* in forests will reduce the infestation of the trees by bark beetles and other wood-boring beetle species, but also the fungal infestation linked to these beetles. To test the role of this wood ant species as a biological control agent, we carried out a large-scale study in which we measured the size and number of *F. polyctena* nests, the infested trees and the cause of their infestation (type of wood-boring beetles or fungus), as well as the physical damages of the infested trees in 12 regions belonging to three European

countries (Hungary, Slovakia, Poland). Additionally, within this study, we made an attempt to reinforce the knowledge about the relevant ecological role of red wood ants in forest ecosystems and highlight the importance of the *Formica rufa* group in habitat conservation and forest pest management as a biological protective agent.

Materials And Methods

The sampling was performed during the summer months (June-July) of 2017 and 2019. The study was carried out in 31 forest patches from 12 regions located across a latitudinal gradient (46.215283°N – 54.069650°N) crossing three different Central-European countries (Hungary, Slovakia, Poland). The lowest latitude corresponded to Hungary, where two regions (Ásotthalom and Kiskunság) were sampled. At the middle latitude of our gradient, we sampled the Carpathians, with Mátra and Bükk Mountains in the Hungarian area, Fatra Mountains in the Slovakian area, and Tatra, Pieniny, and Gorce Mountains in the Polish area. The other sampled areas encompassed the middle of Poland to the Baltic Sea and corresponded to Świętokrzyska, Kampinos, Białowieża, and Koszalin at the highest latitude.

In each region, we selected mixed forests that are under forestry management. These study sites are composed of *Picea abies*, *Pinus sylvestris*, *P. nigra*, *Abies alba* and *Larix decidua* as the most common coniferous species, and *Betula pendula*, *Robinia pseudoacacia* and *Quercus* spp. as the most common non-coniferous ones (according to the local forestry information: NÉBIH, Mapový portal KIMS, Bank Danych o Lasach).

To carry out the sampling, in each study site we marked plots of 150 m × 150 m with the help of a GPS (GARMIN Oregon 700t). This plot size was determined to be a good representation of the territory of *F. polyctena* (86). In accordance with the presence of *F. polyctena* populations, in most regions (Ásotthalom, Kiskunság, Bükk, Fáttra, Pieniny, Świętokrzyska, Kampinos, Białowieża), we could sample three plots, while in Gorce, Tatra and Mátra Mountains we found only two populations, and in Koszalin only one population. Within the plots, we recorded the GPS location of each *F. polyctena* nest and measured their dimensions (two perpendicular diameters and the height). The above-ground nest volume (i.e., semi-ellipsoid) was determined using the following equation:

$$V = \frac{0.75 * \pi * r_1 * r_2 * h}{2}$$

where h is the height of the nest, and r1 and r2 are the two perpendicular nest radii. We used this equation because the above-ground nest volume is closely related to the red wood ant colony size (35, 36, 71).

To test the relationship between the presence of *F. polyctena* nests and the tree infestation, we recorded the number and GPS location of every infested tree within a plot and noted down the type of parasite infestation (bark beetle, longhorn beetle, jewel beetle, or fungus). For a more precise characterization of the health status of forests, we also recorded the status of the infested trees (Alive or Dead) and their position (Standing or Laying). Finally, we determined the latitude and altitude of the sampling sites with

the help of Google Earth (Google 2019) and established a “latitude value” as an increasing distance value starting from the southernmost study area (Ásotthalom: value 1) and added + 1 value with every 20 km (in beeline) passing to the north, finishing in Koszalin (North Poland, value 61; 35). In a previous study, we found a negative correlation between the latitude and the large scale environmental variables like irradiation and temperature (35). The average age of the forests was gathered from local forestry databases (NÉBIH, Mapový portal KIMS, Bank Danych o Lasach).

Statistical analysis

First, we were interested in whether the degree of the beetle infestation is correlated with the latitudinal and altitudinal gradient of the study sites and the forest age. To test this, we built separate GLM models (negative binomial error, maximum likelihood fit) for each parasite group with the proportion of trees infested by *Ips* spp., *Cerambycidae*, *Buprestidae*, and fungi as dependent variables, whereas the log + 1 transformed latitude value, altitude, and age of the forest as explanatory variables (N = 12). We used a Canonical Correspondence Analysis (CCA, N = 31) to test the association between the number of trees affected by both biotic and abiotic factors by using the function *cca*. In the model, a matrix built with the average frequency of the trees affected by each beetle and fungi species from each study plot within the study sites was used as a dependent variable. The matrix was built with log-transformed averages of the following explanatory variables: the log + 1 transformed number of nests (Nests number), nests size (Nest volumes), the perimeter of the tree trunks (Perimeter), the ratio of alive trees to the total number of affected trees (Alive), the ratio of the standing trees to the total number of affected trees (Stand), and the ratio of conifers to the total number of affected trees (Conifer). The significance tests for the general model, in order to calculate the effect of the explanatory variables on each of the dependent variables (number of *Ips*, *Buprestidae*, *Cerambycidae* and Fungal infested trees), were based on permutational ANOVA tests performed with *adonis2* function from the *vegan* package (61).

We also checked whether the infestation by bark beetles varies depending on the status and characteristics of the trees. In the GLM model (Poisson error, maximum likelihood, N = 31), the number of infested trees by *Ips* spp. was used as a dependent variable, whereas the log + 1 transformed number of alive trees and the perimeter of the trees as explanatory variables. The same approach was used to test the relationship between the *Cerambycidae*, *Buprestidae* and fungal infestation and the characteristics of the trees. In the models, the number of infested trees by *Cerambycidae*, by *Buprestidae* and by fungus were used as dependent variables.

A GLM model (Poisson error, maximum likelihood, N = 31) was built to check whether the beetle parasitism facilitates the fungal parasitism. In the model, the number of trees affected by fungi was used as dependent variable and the number of trees affected by beetles was used as explanatory variable.

We were interested in whether a larger number of *F. polychaeta* nests provides stronger pest control in the forests by a reduction of the number of infested trees. We used Generalized Linear Mixed Models (GLMMs; binomial error, maximum-likelihood fit, N = 31) to check whether the number of *F. polychaeta*

nests exert an effect on the number of trees parasitized by each beetle group or fungi. In the models, the ratio of parasitized trees with the *Ips* spp., *Cerambycidae* spp., *Bupresidae* spp. or fungi to the total number of affected trees were used as dependent variables, the number of *F. polyctena* nests as an explanatory variable and the identity of both the plot and the study area as nested random factors.

We were also interested in whether the number of *F. polyctena* nest decreases while increasing the dimensions of the nests present within the study plots, and whether larger *F. polyctena* nests reduce more effectively the infestation of the trees by either beetles or fungi. To test the effect of the nest size on the infestation of the trees with the *Ips* spp., *Cerambycidae* spp., *Bupresidae* spp., fungi or by all beetle groups in general, we carried out GLMMs (binomial error, maximum-likelihood fit, $N = 31$). In the models, the ratio of the parasitized trees (*Ips* spp., *Cerambycidae* spp., *Bupresidae* spp., fungi or by all beetle groups) to the total number of affected trees were used as dependent variables and the nest size (m^3) as the explanatory variable. Additionally, we checked whether the number of *F. polyctena* nests influence their size. To test it, we carried out a GLMM (Poisson error, maximum likelihood, $N = 31$) in which the size of the nests (measured in volume, m^3) was used as a dependent variable and the number of *F. polyctena* nests as an explanatory variable.

Finally, to test whether the number of the wood ant nests or size have an influence on the number of parasite groups, we used a GLMM (Poisson error, maximum likelihood, $N = 31$) with the number of parasite groups as a dependent variable and the number and size of the nests as explanatory variables.

The statistical analyses were carried out in the R Statistical Environment (68). The multivariate statistic (CCA) and the PERMANOVA were carried out by using the *vegan* package (61). Generalized Linear Mixed Models were built with the *glmer* function from *lme4* package (7). When the explanatory variables in a model had different characteristics, all explanatory variables were previously $\log + 1$ transformed to handle the bias in our results. In all the models we used the identity of the plots and the study area as nested random factors. All Poisson models were tested for model overdispersion. If model overdispersion occurred, negative binomial error distribution was used (43). In these latter cases, the models were built with the *glmer.nb* function from *MASS* package (93). The graphical representation of the results was performed by using the function *ggplot* in the R package *ggplot2* (96).

Results

Our study covered a total of 63 ha and was distributed in 12 regions located in a latitudinal gradient of 900 km in beeline crossing three countries. A total of 393 *F. polyctena* nests and 3639 trees were measured and searched for parasite infection. Considering all the affected trees, 74.9% were parasitized by beetle species. The most common pest species belonged to the bark beetle *Ips* spp., which parasitized 51.3% of the trees.

Our results show that the infestation by *Ips* spp. is not influenced by the increasing latitude, altitude, or the average age of the forests under study. The same was found for the infestation by the *Cerambycidae*,

Buprestidae and fungi species (Table 1).

Table 1
The effect of latitude, altitude and the average forest age on the number of trees infected by boring beetles (*Ips*, *Cerambycidae*, *Buprestidae*) and fungi. The results are based on the GLMM models.

Pest groups	Latitude		Altitude		Forest age	
	z	p	z	p	z	p
<i>Ips</i> spp.	-0.27	0.784	0.24	0.807	-0.30	0.765
<i>Cerambycidae</i> spp.	-0.15	0.884	-0.20	0.845	0.19	0.848
<i>Buprestidae</i> spp.	-0.12	0.904	-0.12	0.910	0.11	0.913
Fungi	-0.43	0.671	0.20	0.841	0.46	0.644

Overall the results of the Canonical Correspondence Analysis (CCA) showed that there is a significant relationship ($F = 2.29$, $p = 0.001$; Fig. 1) between the trees affected by the beetle groups and fungi and the explanatory variables (Nests Number, Nest Volume, Conifers, Alive, Stand, and Tree Perimeter). The first three CCA axis explained in total 82.56% of the variation of the number of trees affected: the first one explained 41.6%, the second 26.9%, and the third 14%. The Nest Number ($F = 4.12$, $p = 0.003$), the number of Alive trees ($F = 2.59$, $p = 0.040$), and the Perimeter of the trees ($F = 2.96$, $p = 0.022$) were significantly associated with the number of trees affected by beetles and fungi, whereas the frequency of Conifer trees, the Nests volume of *F. polyclena*, and the Standing infested trees had no significant effect in this respect (Table 2).

Table 2

The effect of red wood ant nest (nest frequency and size) and tree characteristics (proportion of conifers, alive trees, and standing trees but also tree perimeter) on the dissimilarities in the number of trees infected by beetle families and fungi. The results are based on the PERMutational ANOVA.

Characteristics	R^2	F	p
Nests frequency	0.07	3.11	0.007
Nests volume	0.03	1.16	0.339
Conifers	0.02	0.98	0.422
Alive trees	0.12	5.61	0.002
Standing trees	0.04	1.76	0.118
Tree perimeter	0.05	2.43	0.027
*Significant results are with bold font			

Moreover, the number of trees infested by *Ips* spp. showed to be positively related to the proportion of Alive trees and with the trunk Perimeter of the trees (Table 3). The same trend was found in the trees infested by the *Cerambycidae* and *Buprestidae* groups. However, no significant results were found in fungal infestations (Table 3). Notwithstanding, our results do not show any significant relationship between the beetle infestation and the fungal infestation in the studied areas ($z = 0.52$, $p = 0.610$).

Table 3

The effect of the tree characteristics (tree perimeter and proportion of alive trees) on the effect of the different pest groups (*Ips*, *Cerambycidae*, *Buprestidae*, and fungi). The results are based on the GLMM models.

Pest groups	Tree perimeter		Alive trees	
	z	p	z	p
<i>Ips</i> spp.	2.87	0.004	-4.98	> 0.001
<i>Cerambycidae</i> spp.	4.09	> 0.001	-2.16	0.031
<i>Buprestidae</i> spp.	6.65	> 0.001	-3.71	0.001
Fungi	-0.67	0.506	1.25	0.211
*Significant results are with bold font				

The increasing number of *F. polyctena* nests present in the study areas led to a significant reduction in the number of infested trees ($z = -3.83$, $p < 0.001$; Fig. 2a). Moreover, the number of infested trees by *Ips* spp. showed to be significantly reduced by the increasing number of *F. polyctena* nests ($z = -4.01$, $p < 0.001$, Fig. 2b). However, no significant negative effect of the number of *F. polyctena* nests was found on the *Cerambycidae* ($z = -1.140$, $p = 0.160$; Fig. 2c) or *Buprestidae* ($z = -0.135$, $p = 0.893$; Fig. 2d) infestations, nor the number of beetle groups infesting the trees was reduced ($z = -0.21$, $p = 0.838$). However, in fungal infestation, the results showed a marginally significant reduction caused by the increasing number of *F. polyctena* nests ($z = -1.91$, $p = 0.056$, Fig. 2e). Moreover, the increasing number of *F. polyctena* nests was correlated with a decrease of their size ($z = -2.41$, $p = 0.016$, Fig. 3)

The nests size did not have any significant effect on the number of trees affected by *Ips* spp. ($z = 0.63$, $p = 0.527$), *Cerambycidae* ($z = -1.20$, $p = 0.235$) and *Buprestidae* ($z = -1.40$, $p = 0.160$) groups separately, nor on the number of infested trees ($z = -1.84$, $p = 0.065$). Similarly, the increase in the nest size did not affect the number of trees infested by fungi ($z = 0.82$, $p = 0.412$). Finally, the number of parasite groups infesting the trees was not affected by the number ($z = 0.39$, $p = 0.69$) or size ($z = 0.29$, $p = 0.767$) of the *F. polyctena* nests.

Discussion

In our study, we tested the role of *F. polyctena* as pest control for bark beetles in 12 regions located along a latitudinal and altitudinal gradient from South-Hungary to North-Poland. Our results show that the beetle community was mainly shaped by the number of *F. polyctena* nests, the percentage of alive affected trees and the perimeter of the affected tree trunks present within the study areas. The increasing number of *F. polyctena* nests led to a reduction in the number of trees infected by bark beetles and, despite the fungal infestation is not significantly reduced, it also seems to be affected. However, the number of wood ant nests did not affect the number of trees infected by other beetle species. Moreover, neither the nest size, age of the forests, the altitude or the latitudinal location of the study sites showed to be related to the degree of beetle or fungal infestation.

Wood-boring beetles, especially the bark beetles of the *Ips* genera can show an exponential population growth that leads to massive loss of trees in the forests they inhabit (11, 16, 46, 50). Moreover, the infestation by bark beetles is often associated with assemblages of fungi, bacteria, and mites which determine their successful tree colonization and reproduction (78, 79). The death of trees is the result of a double effect: a direct one by the bark beetle boring action and an indirect one by the inoculation with phytopathogenic fungi used to feed their broods (26). Notwithstanding, the degree of the infestation by these wood-boring beetles can be determined by their local community structure and composition, as found also in other arthropod groups (12, 29, 82, 97). Moreover, the wood-boring beetles can be regulated also by different habitat characteristics like the health status of the trees, the abundance of host plant species, natural predators or even interspecific competition (20, 77). From these possible effects, our results indicate that the infestation by the wood-boring species parasitizing the studied forests was

shaped in a different extent by the number of red wood ant nests, percentage of alive infested trees and the perimeter of the affected trees.

In our study, though the highest percentage of infestation was carried out by the bark beetles (*Ips* species), other wood-boring species belonging to the families *Cerambycidae* (Latreille, 1802) and *Buprestidae* (Leach, 1815) were also present. Due to the higher abundance of *Ips* species, the other wood-boring species would be more successful by avoiding nesting close to the bark beetles to reduce the larval competition for resources (77), which might result in niche partitioning by the species in their search for an optimal reproduction rate. If we take into account that conifers are the main nesting target for bark beetles (60, 65) and the most abundant trees in our studied forests, this partitioning can be even more accentuated. Furthermore, as it was formerly mentioned, wood-boring beetles mainly attack dead and weakened trees. Notwithstanding, healthy alive trees and shrubs can be also attacked when the beetle population reaches a high abundance receiving the nomination of “primary invaders” (21, 26, 67). For example, *Dendroctonus frontalis*, a *Curculionidae* that produces galleries with an “S” pattern, quickly disrupts the cambium (21). Moreover, our results show that boring beetles are benefited by trees with a larger perimeter. Larger trees can offer a more suitable nesting place (higher amount of older tissues) for the boring beetle larvae and adults are more attracted to carry out their oviposition in them. For example, the species of the genera *Agrilus* tend to lay their eggs on the south side of large living-trees with thick bark (22).

Ants are known as natural enemies of insect pests worldwide (15, 28, 48, 58, 73, 76, 94) mainly because they disturb pests during their oviposition and feeding (15). Ants possess a series of characteristics that make them very efficient in this matter, such as their vast abundance in many ecosystems, a quick reaction to the increasing prey abundance by using chemical communication, the effective retrieval of prey individuals even when these are present in low numbers, their capability of switching preys when the source is depleted and modifying their foraging behaviour to increase the contact with prey species (70, 94). These valuable properties made them largely used in agriculture pest (species that are usually present in high abundance) control (29). For example, some species have been incorporated into integrated pest management programs to control sweet potato and banana weevils in Cuba or apple plantations in Denmark (15, 57, 58). In forests, red wood ants can shape the invertebrate community of trees by reducing their species richness through different interactions at multi-trophic levels that also includes the predation on forest pests (2, 25, 94, 89). Additionally, the supercolonies of the red wood ants show characteristics (such as large biomass of colonies, long-term stability and high predation on herbivores) that make these species even more suitable as biocontrol agents (73). For example, *Formica yessensis* has been described to reduce the species number and abundance of weevils (34), and ant-predation on herbivores improved the growth and performance of trees (53). Similarly, our results show that the presence of *F. polyctena* nests reduced the number of infected trees by bark beetles. However, in our scenario, the reduction of this other arthropod groups is the result of an indirect effect of the monopolization of resources and dominance of the red wood ants (47). The complex polydomous system of *F. polyctena* requires a large amount of food that is provided by foraging in mass (19, 72), covering an extensive area of the forest. The vast number of workers moving to the tree canopy to collect

the honeydew from the aphids covers almost the totality of the trunk (19, authors pers. observ.), making extremely difficult for other arthropods to perch. Moreover, the *F. polyctena* workers tend also to attack insects when they perceive their movement (4). As a result, the number of available trees for the oviposition of the bark beetle is strongly reduced, so their abundance is as well negatively affected. This situation can lead to an increase in tree survival and forest health. This indirect protection from pests has been already used in agricultural practices, e.g. *F. polyctena* has been used for pest control in apple plantations in Denmark, where its presence led to greater production in the first year (58).

Notwithstanding, the number of trees affected by longhorn and jewel beetle populations were not affected by *F. polyctena*, though the relationship between the trees affected by jewel beetles and the ants showed a negative trend. The reduced presence of this group, compared to the bark beetles, could be linked to this soft reduction of their populations. Additionally, the chemical defences against predators secreted by the species of the superfamily *Chrysomeloidea* (here belong the *Cerambycidae*), might also be involved in the reduction of the effect of red wood ants on their populations (64). On the other hand, another underlying mechanism might be related to the protection of the wood ants' food sources, mainly aphids of conifers; an activity that can lead to a reduction in the bark beetle abundance (48) but this can be also responsible for regulating the other two wood-boring beetle families. Additionally, the capacity of red wood ants to focus their foraging activity and predation on the location of the most abundant food sources can be also involved (15), which in our case corresponds with the presence of aphids in the conifers canopy. This might be the main reason behind the intensive foraging to the canopy and its negative effect found on the *Ips* spp., the most abundant beetle infesting our study forests.

The presence of red wood ants is strongly linked to habitat features which is the main reason why the changes in their habitat had strongly affected their populations, resulting in their current threatened status (33). Besides factors like the availability of proper food sources, nesting places, and the material for the construction of their mounds (85), also the temperature and isolation are important determinants of the presence of the red wood ant nests both at local and at larger scales (35, 36, 71). Moreover, the combination of the large and small scale factors, like the reduction of the insolation on a local scale due to the shading by the tree canopy has been demonstrated to exert an important effect on the *F. polyctena* nests size and distribution (35). However, the latitudinal and altitudinal location as well as the average age of the forests were not related to the infestation of trees by beetles or fungi. This could be due to anthropogenic climate change which promotes higher generation rates in bark beetle populations (three generations instead of two in lower latitudes and two instead of one in higher latitudes, 63), and make possible to these species to become abundant in a wide range of habitats.

In conclusion, our study demonstrates for the first time the high effectiveness of red wood ants as pest control agents in mixed coniferous forests. The increasing number of *F. polyctena* nests, regardless of their size, leads to a severe reduction of the number of infested trees, demonstrating the protective role of *F. polyctena* nests mostly against bark beetles. Moreover, it seems that this effect is species-specific and is also influenced by other habitat characteristics. Based on these results we can tell that red wood ants can be valuable tools in the development of forest management plans for the control of pest species,

such as *Ips* spp. that are globally a major cause of tree mortality (3, 50, 51, 60, 90). Moreover, our study also highlights the importance of the conservation plans for red wood ant species due to their important role in preserving forests health, essential for the forests communities in the light of the threat of global climate change.

Declarations

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Authors' contributions:

IM and OJ designed the experiments; GTP, OJ, PJK, GM, AT, and IM carried out the field experiments and the data collection; GTP and IM carried out the data analysis; GTP prepared figures and tables; GTP, OJ and IM wrote the manuscript. All authors participated in the revision of the final version and approved the final manuscript.

Competing interests:

The authors declare that there are no conflicts of interest.

Availability of data and material:

Raw data were generated at Department of Social and Myrmecophilous Insects, at the Museum and Institute of Zoology (PAS). Derived data supporting the findings of this study are available from the corresponding author [GTP] or the senior author [IM] on request.

References

1. Abdullah, H., Darvishzadeh, R., Skidmore, A. K., Groen, T. A. & Heurich, M. European spruce bark beetle (*Ips typographus*, L.) green attack affects foliar reflectance and biochemical properties. *Int. J. Appl Earth Obs.* 64, 199–209 (2018).
2. Adlung, K. G. A critical evaluation of the European research on use of red wood ants (*Formica rufa* group) for the protection of forests against harmful insects. *Z. Angew Entomol.* 57, 167–189 (1966).

3. Anderegg, W. R. L., Hicke, J. A., Fisher SA et al. Tree mortality from drought, insects, and their interactions in a changing climate. *New Phytol.* 208, 674–683 (2015).
4. Ayre, G. Response to Movement by *Formica polycтена* Forst.. *Nature* 199, 405–406 (1963)
5. Bale, J. S., Masters, G. J., Hodkinson, I. D., Awmack, C. et al. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Glob. Chang. Biol.* 8, 1–16 (2002).
6. Balletto, E., Barbero, F., Casacci, L. P., Cerrato, C., Patricelli, D. & Bonelli, S. L'impatto dei cambiamenti climatici sulle farfalle italiane. *Studi Trent Sci Nat.* 86, 2–6 (2009).
7. Bates, D., Maechler, M., Bolker, B. & Walke, S. Fitting Linear Mixed-Effects Models Using lme4. *J. Stat. Softw.* 67(1), 1–48 (2015).
8. Becker, G. Untersuchungen über die Ernährungsphysiologie der Hausbockkäferlarven. *Z. Vgl. Physiol.* 29, 315–388 (1942).
9. Bellamy, C. L. & Nelson, G. H. Buprestidae Leach 1815 in American Beetles, Volume 2, Polyphaga: Scarabaeoidea through Curculionoidea. (ed. Ross, H., Arnett, J. R., Michael, C., Thomas, P. E., Skelley, J. & Howard, F.) 98–112 (CRC Press, 2002).
10. Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp. F. Impacts of climate change on the future of biodiversity. *Ecol. Lett.* 15, 365–377 (2012).
11. Bentz, B. J. & Jönsson, A. M. Modeling bark beetle responses to climate change. In: *Bark beetles: biology and ecology of native and invasive species* (ed. Vega, F. & Hofstetter, R.) 533–553 (Elsevier Academic Press, 2015).
12. Casacci, L. P., Witek, M., Barbero, F., Patricelli, D., Solazzo, G., Balletto, E. & Bonelli. S. Habitat preferences of *Maculinea arion* and its *Myrmica* host ants: implications for habitat management in Italian Alps. *J. Insect Conserv.* 15, 103–110 (2011).
13. Cline, A., Ivie, M. A., Bellamy, C. L. & Scher, J. A Resource for Wood Boring Beetles of the World: Wood Boring Beetle Families, Lucid v. 3.4. USDA/APHIS/PPQ Center for Plant Health Science and Technology, Montana State University, and California Department of Food and Agriculture. <http://www.lucidcentral.org/keys/v3/WBB> (2009).
14. Cebeci, H. H., Ayberk, H., Rapuzzi, P., Baiocchi, D., Magnani, G. & Göltas, M. The wood boring insects (Coleoptera: Cerambycidae and Buprestidae) recorded as the new pests for acer *Undulatum* Pojark from the Babadag mountain (SW Turkey). *Fresenius Environ. Bull.* 27, 9325–9328 (2018).
15. Choate, B. & Drummond, F. A. Ants as biological control agents in agricultural cropping systems. *Terrestrial Arthropod Rev.* 4, 157–180 (2011).
16. Christiansen, E. & Bakke, A. The spruce bark beetle of Eurasia. In: *Dynamics of Forest Insect Populations* (ed. Berryman, A. A.) 479–503 (Plenum Publishing, 1988).
17. Cilbircioglu, C. & Ünal, S. Bark beetles and their natural enemies on oriental spruce from the Black Sea region of Turkey. *J. Agric. Urban Entomol.* 28, 42–56 (2012).
18. Curtsdotter, A., Banks, H. T., Banks, J. E., Jonsson, M., Jonsson, T., Laubmeier, A. N., Traugott, M. & Bommarco, R. Ecosystem function in predator–prey food webs confronting dynamic models with

- empirical data. *J. Anim. Ecol.* 88, 196–210 (2018).
19. Czechowski, W., Radchenko, A., Czechowska, W. & Vepsäläinen, K. The ants of Poland with reference to the myrmecofauna of Europe. *Fauna Poloniae* 4 (Natura optima dux Foundation, 2012).
 20. Denno, R. F., McClure, M. S. & Ott, J. R. Interspecific interactions in phytophagous insects: Competition Reexamined and Resurrected. *Annu. Rev. Entomol.* 40, 297–331(1995).
 21. Drees, B. M., Jackman, J. A. & Merchant, M. E. Wood-Boring Insects of Trees and Shrub. Texas Agricultural Extension Service. <http://hdl.handle.net/1969.1/160397> (1994).
 22. Evans, H. F., Moraal, L. G. & Pajares, J. A. Biology, ecology and economic importance of Buprestidae and Cerambycidae. In: *Bark and Wood Boring Insects in Living Trees in Europe, a Synthesis* (ed. Lieutier, F., Day, K. R., Battisti, A., Grégoire, J. C. & Evans, H. F.) 447–474 (Springer PO Box 17, 2004).
 23. FAO (Food and Agriculture Organization of the United Nations) Global review of forest pests and diseases. *FAO Forestry Paper* 156 (2009).
 24. Fayt, P., Machmer, M. M. & Steeger, C. Regulation of spruce bark beetles by woodpeckers - a literature review. *For Ecol. Manag.* 206, 1–14 (2005).
 25. Frizzi, F., Masoni, A., Quilghini, G., Ciampelli, P. & Santini, G. Chronicle of an impact foretold: the fate and effect of the introduced *Formica paralugubris* ant. *Biol. Invasions* 20, 3575–3589 (2018).
 26. Goldazarena, A., Romón, P. & López, S. Bark beetles control in forests of Northern Spain. *Integrated Pest Management and Pest Control - Current and Future Tactics*, Dr. Sonia Soloneski (Ed), ISBN: 978-953-51-0050-8, In Tech. <http://www.intechopen.com/books/integrated-pest-management-and-pest-control-current-and-future-tactics/bark-beetles-control-in-forests-of-northern-spain> (2012).
 27. Grégoire, J. C. & Evans, H.F. Damage and control of bark bilt organisms an overview. In: *Bark and Wood Boring Insects in Living Trees in Europe, a Synthesis* (ed. Lieutier, F., Day, K. R., Battisti, A., Grégoire, J. C. & Evans, H.F.) 19–38 (Springer PO Box 17, 2004).
 28. Haddan, M., Fraval, A. & Thevenot, M. Ennemis naturels de *Phoracantha semipunctata* (F.) (Col., Cerambycidae), ravageur xylophage des eucalyptus au Maroc. *Bull. Inst Sci.* 12, 167–70 (1988).
 29. Hölldobler, B. & Wilson, E. O. *The Ants*. (Harvard University Press, 1990)
 30. Holmes, T. & Koch, F. Bark Beetle Epidemics, Life Satisfaction, and Economic Well-Being. *Forests* 10, 696 (2019).
 31. Hougardy, E. & Grégoire, J. C. Biological differences reflect host preference in two parasitoids attacking the bark beetle *Ips typographus* (Coleoptera: Scolytidae) in Belgium. *Bull. Entomol Res.* 94, 341–347 (2004).
 32. Huber, D. P. W., Aukema, B. H., Hodgkinson, R. S. & Lindgren, B. S. Successful colonization, reproduction, and new generation emergence in live interior hybrid spruce, *Picea engelmannii* x *glauca*, by mountain pine beetle, *Dendroctonus ponderosae*. *Agric. For Entomol.* 11, 83–89 (2009).
 33. IUCN 2020. The IUCN Red List of Threatened Species. Version 2020-1. <https://www.iucnredlist.org> (2020).

34. Ito, E. & Higashi, S. Effects of red wood ants on weevil community inhabiting oak trees. *Zeitschrift für Angew.* 110, 483–488 (1990).
35. Juhász, O., Bátori, Z., Trigos-Peral, G., Lőrinczi, G., Módra, G., Bóni, I., Kiss, P. J., Aguilon, D. J., Tenyér, A. & Maák, I. Large- and small-scale environmental factors drive distributions of ant mound size across a latitudinal gradient. *Insects* 11, 350 (2020a).
36. Juhász, O., Fürjes-Mikó, A., Tenyér, A., Somogyi, A. Á., Aguilon, D. J., Kiss, P. J., Bátori, Z. & Maák, I. Consequences of climate change-induced habitat conversions on red wood ants in a Central European mountain: a case study. *Animals* 10, 1677 (2020b).
37. Kahuthia-Gathu, R., Kirubi, D. T. & Gitonga, D. Composition and abundance of wood-boring beetles of *Acacia xanthophloea* and their associated natural enemies in Thika, Kenya. *J. Asia Pac Biodivers.* 11, 248e254 (2018).
38. Khanday, A. L., Sureshan, P. M., Buhroo, A. A., Ranjith, A. P. & Tselikh, E. Pteromalid wasps (Hymenoptera: Chalcidoidea) associated with bark beetles, with the description of a new species from Kashmir, India. *J. Asia Pac Biodivers.* 12, 262–272 (2019).
39. Kroll, J. C. & Fleet, R. R. Impact of woodpecker predation on over-wintering within-tree populations of the southern pine beetle (*Dendroctonus frontalis*) (ed. Dickson, J. G., Connor, R. N., Fleet, R. R., Jackson, J. A. & Kroll, J. C.) *The role of insectivorous birds in forest ecosystems*, 269–281 (Academic Press, 1979).
40. Kroll, J., Conner, R. N. & Fleet, R. R. Woodpeckers and the southern pine beetle (*Agric Handb* 564 (1980).
41. Leather, S. R., Day, K. R. & Salisbury, A. N. The biology and ecology of the large pine weevil, *Hylobius abietis* (Coleoptera: Curculionidae): a problem of dispersal? *Bull. Entomol Res.* 89, 3–16 (1999).
42. Leong, M., Bertone, M. A., Savage, A. M., Bayless, K. M., Dunn, R. R. & Trautwein, M. D. The Habitats Humans Provide: Factors affecting the diversity and composition of arthropods in houses. *Sci Rep* 7, 15347 (2017).
43. Lindén, A. & Mäntyniemi, S. Using the negative binomial distribution to model overdispersion in ecological count data. *Ecology* 97, 1414–1421 (2011).
44. Linder, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Garcia-Gonzalo, J., Seidl, R., Delzon, S., Corona, P., Kolström, M. et al. Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. *For Ecol. Manag.* 259, 698–709 (2010).
45. Lindgren, B. & Raffa, K. Evolution of tree killing in bark beetles (Coleoptera: Curculionidae): Trade-offs between the maddening crowds and a sticky situation. *Can. Entomol.* 145, 471–495 (2013).
46. Logan, J. A. & Bentz, B. J. Model analysis of mountain pine beetle (Coleoptera: Scolytidae) seasonality. *Environ. Entomol.* 28, 924–934 (1999).
47. Maák, I., Tóth, E., Lenda, M., Lőrinczi, G., Kiss, A., Juhász, O., Czechowski, W. & Torma, A. Behaviours indicating cannibalistic necrophagy in ants are modulated by the perception of pathogen infection level. *Scientific Reports* 10, 17906 (2020).

48. Maňák, V., Björklund, N., Lenoir, L. & Nordlander, G. The effect of red wood ant abundance on feeding damage by the pine weevil *Hylobius abietis*. *Agric. For Entomol.* 17, 57–63 (2015).
49. Marini, L., Lindelöw, A., Jönsson, A. M., Wulff, S. & Schroeder, L. M. Population dynamics of the spruce bark beetle: a long-term study. *Oikos* 122, 1768–1776 (2013).
50. Marini, L., Økland, B., Jönsson, A. M., Bentz, B., Carroll, A., Forster, B., Grégoire, J. C., Hurling, R., Nageleisen, L. M., Netherer, S. et al. Climate drivers of bark beetle outbreak dynamics in Norway spruce forests. *Ecography* 40, 1426–1435(2017).
51. Meddens, A. J., Hicke, J. A. & Ferguson, C. A. Spatiotemporal patterns of observed bark beetle-caused tree mortality in British Columbia and the western United States. *Ecol. Appl.* 22, 1876–1891(2012).
52. Mikkelsen, K. M., Bearup, L. A., Maxwell, R. M., Stednick, J. D., McCray, J. E. & Sharp, J. O. Bark beetle infestation impacts on nutrient cycling, water quality and interdependent hydrological effects. *Biogeochemistry* 115, 1–21(2013).
53. Moreira, X., Alfaro, R. I. & King, J. N. Constitutive defenses and damage in Sitka spruce progeny obtained from crosses between white pine weevil resistant and susceptible parents. *Forestry* 85, 87–97 (2012).
54. Nardi, J. B., Mackie, R. I. & Dawson, J. O. Could microbial symbionts of arthropod guts contribute significantly to nitrogen fixation in terrestrial ecosystems? *J. Insect Physiol.* 48, 751–763 (2002).
55. Nordlander, G., Bylund, H., Örlander, G. & Wallertz, K. Pine weevil population density and damage to coniferous seedlings in a regeneration area with and without shelterwood. *Scand. J. For. Res.* 18, 438–448 (2003).
56. Nordlander, G., Hellqvist, C., Johansson, K. & Nordenhem, H. Regeneration of European boreal forests: effectiveness of measures against seedling mortality caused by the pine weevil *Hylobius abietis*. *For. Ecol. Manag.* 262(12), 2354–2363 (2011).
57. Offenberg, J. Ants as tools in sustainable agriculture. *J. Appl Ecol.* 52, 1197–1205 (2015).
58. Offenberg, J., Nielsen, J. S. & Damgaard, V. Wood Ant (*Formica polyctena*) services and disservices in a danish apple plantation. *Sociobiology* 66, 247–256 (2019).
59. Økland, B. & Berryman, A. Resource dynamics plays a key role in regional fluctuations of the spruce bark beetle *Ips typographus*. *Agric. For Entomol.* 6, 141–146 (2004).
60. Økland, B., Erbilgin, N., Skarpaas, O., Christiansen, E. & Langstrom, B. Inter-species interactions and ecosystem effects on non-indigenous invasive and native tree-killing bark beetles. *Biol. invasions* 13, 1151–1164 (2011).
61. Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., Wagner, H. *Vegan: Community Ecology Package* (2019).
62. O'Neill, K. M., Fultz, J. E. & Ivie, M. A. Distribution of adult *Cerambycidae* and *Buprestidae* (Coleoptera) in a subalpine forest under shelterwood management. *Coleopt. Bull.* 62(1), 27–36 (2008).

63. Overbeck, M. & Schmidt, M. Modelling infestation risk of Norway spruce by *Ips typographus* (L.) in the Lower Saxon Harz Mountains (Germany). *For. Ecol. Manag.* 266, 115–125 (2012).
64. Pasteels, J. M., Braekman, J. C. & Daloze, D. Chemical defense in the *Chrysomelidae* (ed. Jolivet P., Petitpierre, E. & Hsiao, T. H.) *Biology of Chrysomelidae*, 233-252 (Kluwer Academic, 1988).
65. Raffa, K. F., Aukema, B. H., Bentz, B. J., Carroll, A. L., Hicke, J. A., Turner, M. G. & Romme, W. H. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *BioSci* 58, 501–517(2008).
66. Raffa, K. F., Grégoire, J. C. & Lindgren, B. S. Natural history and ecology of bark beetles (ed. Vega, F. E. & Hofstetter, R. W.) *Biology and ecology of native and invasive species*, 1–40 (Elsevier, 2015).
67. Ray, C., Cluck, D. R., Wilkerson, R. L., Siegel, R. B., White, A. M., Tarbill, G. L., Sawyer, S. C. & Howell, C. A. Patterns of woodboring beetle activity following fires and bark beetle outbreaks in montane forests of California, USA. *Fire Ecol.* 15, 21 (2019).
68. R Core Team. R: A Language and Environment for Statistical Computing. <https://www.R-project.org/> (2020)
69. Reeve, J. D. Predation and Bark Beetle Dynamics. *Oecologia* 112, 48–54 (1997).
70. Risch, S. J., Carroll, C. R. The ecological role of ants in two Mexican agroecosystems. *Oecologia* 55, 114–19 (1982).
71. Risch, A., Ellis, S. & Wiswell, H. Where and why? Wood ant population ecology. In: *Wood Ant Ecology and Conservation* (ed. Stockan, A. & Robinson, E. J. H.) 81-105 (Cambridge University Press, 2016).
72. Robinson, E. J. H. & Stockan, J. A. Future directions for wood ant ecology and conservation In: *Wood Ant Ecology and Conservation* (ed. Stockan, A. & Robinson, E. J. H.) 287–299 (Cambridge University Press, 2016).
73. Robinson, E. J. H., Stockan, J. A. & Glenn, R. I. (2016) Wood ants and their interaction with other organisms. In: *Wood Ant Ecology and Conservation* (ed. Stockan, A. & Robinson, E. J. H.) 177-206 (Cambridge University Press, 2016).
74. Roura-Pascual, N., Suarez, A. V., Gómez, C., Pons, P., Touyama, Y., Wild, A. L. & Townsend, P. A. Geographic potential of Argentine ants (*Linepithema humile* Mayr) in the face of global climate change. *Proc. R. Soc. Lond. B.* 271(1557), 2527–2535 (2004).
75. Rudinski, J. A. Ecology of *Scolytidae*. *Annu. Rev. Entomol.* 7, 327–348 (1962).
76. Schifani, E. Exotic ants (Hymenoptera, Formicidae) invading Mediterranean Europe: A brief summary over about 200 years of documented introductions. *Sociobiology* 66, 198–208 (2019).
77. Schlyte, F., Anderbrandt, O. Competition and niche separation between two bark beetles: Existence and mechanisms. *Oikos* 68, 437–447 (1993).
78. Schowalter, T. D. *Insect ecology: an ecosystem approach*, 3rd ed. (ed. Schowalter, T. D.) (Academic press, 2011).
79. Schowalter, T. D. Ecology and Management of Bark Beetles (Coleoptera: Curculionidae: Scolytinae) in Southern Pine Forests. *J. Integ. Pest Mngmt.* 3, 1–7 (2012).

80. Schweiger, O., Maelfait, J. P., van Wingerden, W., Hendrickx, F., Billeter, R., Speelmans, M., Augenstein, I., Aukema, B., Aviron, S., Bailey, D., Bukacek, R., Burel, F., Diekötter, T., Dirksen, J., Frenzel, M., Herzog, F., Liira, J., Roubalova, M. & Bugter, R. Quantifying the impact of environmental factors on arthropod communities in agricultural landscapes across organisational levels and spatial scales. *J. Appl. Ecol.* 42, 1129–1139 (2005).
81. Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., Lexer, M. J., Trotsiuk, V., Mairota, P., Svoboda, M., Fabrika, M., Nagel, T. A. & Reyer, C. P. O. Forest disturbances under climate change. *Nat. Clim. Chang.* 7, 395–402 (2017).
82. Siemann, E., Haarstad, J. & Tilman, D. Dynamics of Plant and Arthropod Diversity during Old Field Succession. *Ecography* 22, 406–414 (1999).
83. Sommerfeld, A., Senf, C., Buma, B. et al. Patterns and drivers of recent disturbances across the temperate forest biome. *Nat. Commun.* 9, 4355 (2018).
84. Sømme, L. & Block, W. Adaptations to Alpine and Polar Environments in Insects and Other Terrestrial Arthropods. In: *Insects at Low Temperature* (ed. Lee, R. E. & Denlinger, D. L.) (Springer, 1991).
85. Sorvari, J. & Hakkarainen, H. Wood ants are wood ants: deforestation causes population declines in the polydomous wood ant *Formica aquilonia*. *Ecol. Entomol.* 32, 707–711 (2007).
86. Sorvari, J. Foraging distances and potentiality in forest pest insect control: an example with two candidate ants (Hymenoptera: Formicidae). *Myrmecol. News* 12, 211–215 (2009).
87. Springer, M. Marine Insects. In: *Marine Biodiversity of Costa Rica, Central America*. (Wehrtmann, I. S. & Cortés, J.) *Monographiae Biologicae*, vol 86. (Springer, 2009).
88. Stork, N. E., McBroom, J., Gely, C. & Hamilton, A. J. New approaches narrow global species estimates for beetles, insects, and terrestrial arthropods. *PNAS* 112, 7519–752 (2015).
89. Styrsky, J. D. & Eubanks, M. D. Ecological consequences of interactions between ants and honeydew-producing insect. *Proc. Royal Soc. B: Biological sciences* 274, 151–164 (2007).
90. Thom, D., Seidl, R., Steyrer, G., Krehan, H. & Formayer, H. Slow and fast drivers of the natural disturbance regime in Central European forest ecosystems. *For. Ecol. Manage.* 307, 293–302 (2013).
91. Toth, D., Maitah, M., Maitah, K. & Jarolínová, V. The impacts of calamity logging on the development of spruce wood prices in czech forestry. *Forests* 11, 283 (2020).
92. Trigos-Peral, G., Rutkowski, T., Witek, M., Ślipiński, P., Babik, H., Czechowski, W. Three categories of urban green areas and the effect of their different management on the communities of ants, spiders and harvestmen. *Urban Ecosyst* 23, 803–818 (2020).
93. Venables, W. N. & Ripley, B. D. *Modern Applied Statistics with S-plus*, Fourth Edition ed. Venables, W. N.) (Springer, 2002).
94. Way, M. J. & Khoo, K. C. Role of ants in pest management. *Annual Rev. Entomol.* 37, 479–503 (1992).
95. Wermelinger, B., Duelli, P. & Obrist, M. K. Dynamics of saproxylic beetles (Coleoptera) in windthrow areas in alpine spruce forests. *For. Snow Landsc.* 77, 133–148 (2002).

96. Wickham, H. ggplot2: Elegant Graphics for Data Analysis (Springer-Verlag, 2016).

97. Zurbrügg, C. & Frank, T. Factors influencing bug diversity (Insecta: Heteroptera) in semi-natural habitats. Biodivers. Conserv. 15, 261–280 (2006).

Figures

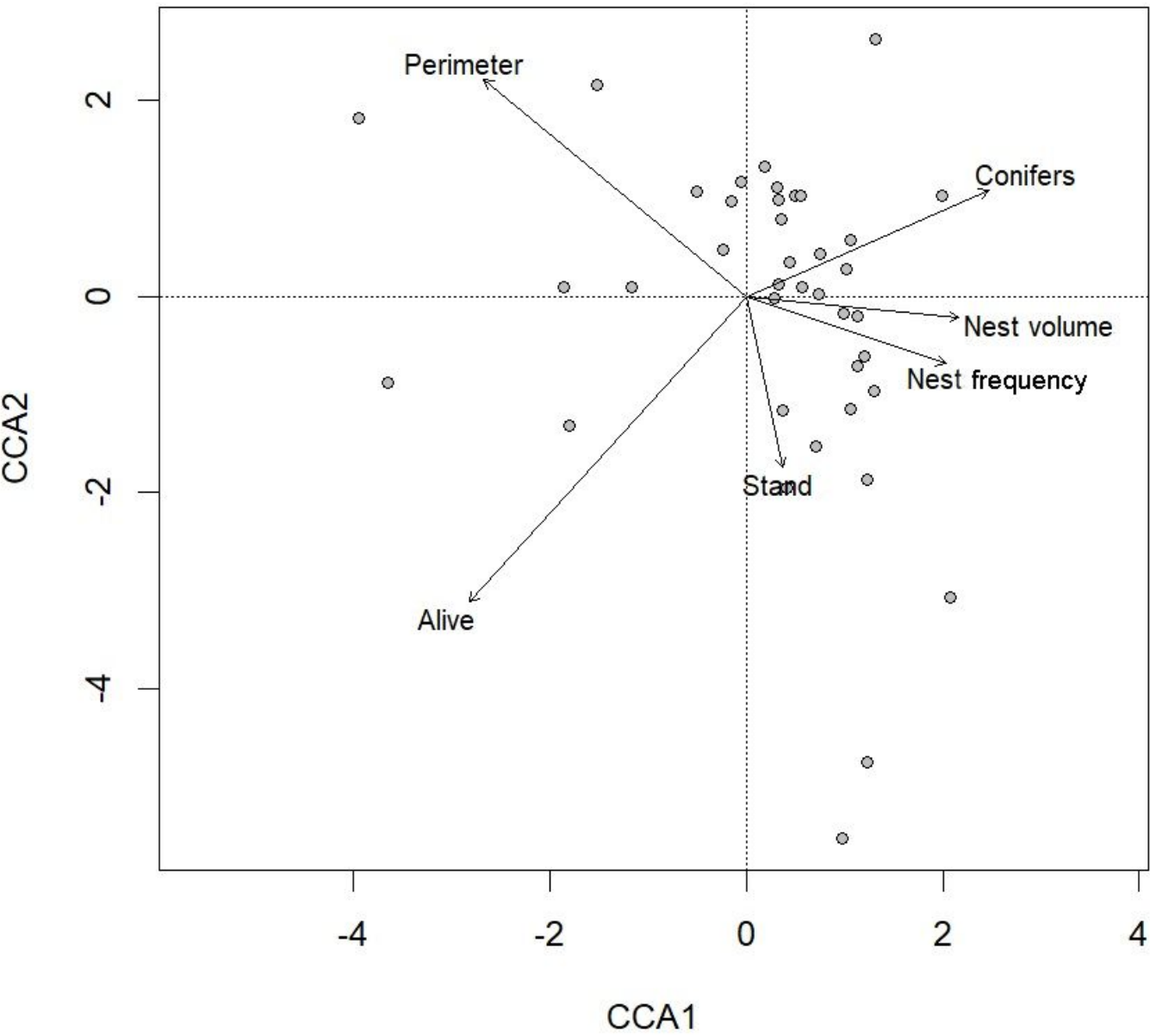


Figure 1

Graphical representation of the Canonical Correspondence Analyses on the biotic and abiotic variables.

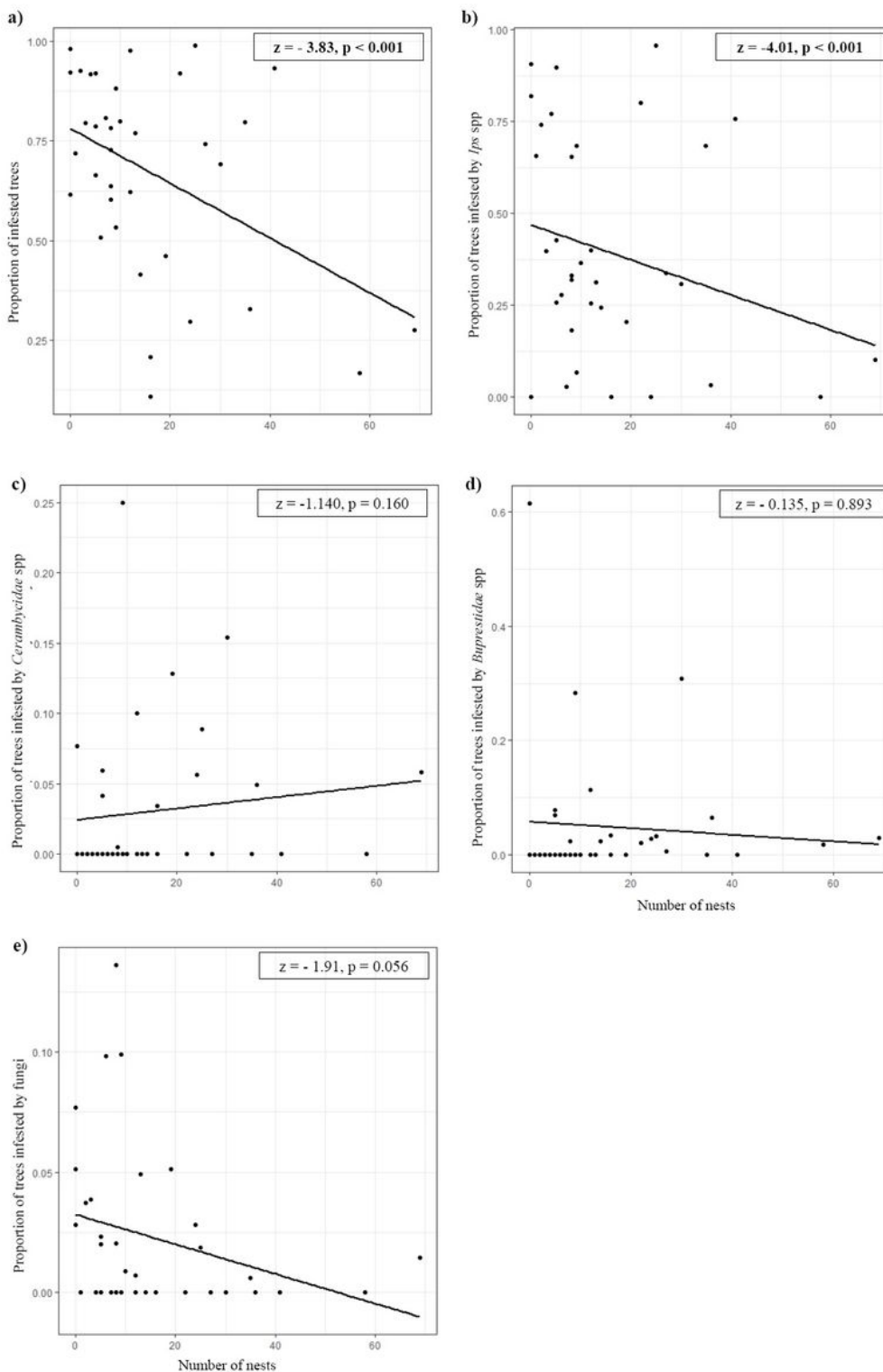


Figure 2

Scatterplot with fitted regression line illustrating the relationship between the number of *F. polycetna* nests and the proportion of infested trees by a) some of the studied pest groups, b) bark beetle (*Ips* spp), c) boring beetles of the *Cerambycidae* group, d) boring beetles of the *Buprestidae* group, e) fungi.

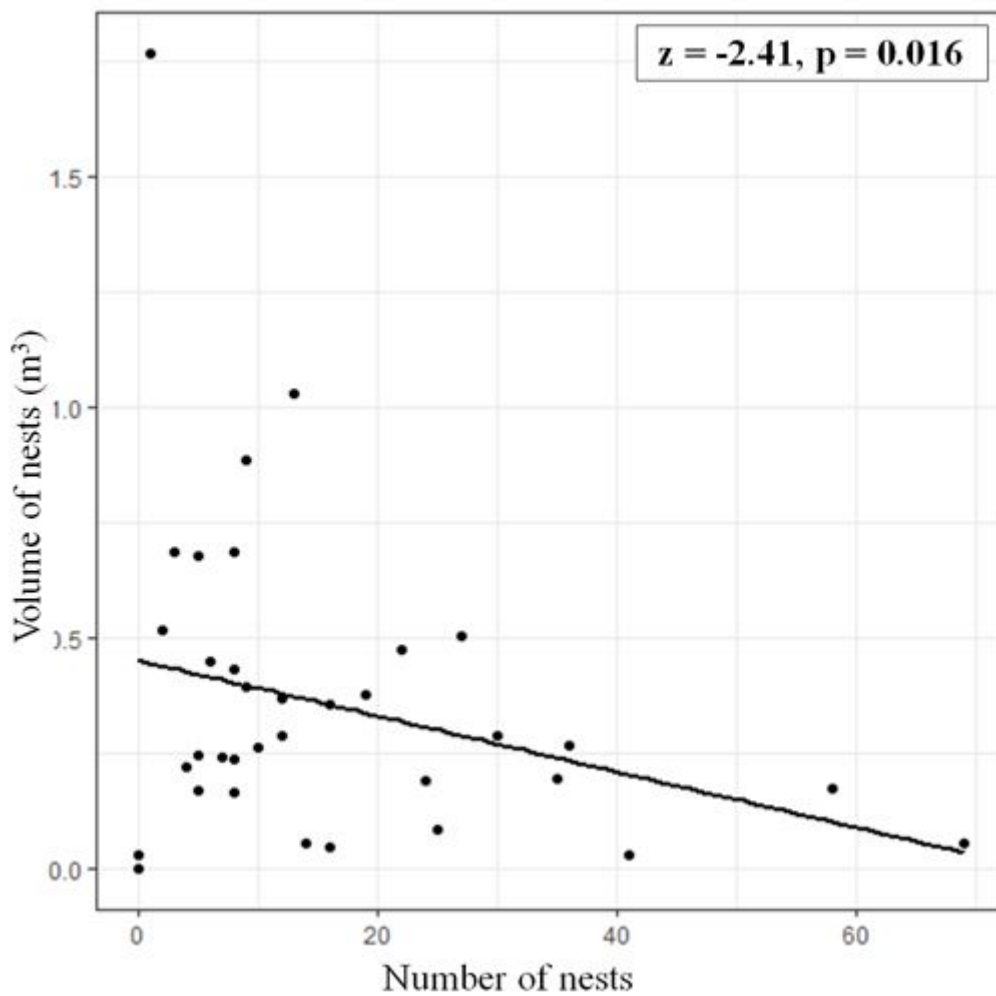


Figure 3

Scatterplot with fitted regression line illustrating the relationship between the number of *F. polycytena* nests and their size.