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Testing temperature effects on woodboring beetles associated with oak dieback

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Abstract
A warmer climate may potentially have a strong effect on the health status of European oak forests by weakening oak trees and facilitating mass reproduction of wood boring insects. We did a laboratory experiment in Slovakia to study the response of major pest beetles of oak and their parasitoids to different temperature regimes as background for predicting climatic effects and improving management tools of European oak forests. With higher temperatures the most important oak pest *Scolytus intricatus* emerged much earlier, which indicate that completion of a second generation and increased damage further north in European oak forests may be possible. Lower temperatures gave longer larval galleries and more offspring per parents but still lower beetle production due to semivoltine life cycle. For buprestids and longhorn beetles warmer temperatures resulted in more emerging offspring and a shift towards earlier emergence in the same season, but no emergence in the first season indicated that a change to univoltine populations is not likely. Reduced development success of parasitoids at the highest temperatures (25/30 °C) indicates a loss of population regulation for pest beetle populations. A warmer climate may lead to invasion of other population-regulating parasitoids, but also new serious pest may invade. With expected temperature increases it is recommended to use trap trees both in April and in June, and trap trees should be removed within 2 months instead 1 year as described in the current standard.

Keywords *Quercus* · Temperature · *Scolytus intricatus* · Cerambycids · Buprestids · Parasitoids

Introduction

The possible effects of climate change on European oak forests are of deep concern. Oak trees constitute a significant part of mixed hardwood forest, which is the most widespread forest type in the lowlands of Central Europe (Godwin 1975). For example, in Slovakia oak forest includes nine indigenous species and covers 254,000 ha or 13.1% of the area of mixed hardwood forests (National Forest Centre data). Oak dieback occurs throughout most of Europe, causing extensive tree

mortality and within the Slovak Republic it accounts for 1.4 mil m^3 over the years 1980–1985. The situation was particularly severe in 1984 when 73,000 ha of oak stands were infested (National Forest Center data). Oak dieback is caused by a complex interaction of abiotic and biotic factors such as attack by wood boring and defoliating insects, fungal infestations, drought stress due to low groundwater, and more often warm and dry weather that may be associated with climate change.

Compared to other hardwood trees, oak is host to a very broad spectrum of bark- and wood-boring beetles (Jurc et al. 2009; Marković and Stojanović 2011). The oak splendor beetle *Agrilus biguttatus* (F., 1777) (Coleoptera: Buprestidae), breeds underneath the bark and is one of the most damaging borers in oak trees (Brown et al. 2014). It usually attacks young oak stands (30–40 years old, Hilszczański and Sierpinski 2007) and its occurrence in Europe is increasing (Moraal and Hilszczański 2000). The most abundant beetle breeding within Slovakian oaks is the European oak bark beetle, *Scolytus intricatus* (Coleoptera: Curculionidae: Scolytinae) (Gogola and Chovanec 1987; Gogola and Brutovský 1999; Galko 2008; Galko et al. 2009, 2012).

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S. intricatus is a secondary pest that develops within physiologically weakened trees and freshly felled material (Marković and Stojanović 2003). Of the many factors contributing to oak decline in Europe, *S. intricatus* is considered as the most important (Leontovyč 1990). After emerging from its host, *S. intricatus* flies to the canopy of healthy oak trees where it will do maturation feeding on twigs 3–5 of mm diameter and thereby vector Ophiostomatales fungi that will weaken the tree (Doganlar and Schopf 1984; Doganlar et al. 1984; Gibbs et al. 1984; Yates 1984; Gogola and Chovanec 1987; Habermann and Schopf 1988; Galko 2008). Maturation feeding is required to complete sexual development, and mating occurs on the surface of attractive oak material. The maternal galleries are about 1 to 2 cm long, in which the females lay eggs in niches along both sides. After laying eggs, the female dies in the entrance hole and her dead body protects the offspring from predators and parasitoids (Gogola and Chovanec 1987; Galko 2008).

The temperature responses of the most important insect pests in oak are not well known. Since oak dieback also involves wood boring pest beetles, it is useful to get more insight in the temperature requirements of these pests; and in particular the most significant inhabitants, such as *S. intricatus*. Since this pest prefers to attack weakened trees, forest managers use oak trap trees to reduce populations. Standing, live oak trees are girdled, creating an attractive habitat for colonization of female beetles (Gogola and Chovanec 1987). The trap trees are destroyed before emergence of adult bark beetles, thereby reducing the population of *S. intricatus* and preventing the spread of pathogenic fungi (Galko 2008; Galko et al. 2009). Thus, it is of special interest to understand how a warmer climate will impact the development of bark beetle species and thereby the optimal timing of the trap trees (Holuša et al. 2017). Better knowledge of the temperature requirements may improve our prediction of climatic effects on insects associated with oak dieback and if the efficiency of the established method of using trap trees will change as the climate becomes warmer. Furthermore, parasitoids that are important for population regulation of pest insects might be affected by a warmer climate (Jeffs and Lewis 2013). There is a rich literature on the biology of parasitoids of oak bark and wood boring beetles (hereafter shortened as BAWBB) (Čapek and Leontovyč 1987; Čapek 1999; Zach 1994; Marković and Stojanović 2003, 2011; Galko 2008; Galko and Pavlík 2009), but few authors have compared development at different temperatures.

Here we performed an experiment to determine the effects of temperature on the abundance, diversity and emergence of various oak BAWBB and their parasitoids. We studied in particular how temperature affects the abundance and distributions of *S. intricatus*. Based on the results, we discussed possible effects of global warming on the insects associated with oak dieback and the efficiency of the current use of trap trees against the most serious oak insect pests.

Materials and methods

Preparation of experimental trap tree and samples

We selected a healthy standing oak tree of *Quercus robur* L. in the Duchonka district, (48°36′37.80″N; 18°02′59.05″E, 345 m a.s.l.) in western Slovakia. The selected tree had a high density of *S. intricatus* and other BAWBB. The diameter of the tree was 30 cm at breast height, the height was 24 m and calculated surface area ~ 1100 dm^2. We selected by intention only one experimental tree in order to make micro-climate and other environmental factors as equal as possible, while the insect individuals constituted the unit of repetitions in the experiment. The surrounding forest of the experimental tree is dominated by broadleaved trees, in particular the oak species *Q. dalechampii* Tenore, *Q. petraea* Mattuschka (Lieblein), *Q. robur* L. and *Q. cerris* L.

At the end of April 2012, we used a chainsaw to damage the vascular tissue of the experimental tree in order to disturb the flow of nutrients and water within the tree. Gradually the tree started to decay and emit primary attractants that are used by the female *S. intricatus* beetles to find suitable brood trees. This method is recognized as efficient for capturing and monitoring *S. intricatus* and others BAWBB in Slovakian oak forests (Turčáni 2000; Galko 2008; Galko et al. 2009).

After infestations by *S. intricatus*, the experimental tree was felled 15 June and sawn into bolts of 50–80 cm length. The bolts were divided into four groups (I, II, III, IV), where each group contained one bolt with each of the following diameters: 15 cm, 19 cm (control bolt), 22 cm and 25 cm (Table 1). The control bolts (4) were 50 cm long, while all other bolts (12) were 80 cm long (Table 1). Based on experiences from previous studies and monitoring (Turčáni 2000; Galko 2008; Galko et al. 2009), it is assumed that the attack densities of *S. intricatus* and others BAWBB were uniformly distributed along the trunk section used for the experiment. One group of sample bolts (IV) was left in the forest to simulate outdoor conditions (marked in this publication as ext.). Bolts in the other three groups (I, II, III) were transported to the Forest Protection Service laboratory in Banská Štiavnica (National Forest Centre, Forest Research Institute Zvolen, Slovakia). On 19 June, these bolts were placed into mesh bags with plastic containers attached to the outside of the bags to capture emerging insects, and each group of bolts were placed within 700 L growth chambers (Climacell 707 – BMT Medical Technology, Brno, Czech Republic) at different temperature conditions (Table 1). The group IV bolts (ext.) were transported to the laboratory after the first exit holes of *S. intricatus* were recorded on July 20 (after 35 days in the forest). These samples were placed in dark rearing chambers (photo eclectors) and kept at 20–22 °C and 40–50% humidity in the laboratory. Each rearing chamber had 1 or 2 small holes,

Table 1 Surface area (dm^2) of bolts assigned to each group of the experiment

Group	Temperature (night/day)	Diameter				Total
		15 cm	22 cm	25 cm	19 cm (control)	
I	15/20 °C	37.80	56.00	64.93	29.40	188.13
II	20/25 °C	38.70	57.51	74.76	28.91	199.88
III	25/30 °C	45.90	62.31	66.00	30.78	204.99
IV	ext.	52.52	66.24	76.63	30.24	225.63
Total		174.92	242.06	282.32	119.33	818.63

ext. – field conditions

through which emerging insects were entering into collection plastic containers. All of the laboratory growth chambers (group I, II, III) were run under the similar conditions with 24 h regime of 9/15 h (night/day), where moisture was set at 95/65%, ventilation at 10/20%, and light at 0/100%.

The control bolts were debarked in order to determine the developmental stage of the insects. The surface areas of each bolt were calculated and are presented in Table 1.

During 2012, insects were collected from the rearing and growth chambers every week for 8 weeks (23 July to 10 September). Adults from each group and diameter class were placed in separate, labeled tubes filled with propylene glycol (C$_3$H$_8$O$_2$, 99.5%) (Penta-Ing. Petr Švec, Prague, Czech Republic). On 12 September 2012 the bolts from all four groups were removed from the rearing and growth chambers and stored outside in partial shade until 22 April 22 2013 (224 days), thereby exposing undeveloped instars to winter conditions. All the samples were covered with mesh net as a protection against woodpeckers.

On 22 April 2013, all bolts were placed back in the rearing and growth chambers. The conditions in the growth chambers were the same as in the previous year. Insects started to emerge on 6 May 2013 and adults were collected at weekly intervals until 20 August, after which insects ceased to emerge from the bolts.

Insect identification

The following keys were used to identify insects to species: bark beetles (Pfeffer 1989); buprestids (Bílý 1989); cerambycids (Sama 2002); chalcids (Hedqvist 1963); and braconids (Čapek 1996; Hedqvist 1998).

Assessment of *S. intricatus* galleries

All bolt samples were debarked using knife and axe. Frass and debris were removed from galleries using a soft brush. We measured the length of maternal galleries (mm) and larval tunnels (mm) and calculated the density of maternal galleries per dm^2 (m.g./dm^2). Only *S. intricatus* galleries were assessed since these larvae consumed most of the inner bark and outer sapwood, making it impossible to measure the galleries of buprestids and cerambycids.

Statistical analyses

All statistical analyses were performed using Statistica 10 (StatSoft Inc., Oklahoma, USA). The results were statistically evaluated using one-factor analyses of variance (ANOVA). Log(x + 1) transformation was used to normalize for variance analyses, but untransformed data are presented in the tables. We used the HSD (Honestly Significant Difference) Tukey test to determine the minimum difference between means. In all cases, $p \leq 0.05$ was used to determine statistical significance.

Results

Influence of temperature on the emergence of BAWBB and their parasitoids

Only *S. intricatus* emerged from the experimental bolts in the first year; the beetles started to emerge on 23 July, after 35 days in growth chambers (Fig. 1a). The majority of the adults were collected from bolts placed in the warmest conditions (25/30 °C) and peak emergence occurred on 6 August (Fig. 1a). In 2012, a total of 1714 *S. intricatus* were collected from the samples stored at 25/30 °C. This is markedly more than from samples stored at 20/25 °C (487 beetles) and 15/20 °C (122 beetles) (Table 2). Only 283 *S. intricatus* were recorded from the samples stored outdoors (Table 2) with peak activity occurring much later on 27 August. Emergence continued until mid-September (Fig. 1a). There were no buprestids and cerambycids recorded in 2012 (Fig. 1b, c).

In 2013, the emergence of *S. intricatus* continued the year after overwintering (Fig. 1a). A total of 8838 *S. intricatus* adults were collected in this year (2987 at 15/20 °C; 2336 at 20/25 °C; 1034 at 25/30 °C and 2481 from bolts placed outdoors) (Table 2).

Buprestids started to emerge in 2013 (Fig. 1b); a total of 2637 jewel beetles were collected (Table 2). At the warmest

Fig. 1 Emergence of insects under different temperature conditions (ext. - field conditions)
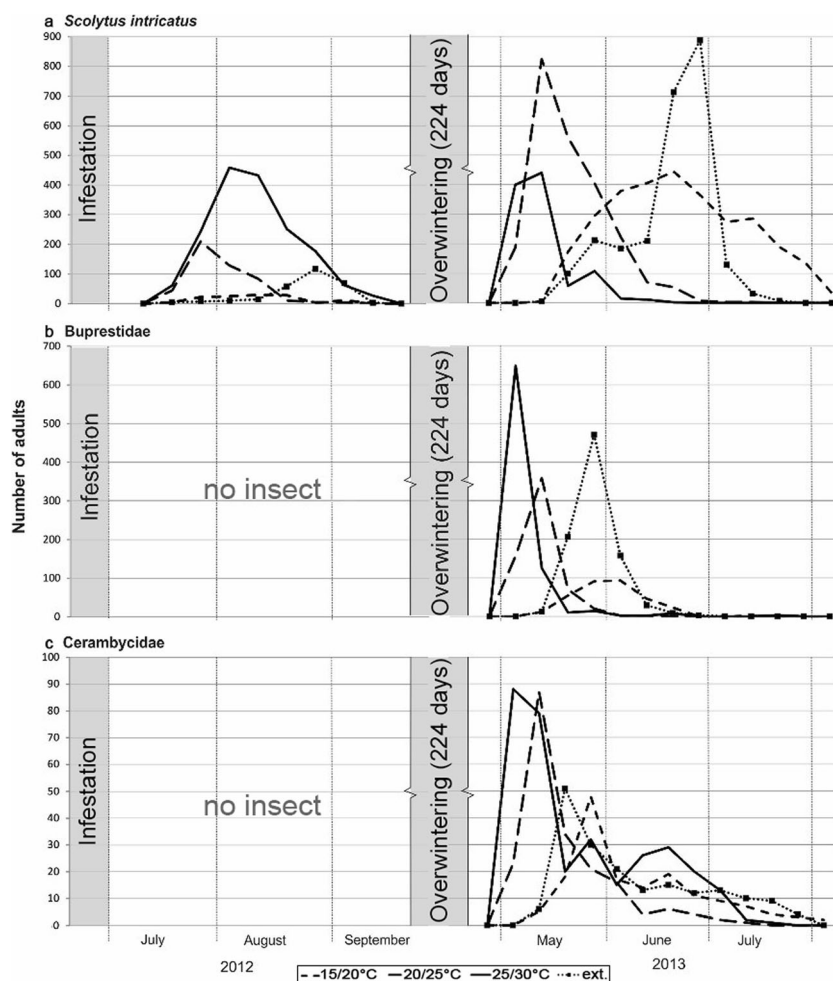
temperatures (25/30 °C), peak emergence occurred on 6 May, while no beetles had emerged during visual inspection a few days beforehand. Peak emergence at 20/25 °C was recorded 1 week later on 13 May, while at the coolest temperatures (15/20 °C) emergence was highest on June 3 (Fig. 1b). The abundances were significantly lower at the cooler temperatures (Table 2). Within the bolts placed outdoors, peak emergence occurred on May 27 (Table 2).

A total of 870 longhorns from 5 different species were collected in 2013 (Fig. 1c, Table 2). As with the jewel beetles, cerambycid emergence started and peaked earlier from bolts placed at warmer temperatures (Fig. 1c).

Almost 16,000 adults from six orders were collected (Table 2) with *S. intricatus* as the most commonly collected insect (72.01% - 11,444 adults). In both years there were no significant differences in the number of *S. intricatus* emerging from bolts held at colder or warmer temperatures (Fig. 2a). Regardless of temperature, an average 14 beetles/dm^2 emerged from our samples.

Following *S. intricatus*, buprestids were the second most abundant taxon accounting for 16.6% (2637 adults) of all adults, with *A. laticornis* (1210 beetles) and *A. sulcicollis* (1212 beetles) being the most dominant species (Table 2). The number of emerged jewel beetles was significantly higher ($p \leq 0.0055$) as temperatures increased (Fig. 2b). Statistical significance ($p \leq 0.0089$) was recorded between 15/20 °C (1.80 beetles/dm^2) and 25/30 °C (3.88 beetles/dm^2). There was no significant difference between 15/20 °C and 20/25 °C or between 15/20 °C and bolts placed outdoors.

The most abundant longhorn beetles (5.47%) were *P. testaceus* (3.65% - 579 beetles) and *X. antilope* (1.78% - 283 beetles) (Table 2). The highest number of longhorn beetles recorded was at the warmest temperature 25/30 °C (Fig. 2c). All other comparisons were not significant.

A total of 729 parasitoids of BAWBB were collected. The most abundant taxon was braconids, *Doryctes* sp. (199 wasps) and *D. protuberans* (149 wasps). The most abundant chalcid was *Entedon tibialis* (1.33% - 212 wasps) (Table 2). The most parasitoids (396) emerged from bolts placed outdoors (1.89 wasps/dm^2) (Fig. 2d). This difference was statistically significant compared to bolts placed at 20/25 °C (0.67 wasps/dm^2, $p \leq 0.0500$) and 25/30 °C (0.2 wasps/dm^2, $p \leq 0.0003$).

Table 2 Abundance (N) and relative percentage (D%) of all reared insects

Species	Conditions				Total N	Total D%
	15/20 °C	20/25 °C	25/30 °C	ext.		
PSOCOPTERA	3			114	117	0.74
RAPHIDIOPTERA						
Raphidia notata (Fabricius, 1781)				2	2	0.01
COLEOPTERA						
Staphylinidae	1	6			7	0.04
Cleridae						
Tilloidea unifasciata (Fabricius, 1787)			5		5	0.03
Thanasimus sp. (Latreille, 1806)	18	4	1	23	46	0.29
Buprestidae						
Chrysobothris affinis (Fabricius, 1794)		1	1	2	4	0.03
Agrilus laticornis (Illiger, 1803)	142	266	396	406	1210	7.62
Agrilus sulcicollis (Boisduval and Lacordaire, 1835)	133	264	382	433	1212	7.63
Agrilus angustulus (Illiger, 1803)	45	80	36	50	211	1.34
Cucujidae						
Silvanus unidentatus (Olivier, 1790)				1	1	–
Cerambycidae						
Pyrrhidium sanguineum (Linnaeus, 1758)	4	2			6	0.04
Phymatodes testaceus (Linnaeus, 1758)	116	150	179	134	579	3.65
Poecilium alni (Linnaeus, 1767)		1			1	–
Plagionotus detritus (Linnaeus, 1758)	1				1	–
Xylotrechus antilope (Schonherr, 1817)	36	45	146	56	283	1.78
Curculionidae, Scolytinae						
Σ *Scolytus intricatus* (Ratzeburg, 1837)	3109	2823	2748	2764	11,444	72.01
2012 *Scolytus intricatus*	122	487	1714	283	2606	
2013 *Scolytus intricatus*	2987	2336	1034	2481	8838	
HYMENOPTERA						
Ichneumonidae				5	5	0.03
Braconidae						
Coeloides scolyticida (Wesmael, 1838)				5	5	0.03
Doryctes sp. (Haliday, 1836)	48	59	36	56	199	1.25
Dendrosoter protuberans (Nees, 1834)		1		148	149	0.94
Eucorystes aciculatus (Marshall, 1888)				7	7	0.04
Ecphylus silesiacus (Ratzeburg, 1848)				68	68	0.43
Eurytomidae						
Eurytoma morio (Boheman, 1836)				1	1	–
Pteromalidae						
Dinotiscus aponius (Walker, 1848)	4	2	2	1	9	0.06
Eulophidae						
Entedon tibialis (Nees, 1834)	68	52	7	85	212	1.33
Entedon ergias (Walker, 1839)	24	23	7	25	79	0.50
LEPIDOPTERA				17	17	0.11
DIPTERA						
Nematocera				9	**9**	0.06
Brachycera		2			**2**	0.01
Total	3752	3781	3946	4412	15,891	100
N species	15	17	13	23	29	

ext. – field conditions

Significant differences in parasitoids emergence also occurred between 15/20 °C and 25/30 °C ($p \leq 0.009$) and between 20/25 °C and 25/30 °C ($p \leq 0.019$) (Fig. 2d).

Fig. 2 Mean ± SE density (adults/dm^2) of *S. intricatus* (**a**), buprestids (**b**), cerambycids (**c**) and their parasitoids (**d**). Bars sharing the same letter are not significantly different ($p \leq 0.05$, HSD Tukey test) (ext. – field conditions)

Assessment of *S. intricatus* galleries

Bolts were debarked after all the insects had emerged from them. The surface area of all the bolts was 816.63 dm^2 (Table 1) which represents 74.24% of total area of the original experimental tree (1100 dm^2). A total of 652 maternal galleries were assessed with an average length of 12.80 ± 3.71 mm. Maternal galleries were significantly longer in bolts placed outdoors (13.70 mm) than those within bolts stored at 25/30 °C (12.43 mm) ($p \leq 0.0074$) or 20/25 °C (12.17 mm) ($p \leq 0.0004$) (Fig. 3a). There was also a significant difference in galleries length from bolts of different diameter: 15 cm (average gallery length = 13.48 mm) and 22 cm (average gallery length = 12.40 mm) ($p \leq 0.0250$). Differences between other diameter categories were not significant (Fig. 3b). The average density of maternal *S. intricatus* galleries was 0.82 ± 0.13 galleries/dm^2 and was almost identical in all sample groups.

A total of 375 larval galleries were assessed with an average length of 68.69 ± 16.45 mm. Significant differences in the length of larvae galleries occurred between 15/20 °C (74.59 mm) and 20/25 °C (67.39 mm) ($p \leq 0.0125$), between 15/20 °C and 25/30 °C (64.45 mm) ($p \leq 0.00001$) and also between 15/20 °C and bolts placed outdoors (68.45 mm) ($p \leq 0.0338$) (Fig. 3c). There were no significant differences in larval gallery length between different bolt diameters (15 cm = 70.66 mm, 22 cm = 66.67 mm, 25 cm = 68.65 mm, control 19 cm = 68.59 mm) (Fig. 3d).

There was a negative relationship between the galleries length and temperature conditions (Fig. 3c). Longer galleries were measured on samples stored in colder conditions was probably caused by slower development rate of larvae. The developmental period is prolonged at lower temperatures and therefore the larvae excavate longer galleries. The length of the galleries did not differ significantly when compared between different bolt diameters (Fig. 3d).

Estimation *S. intricatus* production per oak tree at different temperatures

We estimated the number of *S. intricatus* that possibly could emerge at different temperatures (Fig. 4). Using the results of Fig. 1, our estimate at 25/30 °C is that 62% (> 9000 individuals) of the population will emerge in the first year and the remaining individuals (37.6%) in the second year, which results in a total of 14,740 individuals emerging over 2 years. Conversely, under colder conditions (15/20 °C) only 3.9% of the population emerges in the first year and the remainder (96.1%) overwinters in the tree and emerges in the following year, which makes a total production of 18,131 *S. intricatus* per infested oak tree (Fig. 4).
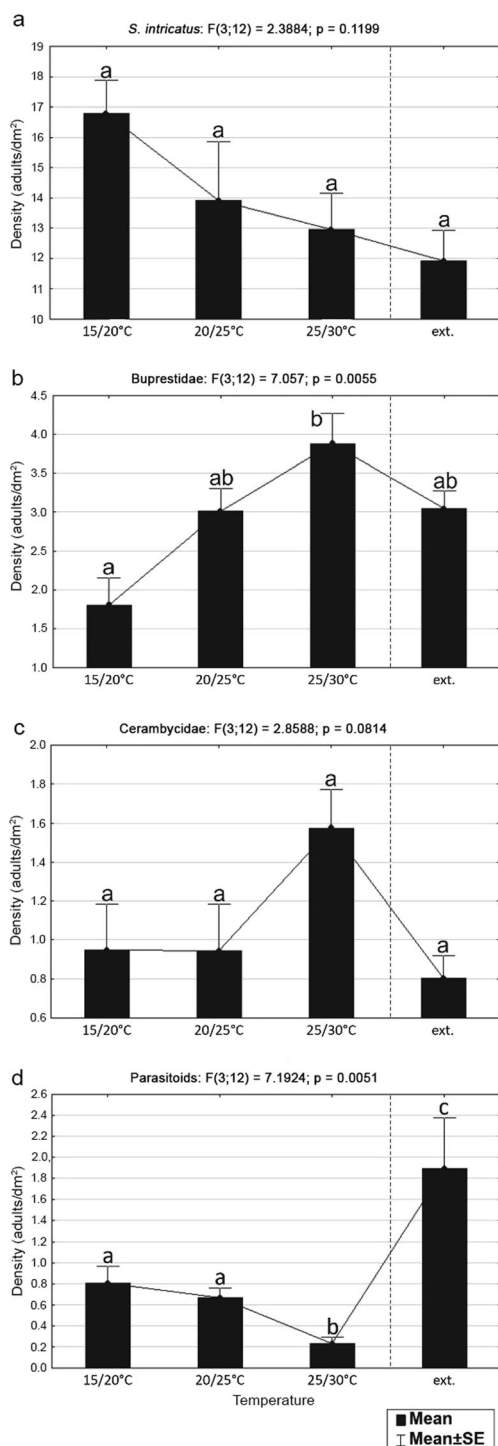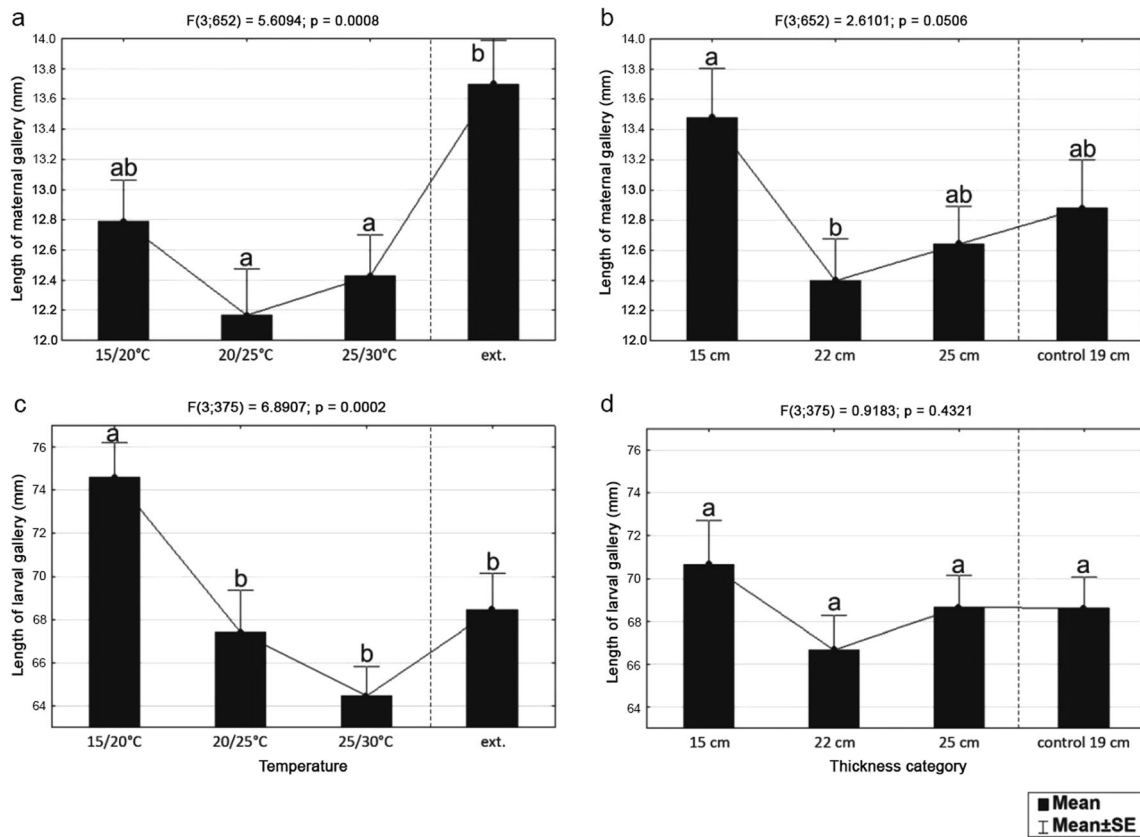
Fig. 3 Mean ± SE length of *S. intricatus* maternal and larval galleries with respect to temperature and bolt diameter. Means followed by the same letter are not significantly different ($p \leq 0.05$, HSD Tukey test) (ext. – field conditions)

Discussion

The strong effect of temperature on development rate of *S. intricatus* observed in the present experiment may indicate that global warming may have strong effects on life cycle
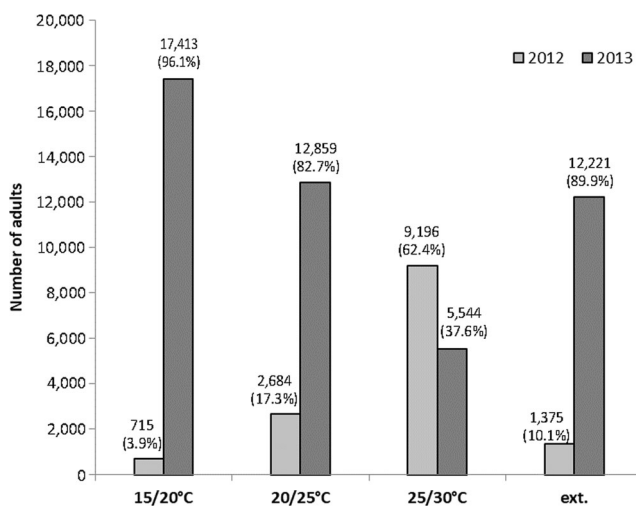

Fig. 4 Estimated numbers of *S. intricatus* beetles emerging from one oak experimental trap tree under different temperature regimes. Percentages indicate the proportion of beetles emerging in either the first year (2012) or in the second year (2013) (ext. – field conditions)

synchrony and development success for this contributing pest species on oaks (Fig. 1a). Under typical forest conditions and under the current climate in Slovakia, *S. intricatus* begins to emerge from infested material during the first half of May following female colonization (Galko 2008). We found that development of *S. intricatus* in the warmest conditions (25/30 °C) was completed in 45–50 days after initial infestation (Fig. 1a). These findings correspond with work of Doganlar and Schopf (1984) and Yates (1984). During warmer years, some *S. intricatus* are able to emerge and establish a second generation in the same year of the initial infestation, but development cannot be completed until the following spring (Gogola and Chovanec 1987; pers. obs.). However, in more southern parts of Europe (e.g. Serbia), *S. intricatus* is able to successfully complete two generations in 1 year (Marković and Stojanović 2003). If the average temperature increases as expected with climate change, we assume that *S. intricatus* will be able to complete a second generation also in Slovakia. Degree day modelling may be good tool determine the temperatures at which this will happen.

The question may be the physical condition of new *S. intricatus* adults that have developed under different temperature conditions (Fig. 1a). We did not find any differences in the weight of the beetles developed under different temperature conditions, but we visually recorded significant

differences in the color of the beetles. Those with the shortest development time under warmer conditions have not been fully colored in contrast to slowly developed beetles in colder conditions. Can these color differences of faster developed beetles reflect also their physical condition? This may be the subject of further study.

A change in development of buprestid due to global warming is also indicated (Fig. 1b), even though the effects in the experiment were not as distinct as for *S. intricatus*. Warmer temperatures resulted in a shift towards earlier emergence in the same season, while a change of voltinism was not observed. The peak emergence at 25/30 °C occurred 1 week earlier than for 20/25 °C. During the first week, 650 jewel beetles emerged at 25/30 °C, 187 beetles at 20/25 °C, while none emerged at 15/20 °C (Fig. 1b). The number of emerging jewel beetles increased with warmer temperature (Fig. 2b), which is completely different from the trends of *S. intricatus* emergence (Fig. 2a). It is known that warmer temperatures are especially conducive for adult flight and larval development of jewel beetles (Hawkeswood 1978; Bílý 1989). We did not observe that increased temperatures could lead to emergence of *Agrilus* or other jewel beetles in the first year instead of the second year (Fig. 1b). This is however not unexpected, since most *Agrilus* species require at least one full year to develop in infested material (Bílý 1989).

Also for longhorn beetles we expect that global warming will impact the timing of the development. In the same way as for the buprestids warmer temperatures resulted in a shift towards earlier emergence in the same season, while no emergence in the first season indicated no change of voltinism for the temperatures tested (Fig. 1c). The longhorn beetles showed a marked response to higher temperatures, as demonstrated by the largest number of beetles emerged at the warmest temperature (25/30 °C) (Fig. 2c). However, we did not find any emergence of cerambycids in the year when the samples were infested. This agrees with existing literature, since it is known that most longhorn beetles require two to 3 years to complete development (Heyrovský and Sláma 1992; Sama 2002).

The experiment indicates that a warmer climate may possibly weaken the population regulation effects by parasitoids and thereby release some of their host species out of control. According to the results, higher temperatures were not suitable for the development of most of parasitoid species included in the experiment, especially those in Eulophidae family (Table 2). As temperatures increased, the number of emerging *S. intricatus* (Fig. 2a) and parasitoids (Fig. 2d) decreased and conversely, the number of emerging buprestids (Fig. 2b) and cerambycids (Fig. 2c) increased. This interpretation should however be treated with care; as warmer climate may also involve a shift in the species composition of parasitoids. Furthermore, the parasitoid fauna included in the experiment is apparently not the complete fauna of parasitoids that could be involved. In our experiment, only one set of samples

remained in the forest while all other bolts were placed indoors immediately after infestation. From samples placed outdoors for extended 35 days, we found much higher numbers of BAWBB parasitoids emerged compared to indoor samples (Fig. 2d, Table 2). This was expected because these bolts were exposed to parasitoids for a much longer period than those placed within the growth chambers. *Dendrosoter protuberans* parasitizes *S. intricatus* larvae in the year following oak tree colonization (Čapek 1986). However, *S. intricatus* larvae kept outdoors were already parasitized by this species 2 months after the oak tree was infested by *S. intricatus* (Table 2). Only a small number of parasitoids developed in the warmest conditions 25/30 °C (Table 2, Fig. 2d).

There are obviously several more factors that may be involved in the development of oak dieback under a future climate. Due to the multitude of interactions, we do not expect that the results of our temperature experiments on the involved insects can be used to predict the global warming effects on the whole phenomena of oak decline. For example, we may expect changes in the spatial ranges of both pest species and their host tree hosts, which may create new communities and interactions associated with the European oak trees. Also invasive species may be involved. For example, the extensive damages by the oak lace bug *Corythucha arcuata* (Say, 1832) (Heteroptera, Tingidae) is a relatively new phenomenon that affects the health of European oak forests (Hrasovec et al. 2013). This North-American pest was recorded in Europe for the first time in Italy in 2000 (Bernardinelli and Zandigiacomo 2000). Thereafter it has spread rapidly in southeastern Europe and caused severe outbreaks affecting thousands of hectares of oak forests in Hungary, Croatia, Serbia and Krasnodar region in Russia, and further expansions in European oak forests are expected (Csóka et al. 2017). Another pest on the oak foliage is the oak powdery mildew (*Erysiphe alphitoides*), which is one of the most common pathogens on oaks in Europe. Climate change is expected to influence the severity of this disease by altering the host pathogen phenological synchrony (Marçais and Desprez-Loustau 2014). Combined with the expanding effects of oak lace bug and other emerging plant health problems of oaks, more oaks may weakened and become more accessible for breeding of *S. intricatus* and other BAWBB. Considering the spread of new oak pests like this and more frequent weather extremes of heat, drought and storm due to global warming (Lindner et al. 2010), makes it likely that oak decline may be an increasing problem in European oak forests in the future.

Management recommendations

As the *S. intricatus* life cycle can be univoltine (1 generation per year) or semivoltine (generation requiring more than 1 year), it is important for forest protection managers to reduce the populations of both life cycles. According to our previous

studies (Galko 2008; Galko et al. 2009; Galko et al. unpub. data) and current results, we outlined basic management recommendation. One set of trap trees should be created in April to capture the population emerging in the spring, and these trap trees must be subject of sanitation (e.g. removal, chipping, burning) before the F1 population emerges. Another set of trap trees should be created in June to capture the F1 generation that emerges in July from naturally infested oak trees occurring within the forest. Regardless of seasonal temperatures, the 2nd set of trap trees should remain in the forest until the end of September when all F1 beetles have flown and are searching for new hosts to colonize (Fig. 1a). Fig. 4 shows that only 10% of the natural population is univoltine but at 20/25 °C, this increases to 17%. And at 25/30 °C, 63% of the F1 population completed development and emerged within the year of colonization. Therefore, as annual ambient temperatures increase in Europe, managers may have to deploy more traps trees in April and June in order to protect healthy oaks from attack by the European oak bark beetle (Galko et al. unpubl. data). This is important as *S. intricatus* could become more problematic with increasing climate (i.e. more beetles emerge in the same year as initial colonization, more oak can become infected). Based on these results we can conclude that temperature conditions markedly affect the developmental rate of this pest.

Good tools for estimation of pest populations may be important for management of European oak forests in the future. Forest protection managers in Slovakia use the density of maternal gallery of *S. intricatus* to estimate the impact of oak trap trees on reducing *S. intricatus* populations. During the massive oak dieback in Slovakia in the 1980's, a large variation in the measured densities of *S. intricatus* galleries was recorded. Recorded gallery densities on *Q. cerris* were 0.7 m.g/dm^2 (0.5–1.7 m.g./dm^2) (Pavlík 1996), 4.0 m.g./dm^2 (Čapek and Leontovyč 1987), 4.8 m.g./dm^2 (Patočka and Novotný 1987) and even up to 16 (Gogola and Brutovský 1999) or 40 m.g. /dm^2 (Patočka et al. 1999). Average gallery density in recent research ranged from 0.34 to 2.61 m.g./dm^2 (Galko 2008; Galko et al. 2012). The variation in m.g./dm^2 is certainly dependent on population size and many environmental variables, such as suitability of substrate for attack, altitude, material thickness, weather conditions etc. As *S. intricatus* is monogamous (Yates 1984), two individuals (male and female) are associated with a single maternal gallery. Thus, when we multiply the gallery density by two (i.e. 2 beetles per maternal gallery) and then by the surface area of the tree, we can estimate the number of colonizing *S. intricatus* per the trap tree. For example, in our experiment, we estimated that approximately 1804 *S. intricatus* beetles were removed from the environment (0.82 m.g./dm^2 * 2 * 1.100 dm^2). Based on our previous experiments and operational bark beetle population reduction programs, we estimate that an average of 15,400

beetles develop within one oak trap tree, which is 8.5 times greater than the colonizing population.

We recommend maintaining the use of oak trap trees, since we are for the time being not aware of other efficient measures against *S. inticatus* beyond using oak trap trees. So far, scientists have been unsuccessful in finding highly attractive aggregation pheromones for monitoring or mass trapping of this beetle species (Hovorka et al. 2005; Vrkočová et al. 1999, 2002; Galko et al. unpubl. data). In order for oak trap trees to be an effective population management tactic, they have to be processed before the next beetle generation emerges (Galko et al. 2009), and it is important that the use of trap trees in future is adapted to the life synchrony of the pest organisms in a warmer climate. If the processing of infested trees is neglected, especially if many trap trees are utilized, the population of *S. intricatus* can rise rapidly and lead to increased oak mortality. This is the main reason why the forest managers should also remove or treat recently fallen oak trees and logging residues to reduce bark beetle habitat and keep populations at endemic levels. Current forest protection standard for *S. intricatus* in Slovakia (Turčáni 2000) specify that oak trap trees have to be removed till 1 year after the setup, the new recommendation based on our results (experiences) and expected temperature increase is to remove oak trap trees 2 months after they have been established.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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