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## Invasive Northern Red Oaks benefit *Temnothorax crassispinus* (Hymenoptera: Formicidae) ant colonies

Lukasz MYCZKO, Lukasz DYLEWSKI, Sławomir MITRUS & Tim H. SPARKS



### Abstract

Non-native plant species can modify their environment, and their influence on food chains is well recognized. However, the phenomenon of non-nutrient dependent interaction between non-native plants and native animals has received little attention to date. The Northern Red Oak (*Quercus rubra*) is a non-native, invasive tree species in Europe, which strongly negatively influences co-occurring plants. However, a part of the native fauna is able to utilize the resources offered by this species in its non-native range. We studied a common species of wood ant, *Temnothorax crassispinus*, in forests under canopies of non-native Northern Red Oak and native oaks, Pedunculate Oak (*Q. robur*), and Sessile Oak (*Q. petraea*). These ants use acorns previously predated by insect larvae as nest cavities. We used the number of workers and number of larvae as a proxy for colony condition. *Temnothorax crassispinus* benefited from the occurrence of Northern Red Oak; their colonies were significantly more abundant and colony condition was significantly better than under canopies of native oaks. Laboratory experiments confirmed the significant preference of ants for Northern Red Oak acorns compared with native Pedunculate Oak acorns but only if ants had access to whole acorns. We found no significant preference when the choice was restricted to just the cotyledon material of the acorns. This suggests the ability of *T. crassispinus* to evaluate the solidity of a cavity based on the thicker pericarp of Northern Red Oak acorns. Overall, our data show that *T. crassispinus* ants benefit from the occurrence of Northern Red Oak in the environment.

**Key words:** Invasive plant species, cavity-nesting ant, seed damage, acorns.

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### Introduction

The appearance of non-native plants can take the form of invasion and cause marked changes to ecosystems (VILÀ & al. 2011). This invasion, in most cases, leads to negative effects manifested as decreased local plant species diversity (e.g., GAERTNER & al. 2009, HEJDA & al. 2009, POWELL & al. 2011). However, these negative effects do not necessarily apply equally to all native plant species in the environment (POWELL & al. 2013). Non-native plant species can also increase ecosystem productivity (LIAO & al. 2008, EHRENFELD 2010, VILÀ & al. 2011), but, unfortunately, local herbivores are often unable to take advantage of this increased productivity. Therefore, non-native plants may be associated with significantly poorer communities of herbivores in their introduced range compared with their native range (ROQUES & al. 2006, BRANCO & al. 2015). This means that their resources are not fully utilized by locally occurring herbivores and may result in a reduction of biodiversity in the ecosystem and a simplification of trophic relationships. A very good example of such a non-native plant is the Northern Red Oak (*Quercus rubra*). This species does not have

a positive effect on the occurrence of any vascular plants in the forests of Central Europe (WOZIWODA & al. 2014). Additionally, Northern Red Oak regenerates naturally very well in Central Europe, much better than the native species of oak (MAJOR & al. 2013). The acorns of Northern Red Oak are used by local herbivores much less than those of native species of oak (MYCZKO & al. 2014, 2017).

Ants of the genus *Temnothorax* form small colonies, composed of a few dozen to few hundred individuals. Depending on the species, they nest in, for example, fallen twigs, under rocks, or in the ground (SEIFERT 2007, CZECHOWSKI & al. 2012). *Temnothorax crassispinus* is among the most widely distributed and most common ant species, and it lives in light coniferous and mixed forests in Central Europe (SEIFERT 2007, CZECHOWSKI & al. 2012). Colonies of this ant are mainly found in cavities in acorns and sticks, situated in the litter layer (BIALAS & al. 2011, CZECHOWSKI & al. 2012). However, the acorns and sticks should have previously been bored by larvae of insects, whose foraging creates suitable ant cavities (FOITZIK & al. 2004, MYCZKO & al. 2017). The

local density of *T. crassispinus* ant colonies can be higher than 2 nests / m<sup>2</sup> (STRÄTZ & HEINZE 2004, BIALAS & al. 2011), and the ant can disperse seeds of different herbaceous plant species (FOKUHL & al. 2012). Thus, the ants can significantly influence the distribution of myrmecophilic plants and, consequently, the forest ecosystem. The number of good quality nest sites for *Temnothorax* ant colonies is usually limited, and their availability changes seasonally (HERBERS 1989, FOITZIK & HEINZE 1998, HERBERS & JOHNSON 2007). Acorns and small sticks with cavities are typically ephemeral; they could be accidentally crushed or no longer habitable as a result of decaying processes (HERBERS & JOHNSON 2007, LANGRIDGE & al. 2008). For this reason, *Temnothorax* ant colonies can be forced to find a new nest site and migrate to it frequently, even up to several times per year (HERBERS 1989, HERBERS & JOHNSON 2007).

We here report a study of the density and colony condition (using number of workers and larvae as a proxy for condition) of the ant *Temnothorax crassispinus* under canopies of native and non-native oak species in Central Europe. We also experimentally tested ant preferences for acorns of native and non-native oak species.

## Methods

We conducted our study in the oak-pine forests of central Wielkopolska, Poland (52° 26' - 52° 36' N; 16° 48' - 17° 03' E), where mature trees of the non-native Northern Red Oak (*Quercus rubra*), native Pedunculate Oak (*Q. robur*) and some specimens of native Sessile Oak (*Q. petraea*) grow together. In total, we selected 50 Northern Red Oak trees paired with the nearest native oak species; Pedunculate Oak in 46 cases and Sessile Oak in the remaining 4 cases. We decided to include Sessile Oak because the morphological variability of acorns of the two native oaks and their chemical composition almost completely overlap (SHIMADA & SAITOH 2006, ŁUCZAJ & al. 2014). Northern Red Oak trees within the forest stands were selected randomly, but were at least 15 m from each other. The nearest native oak tree of comparable age was selected as the second member of each pair.

Data were collected during October 2015. Under each selected oak tree we established a square study plot of size 2 × 2 m with one corner of the plot adjacent to the trunk and the opposite corner due south. For each plot we recorded: oak species (non-native or native), distance to the nearest mature Northern Red Oak (other than the target tree if appropriate), distance to the nearest mature native oak (other than the target tree if appropriate), diameter at breast height, percent of undergrowth cover, and percent of understory cover. Additionally we took a photo with the camera facing upwards at an angle of 45° to the south using a Sony Cyber-shot DSC-WX60 digital camera. The photographs were taken with 4.5 mm focal length. The digital photos were then converted into black-white mode in Image J software and the percentage of visible sky was used as an estimate of midday insolation of the plot. Then we searched the whole plot and collected all potential nest sites of *Temnothorax* ants into a container for further assessment in the laboratory. During the search for potential nest sites we checked carefully the whole litter layer and also the soil surface. Until assessed in the laboratory, all containers of potential nest site material were kept at a temperature of about 0 °C to avoid migration of ant colonies. In the laboratory we verified the presence of ant colonies and determined the numbers of workers

and larvae in each colony and the presence of queens. Additionally we recorded for each study plot: the number of acorns with holes predated by insects which would be suitable for *Temnothorax* ant colonies, the number of this year's acorns fallen to the ground, the number of sticks collected, and the total length of all sticks.

To determine the ant species, we used RADCHENKO (2004). After confirmation of the ant species, the colonies were divided between two experiments. During the first experiment we used 16 colonies obtained from Northern Red Oak acorns and 16 colonies from acorns of native oak species. Additionally we used 5 colonies extracted from sticks. Because of the unequal number of suitable ant colonies originating from native and non-native acorns, for the second experiment we used 5 colonies from native oak acorns and 25 from Northern Red Oak acorns. For both of these experiments, we recognized the oak species as preferred if it hosted the queen and most of the workers. Each colony was used only once. We extracted the colonies by carefully breaking the acorn shell or the stick with a scalpel and then we excavated the large rests of the nest site using tweezers. In the first experiment we tested the preferences of *Temnothorax crassispinus* for acorns of either Northern Red Oak or Pedunculate Oak. In this experiment we used comparable size acorns of both species. We prepared artificial nests by cutting the acorns 5 mm from the basal edge and then drilling a 10 mm deep hole with a diameter of 8 mm towards the top of the acorn, resulting in the creation of a 0.5 cm<sup>3</sup> volume space within the cotyledons. Additionally we drilled a hole from the outside surface with a diameter of 2 mm as an entry for ants. This hole connected perpendicularly with the previously drilled hole. Then we re-secured the base of the acorn with two metal staples. We placed single acorns of both species together in Petri dishes (n = 37) and introduced a colony of ants. After 24 hours we recorded how many ants were in each acorn and which acorn species hosted the queen, which is a key factor during *Temnothorax* ant colony movement (DOERING & PRATT 2016). In the second experiment we established if ants chose their nest site based on acorn cotyledon composition. We used 2 ml Eppendorf tubes lined with the cotyledon material of either Northern Red Oak or Pedunculate Oak. Firstly, in the tube wall we drilled a 2 mm diameter access hole at a 10 mm distance from the lid. Then, inside the tube we placed a cylinder cut from cotyledons of either Northern Red Oak or Pedunculate Oak sized to fit inside the tube (9 mm diameter 5 mm high) leaving a space above for the ant colony. The tubes were placed in pairs in Petri dishes (n = 30) and a colony of ants was introduced. After 24 hours we recorded how many ants were in each tube and which hosted the queen. For both these experiments, we recognized the acorn species as preferred if it hosted the queen and most of the workers. To test the difference in the thickness of the pericarp (an estimator of the strength of the acorn) we measured, using calipers, the pericarp thickness of randomly chosen Northern Red Oak and Pedunculate Oak acorns (n = 10 each).

We used model selection procedures based on information theory (BURNHAM & ANDERSON 2002) to identify factors affecting the numbers of *Temnothorax crassispinus* colonies in plots (Tab. S1, as digital supplementary material to this article, at the journal's web pages). We used a generalized linear mixed model (GLMM) with a Poisson distribution to determine factors affecting the number of *T. crassispinus* colonies in plots. Additionally, we used the same models to

determine factors affecting the number of ant colonies in acorns (both with (queenright) and without queens (queenless), and in sticks (both queenright and queenless)). We used plot pair as a random factor in all models. As environmental explanatory variables we included: non-native (coded as 1) or native (coded as 0) canopy oak species (oak.species), diameter at breast height (dbh.tree) as a proxy for the age of the tree, distance to the nearest native or non-native oak species as appropriate (dist.anoth.oak) as a proxy for the proportion of native or non native material in the litter layer, distance to the nearest same oak species (dist.oak) as a proxy measure of isolation from the same habitat, distance to the nearest Scots pine (*Pinus sylvestris*) (dist.pine) as a proxy distance to habitat where excavated acorns were not present (or rare), number of acorns with insect predation holes (no.acorn.hole) suitable for *T. crassispinus* colonies, number of this year's fallen acorns (no.acorn) indicating the fruit production of the tree, number of sticks (no.stick) suitable for *T. crassispinus* colonies, percent canopy openness (per.open.area) which was an indirect measure of the amount of sun from the south, percent of undergrowth cover (per.undergrowth) indicating reduced bare ground or leaf litter, percent of understory cover (per.understory) affecting soil insolation. To avoid multicollinearity, we excluded one variable (total length of sticks) from all models. Multicollinearity in the remaining explanatory variables in all models was not excessive (VIF < 2). All distances were measured from the middle of the study plots.

For model selection we used Akaike's Information Criterion adjusted for small sample sizes (AICc) to identify the most parsimonious model from each candidate set. We ranked all possible model combinations according to their  $\Delta$ AICc values and used models with the lowest AICc together with associated weight values (the probability that a given model is the best) as those best describing the data. We considered candidate models differing by less than 2 AICc units ( $\Delta$ AICc < 2.0) to be equally informative and subject to possible model averaging. For averaging, we used models with weights which had  $\Delta$ AICc values lower than 4 (BURNHAM & ANDERSON 2002).

We used a Generalized Linear Model (GLM) with a binomial error structure and logit link function separately for non-native and native oak species to relate the probability of occurrence of ant colonies to acorn volume. The acorn volume was estimated from the formula:  $4\pi / 3 \times \text{length} / 2 \times (\text{width} / 2)^2$ . We used a log transformation of acorn volume to standardize the distribution and a cubic spline to visualize the probability of ant colony occurrence with respect to acorn volume, separately for non-native and native oak species. We used Kruskal – Wallis tests with a post hoc comparison to compare the number of ant workers and larvae between different nest site types (native oak acorn, non-native oak acorn, native oak stick and non-native oak stick). Chi-square independence tests were used to compare the numbers of all colonies and of the colonies with queens, between the non-native and native oak species, for acorns and sticks separately. We used a GLM with Poisson error to compare the number of acorns predated by insects but not used as ant nests between the non-native and native oak species plots. For the experiments we used binomial tests to determine the statistical significance of deviations from equality of observations in the two categories. In the first experiment the categories were artificial nests made from acorns of either Northern Red Oak or Pedunculate Oak. In

the second experiment the categories were artificial nests made from Eppendorf tubes containing cores of cotyledons of each oak species. We used a simple 2 sample t test to compare thickness of acorn pericarp between Northern Red Oak and Pedunculate Oak acorns.

All analysis was carried out in R (R CORE DEVELOPMENTAL TEAM 2015). The model selection procedure was performed in the MuMIn library (BARTOÑ 2016), and the cubic spline visualization was performed in the mgcv package (WOOD 2015). The threshold for significance was  $p = 0.05$  throughout.

## Results

We found 77 colonies of *Temnothorax crassispinus* ants in Northern Red Oak acorns, 33 in acorns of native oak species and 17 in sticks (seven from the Northern Red Oak plots and ten from the native oak plots). The number of acorns with colonies was significantly higher under non-native oak canopies than native oaks ( $\chi^2 = 17.60$ ,  $p < 0.001$ ). In contrast, the number of occupied sticks did not differ significantly between non-native and native oak species ( $\chi^2 = 0.53$ ,  $p = 0.467$ ) (Tab. 1). We also found three colonies in acorns of native oaks occurring under Northern Red Oak canopies; we excluded these from analysis.

Of the detected colonies, a significantly higher occurrence (57) in Northern Red Oak acorns was queenright than in native oak acorns (27) ( $\chi^2 = 10.71$ ,  $p = 0.001$ ). In contrast, the detected number of queenright colonies did not differ significantly between sticks under canopies of the non-native and native oak species (four under Northern Red Oak, nine under native oak;  $\chi^2 = 1.92$ ,  $p = 0.166$ ).

Based on Akaike's Information Criterion for model selection, seven models of the number of ant colonies were equally good and explained 41 - 54% of the variation. Fourteen models of the number of colonies in acorns were equally good and explained 26 - 56% of the variation. Four models of the number of queenright colonies in acorns were equally good and explained 49 - 55% of the variation. Fourteen models of numbers of colonies in sticks were classified as equally good and explained 6 - 28% of the variation.

The total number of colonies, number of colonies in acorns and number of queenright colonies in acorns was positively correlated with the number of acorns with holes, but numbers were lower in native oak species in comparison to Northern Red Oak (Tabs. 2 - 4). The number of colonies in sticks was significantly positively correlated with the number of sticks ( $p = 0.02$ , Tab. 5).

We use both type of colonies (queenright and queenless) to analyze differences in numbers of ant workers and larvae between types of nest sites (non-native oak acorns, native oak acorns, sticks under non-native oak canopies and sticks under native oak canopies) (Tab. 6). We found significant differences both in the number of workers and larvae ( $\chi^2 = 18.18$ ,  $p < 0.001$ ;  $\chi^2 = 14.59$ ,  $p = 0.002$  respectively). The number of workers was significantly higher in non-native oak acorns than native oak acorns ( $p = 0.005$ ) and also in sticks under non-native oak canopies ( $p = 0.005$ ). Additionally, the number of larvae was significantly higher in non-native oak acorns than native oak acorns ( $p = 0.019$ ) and also in sticks under non-native oak canopies ( $p = 0.007$ ).

The GLM for native oak species showed that the probability of colony occurrence was significantly related to acorn volume ( $\beta = 2.052 \pm 0.004$ ,  $Z = 530.1$ ,  $p < 0.001$ , Fig. 1), but the equivalent GLM for Northern Red Oak was not significant ( $\beta = -1.706 \pm 1.620$ ,  $Z = 1.05$ ,  $p = 0.292$ , Fig. 2).

Tab. 1: The mean density of *Temnothorax crassispinus* ant colonies per 1 m<sup>2</sup> on study plots associated with different oak species. SE = standard error.

Oak species	Colonies in acorns	Colonies with a queen in acorns	Colonies in sticks	All ant colonies
	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)
Northern Red Oak	0.39 (0.07)	0.29 (0.05)	0.04 (0.01)	0.43 (0.07)
Native oaks	0.17 (0.03)	0.12 (0.03)	0.05 (0.02)	0.22 (0.04)

Tab. 2: Factors affecting the number of all *Temnothorax crassispinus* colonies in forest plots. Statistically significant values are emboldened. No.acorn.hole – number of acorns with insect predation holes, Oak.species – canopy oak species, Dist.oak – distance to the nearest same oak species, Dist.anoth.oak – distance to the nearest native or non-native oak species as appropriate, Per.undergrowth – percent of undergrowth cover, No.acorn – number of this year's fallen acorns, Dbh.tree – diameter at breast height, Per.open.area – percent canopy openness, Per.understory – percent of understory cover. SE = standard error; Z = Z value; P = probability.

Factors	Estimate	SE	Z	P
No.acorn.hole	<b>0.143</b>	<b>0.018</b>	<b>7.736</b>	<b>&lt; 0.001</b>
Oak.species	<b>-0.866</b>	<b>0.216</b>	<b>3.960</b>	<b>&lt; 0.001</b>
Dist.oak	-0.019	0.011	1.707	0.088
Dist.anoth.oak	-0.012	0.007	1.566	0.117
Per.undergrowth	-0.020	0.013	1.461	0.144
No.acorn	-0.005	0.003	1.399	0.162
Dbh.tree	-0.002	0.001	1.206	0.228
Per.open.area	-0.006	0.007	0.875	0.381
Per.understory	-0.003	0.005	0.617	0.538

Tab. 3: Factors affecting the number of *Temnothorax crassispinus* colonies in acorns in forest plots. Statistically significant values are emboldened. No.stick – number of sticks. For explanations of other variable codes: see Table 2.

Factors	Estimate	SE	Z	P
No.acorn.hole	<b>0.168</b>	<b>0.020</b>	<b>8.289</b>	<b>&lt; 0.001</b>
Oak.species	<b>-1.148</b>	<b>0.254</b>	<b>4.468</b>	<b>&lt; 0.001</b>
No.acorn	-0.006	0.004	1.800	0.072
Dist.oak	-0.017	0.012	1.417	0.156
Dist.anoth.oak	-0.012	0.008	1.465	0.143
Per.undergrowth	-0.018	0.015	1.194	0.233
Per.understory	-0.006	0.006	0.975	0.329
Per.open.area	-0.007	0.008	0.870	0.384
No.stick	-0.032	0.039	0.811	0.417

Tab. 4: Factors affecting the number of *Temnothorax crassispinus* colonies with queen in acorns in forest plots. Statistically significant values are emboldened. For explanations of variable codes: see Table 2.

Factors	Estimate	SE	Z	P
No.acorn.hole	<b>0.154</b>	<b>0.024</b>	<b>6.418</b>	<b>&lt; 0.001</b>
Oak.species	<b>-1.179</b>	<b>0.279</b>	<b>4.174</b>	<b>&lt; 0.001</b>
No.acorn	-0.007	0.004	1.631	0.103
Dist.anoth.oak	-0.017	0.010	1.616	0.106
Per.undergrowth	-0.014	0.014	0.956	0.339
Dist.oak	-0.010	0.011	0.880	0.379

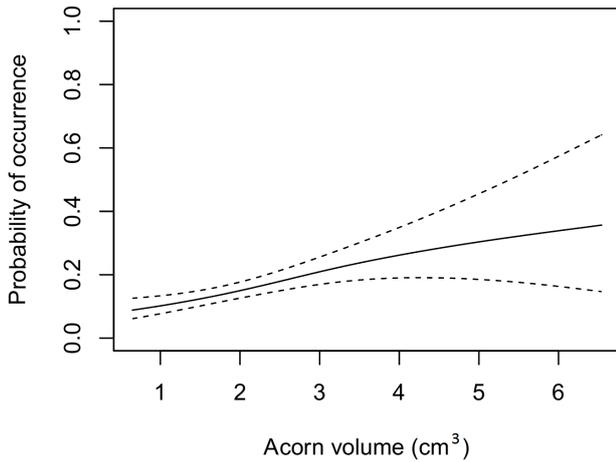


Fig. 1: The probability of occurrence of a *Temnothorax crassispinus* ant colony in relation to the volume of previously insect-bored native oak acorns. The solid curve is based on cubic splines and the dashed lines represent  $\pm 1$  standard error.

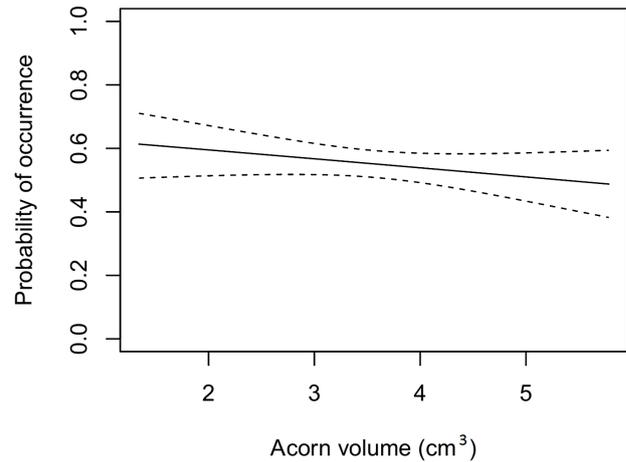


Fig. 2: The probability of occurrence of a *Temnothorax crassispinus* ant colony in relation to the volume of previously insect-bored Northern Red Oak acorns. The solid curve is based on cubic splines and the dashed lines represent  $\pm 1$  standard error.

Tab. 5: Factors affecting the number of *Temnothorax crassispinus* colonies in sticks in forest plots. Statistically significant value is emboldened. No.stick - number of sticks. For explanations of other variable codes: see Table 2.

Factors	Estimate	SE	Z	P
<b>No.stick</b>	<b>0.181</b>	<b>0.077</b>	<b>2.328</b>	<b>0.020</b>
Per.undergrowth	-0.039	0.041	0.954	0.340
Dbh.tree	-0.004	0.004	0.818	0.413
Oak.species	0.466	0.571	0.806	0.420
Per.open.area	0.015	0.020	0.728	0.467
Per.understory	0.009	0.013	0.724	0.469
Dist.oak	-0.040	0.056	0.716	0.474
Dist.anoth.oak	-0.010	0.015	0.660	0.510

Tab. 6: Mean, standard error and 95% confidence intervals (95% CI) of numbers of *Temnothorax crassispinus* workers and larvae in different colonies. SE = standard error.

Nest type	Workers		Larvae	
	Mean (SE)	95% CI	Mean (SE)	95% CI
Northern Red Oak acorns (n = 77)	125.60 (7.59)	110.49 - 140.71	139.57 (9.43)	120.79 - 158.35
Native oak species acorns (n = 33)	84.42 (9.26)	65.57 - 103.28	91.15 (11.64)	67.45 - 114.86
Sticks under Northern Red Oak canopies (n = 7)	43.43 (12.17)	13.66 - 73.20	58.43 (10.19)	33.49 - 83.37
Sticks under native oak species canopies (n = 10)	89.20 (17.96)	48.57 - 129.83	88.10 (22.64)	36.88 - 139.32

We also tested the availability of uncolonised acorn cavities. There were significantly fewer under Northern Red Oak canopies 61 acorns (Mean = 2.18, SE = 0.462) than under canopies of native oak species 202 (Mean = 3.38, SE = 0.577) (Wald  $\chi^2 = 12.74$ ,  $p < 0.001$ ).

The binomial test in the first experiment showed that significantly more ( $p = 0.008$ ) ant colonies chose nests in Northern Red Oak acorns (73%,  $n = 27$ ) than in Pedunculate Oak acorns (27%,  $n = 10$ ). In the second experiment we did not find significant differences ( $p = 0.362$ ) in the choice of artificial nests based on fragments of cotyledons of Northern

Red Oak (40%  $n = 12$ ) or Pedunculate Oak (60%,  $n = 18$ ). Northern Red Oak acorns had a thicker pericarp (Mean = 1.15 mm, SE = 0.03) than Pedunculate Oak acorns (Mean = 0.47 mm, SE = 0.02;  $t = 17.89$ ,  $df = 18$ ,  $p < 0.001$ ).

## Discussion

The occurrence in the environment of invasive Northern Red Oak positively affects the occurrence and colony condition (defined as the number of workers and larvae) of *Temnothorax crassispinus* ants. This is contrary to the most frequently described interactions between native fauna and invasive

plant species (see e.g., SHEA & CHESSON 2002, ROQUES & al. 2006, BRANCO & al. 2015). However, our described situation is not an herbivory interaction, or simple influence of plant cover, but a secondary interaction dependent on utilizing previously insect-infested acorns. This interaction has become possible only after the host range expansion by native insects whose larvae feed on cotyledons within developing acorns of Northern Red Oak (MYCZKO & al. 2017). The appearance of such interactions indicates the inclusion of this non-native species in the network of dependencies in the ecosystem and its “naturalization”. Our results show that acorns of Northern Red Oak are significantly preferred as a colony cavity. Both in the forest and in the first laboratory experiment, colonies had access to whole acorns. The lack of preference for oak species in the second experiment where cotyledons were the only plant tissue provided suggests the ability of *T. crassispinus* ants to assess the durability of acorns. Acorns of native Pedunculate Oak had significantly thinner pericarps compared to Northern Red Oak acorns. Furthermore, ŁUCZAJ & al. (2014) reported a significantly lower proportion of seed material within Northern Red Oak acorns indicating a greater share of pericarp tissue in the total weight of the acorn.

In addition to the robustness of the acorn for *Temnothorax crassispinus* ants, cavity volume also seems to be important. MITRUS (2015) has shown that ants prefer larger artificial nests. However, the volumes tested (up to 1.76 cm<sup>3</sup>) were smaller than the volume of most insect-infested acorns found in our study plots. In the current study, a positive relationship between acorn occupation and acorn volume occurred only in native oaks (Fig. 1). The increased occurrence of ant colonies in larger native acorns may be associated with an increase in “solidity” in larger acorns. However, in the current study we did not collect data on pericarp thickness of all acorns to confirm this statement. In contrast, Northern Red Oak acorn volume did not significantly influence occupation by *T. crassispinus* ants (Fig. 2). This suggests that a factor other than the simple volume difference affects the decision on occupation of an acorn.

We found two key factors affecting the number of ant colonies on our plots, irrespective of whether total number of colonies, number of acorn colonies or number of queen-right acorn colonies was considered. These were the oak species and the number of acorns with holes. Numbers of all types of colony were higher in Northern Red Oak plots. Northern Red Oak acorns were also characterized by significantly higher numbers of both workers and larvae in colonies (proxy for colony condition). This suggests better food resources under Northern Red Oak canopies. This finding is consistent with McCARY & al. (2016) who showed increased abundance of secondary consumers in woodland brown food webs based on invasive plants. Also KJAR & PARK (2016) showed that the ant abundance and species richness can be positively associated with alien plant cover. The second factor significantly affecting the number of all types of ant colony was the number of acorns previously predated by insects. This factor indicates the ability of colonies to more frequently change nest location which should allow avoidance of social parasites, for which the *Temnothorax* ants are particularly vulnerable (BRANDT & FOITZIK 2004, FOITZIK & al. 2004). However, it should be kept in mind that under Northern Red Oak canopies there were significantly fewer potential acorn cavities than under native oaks. This suggests two possibilities or a combination

of them; firstly that the better quality of Northern Red Oak acorns compensated for their smaller number or, secondly, that compensation was via a higher quality of habitat under Red Oak canopies in comparison to habitat under native Oak species.

The colonies located in acorns coexisted on the same plots with colonies located in sticks previously bored by insects. If we analyze only the differences between types of nest choice, the ant colonies located in sticks under Northern Red Oak canopies contained fewer workers and fewer larvae (proxy for colony condition) than colonies in acorns of Northern Red Oak, but these numbers were comparable to those in native oak acorns. Additionally, only the number of sticks significantly explained the number of ant colonies in sticks. This type of cavity may be a refuge for local ant colonies during subsequent non-mast years when acorns may be scarce. The differences in the quality of colonies between Northern Red Oak acorns and native oak acorns should influence sex ratio decisions during production of sexual specimens. STRÄTZ & HEINZE (2004) showed that well-supplied *Temnothorax crassispinus* colonies reared more numerous female sexuals in comparison to weaker colonies which preferably invested in the production of male sexual specimens. This means we can anticipate differences between sex ratio decisions from colonies living under Northern Red Oak canopies and those under native oak canopies, but this question needs future investigation.

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