

# Invasive bark beetle *Dryocoetes himalayensis* (Coleoptera: Curculionidae: Scolytinae) – A threat for walnut trees (*Juglans* spp.) in Europe?

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## Funding information

Forests of the Czech Republic, Grant/Award Number: 84

## Abstract

As walnut trees (*Juglans* spp.) are of high economic importance, considerable attention has been given to invasive pests of these trees in Europe. In 2016, *Dryocoetes himalayensis* Strohmeier, 1908, an alien bark beetle originating from the Himalayas region of India, already present in several European countries, was confirmed to have attacked walnut trees in the Czech Republic. Within the present study, we (i) surveyed the current distribution of *D. himalayensis* in the Czech Republic, (ii) examined *D. himalayensis* phenology by rearing it in trap logs, and (iii) investigated tree level habitat preferences of the species in two study stands with 180 black walnut (*Juglans nigra* L.) trees and 66 common walnut (*Juglans regia* L.) trees sampled. The present study documented the species to be relatively widespread in some warmer lowland regions of the Czech Republic (42 localities found) and to reach high abundance locally. Almost 15 thousand *D. himalayensis* individuals reared from the trap logs showed the species emerging throughout the whole vegetation period with a distinctive peak in June. Even though the species is able to develop in thin stems (diameter <5 cm), it is most numerous in thicker trunk bases and also preferably attacks trees of higher diameters. The species preferred common walnut trees (its native host) with decreased vitality. In contrast, black walnut trees (North American species) were attacked regardless of their vitality, but the vitality of occupied trees successively decreased. Based on our results, *D. himalayensis* should be assumed as a considerable pest of walnut trees (particularly black walnuts), which might become of significant importance in its European invasive range in the future, and thus substantial attention should be given to it.

## KEYWORDS

bionomy, Czech Republic, invasive pest, *Juglans nigra*, *Juglans regia*

## 1 | INTRODUCTION

Globally, walnut trees (*Juglans* spp.) are undoubtedly of considerable economic importance. Among more than 20 distinguished walnut species (Bernard et al., 2018), the Common walnut (*Juglans regia* L.)

(hereinafter, referred to as CW) and Black walnut (*Juglans nigra* L.) (hereinafter, referred to as BW) are particularly significant. CW is cultivated primarily for its high-quality nuts (Pollegioni et al., 2017), and the nuts of this tree are the second most numerous produced nuts in the world (Shah et al., 2020). Correspondingly, CW originated from

a restricted range in southern parts of Europe and Asia and is currently planted throughout large parts of the temperate zone of all continents (Martinez et al., 2010). Thus, it is among the most widespread tree species in the world. Although CW is primarily planted for nutritionally valuable nuts, the tree and products from it (wood, chemical compounds, etc.) are of value in forestry, pest control, medicine, and culture (Abu Taha & Al-wadaan, 2011; de Rigo et al., 2016). BW is native to central and eastern parts of the United States of America (USA) with the centre of its area in Kentucky, Indiana, Illinois, Ohio and West Virginia, but currently is planted in other parts of North America and also in many (at least 14) countries in Europe. BW is planted mainly for its high-quality and very decorative wood. Its wood is considered as the aristocrat of fine hardwoods and is one of the most expensive in the USA and Europe. In addition to wood production, BW is of importance also for nuts in the USA (Nicolescu et al., 2020).

Invasive pathogens and pests represent a substantial threat to the production of plant commodities all over the world (Pimentel et al., 2005). In the case of woody plants, scolytid beetles (Coleoptera: Curculionidae: Scolytinae) undoubtedly are among the organisms that are capable of severely impacting production (Kirkendall & Faccoli, 2010). Invasive species of scolytid beetles with high aggressivity are capable of suppressing their host plant species throughout whole regions within a few years (Cullingham et al., 2011; Montecchio et al., 2016). Such a loss of production (and also costs of related plant protection measures) results in high financial damage and negative social impacts (Marchioro & Faccoli, 2021; Montecchio et al., 2016; Valenta et al., 2017).

As walnuts are typical for the presence of repellent and toxic compounds (e.g. juglone) in all parts of the plant, these tree species are largely not suitable for phytophagous and xylophagous insects (Islam & Widhalm, 2020). Thus, the spectrum of insect species using walnuts as a host tree is species-pure in both its native and introduced ranges and only a few species may be considered as pests (Katovich, 2004; Nicolescu et al., 2020). The husk maggot *Rhagoletis completa* Cresson, 1929 (Diptera: Tephritidae) and the walnut twig beetle *Pityophthorus juglandis* Blackman, 1928 (Coleoptera: Curculionidae: Scolytinae) are by far the most important pests of walnuts in past years. Both these species are native to North America, with an invasive range in Europe. Larvae of *R.completa* damage large portions of the CW nut crop (Duso & Dal Lago, 2006); and *P.juglandis* while developing under the bark in phloem is a vector of a serious pathogenic fungus, *Geosmithia morbida* (Kolařík et al., 2011). This fungus causes thousand canker diseases that lead to massive dieback of walnut trees, accompanied by huge financial losses (Cranshaw, 2011; Randolph et al., 2013). Consequently, both *R.completa* and *P.juglandis* have been labelled as quarantine pests by the European and Mediterranean Plant Protection Organization (EPPO). *Rhagoletis completa* was added to the A1/A2 List of pests recommended for regulation as quarantine pests in 1975 and deleted in 1996; *P.juglandis* was added to the A2 List in 2015 (Eppo, 2023a, 2023b). Besides *P.juglandis*, only *Xylosandrus germanus* (Blandford, 1894) (Coleoptera: Curculionidae: Scolytinae) (reported from the USA by Katovich (2004)) and *Trirachys sartus* (Solsky,

1871) (Coleoptera: Cerambycidae) (reported from Central Asia by Hayat (2022)) are mentioned as considerable bark and wood-boring insect pests of walnuts.

In connection with monitoring a possible spread of *P.juglandis* to the Czech Republic, an increased effort was given to surveying phloeophagous insects colonizing walnuts in recent years. Hence, several BW trees attacked by *Dryocoetes himalayensis* Strohmeier, 1908 (Coleoptera: Curculionidae: Scolytinae) (hereinafter, referred to as DH) were recorded in the southeast part of the Czech Republic in 2016 (Foit et al., 2017). This report represented the first information regarding DH host trees and breeding ecology in its introduced range. This scolytid beetle is native to a restricted range in the Himalayas (India), where it was reported to develop in CW and *Pyrus lanata* D. Don (Wood & Bright, 1992). The species was introduced to Europe in the 1970s and was recorded for the first time in the Czech Republic in 2009 (Knížek, 2011). Surprisingly, it took about 50 years until any host tree of this species was found in its European invasive range. According to Foit et al. (2017), DH developed in lower trunk parts of weakened but still living BW and the presence of the galleries was associated with dark brown (almost black) fluid oozing from entrance holes, while the gallery systems were usually surrounded by dark brown to black necrotic areas, presumed to be caused by an associated fungus. Recently, DH is known from several European countries (Austria, Czech Republic, France, Germany, Slovakia, and Switzerland) and as presumed the species is probably spreading in some regions (Procházka et al., 2018). Additionally, it was documented that DH is able to attack all walnut species in Europe (i.e., BW and CW) (Barnouin et al., 2020), which means a potential economic threat. Although the planting of walnut trees in Europe is currently considered to be threatened mainly by *P.juglandis* and the associated fungus *G.morbida*, distribution of this species is still limited to specific regions of Italy (Montecchio et al., 2016) and France (Saurat et al., 2023). In contrast, DH is present and already naturalized in several European countries (Procházka et al., 2018) and thus may be a threat to walnut tree planting over vast areas.

Although our knowledge on the life history of DH as well as other species from the genus *Dryocoetes* is limited, interesting findings might be inferred from a comparison of these species. To the best of our knowledge, all the *Dryocoetes* species living in Holarctic and Oriental regions (i.e., 46 species) might be characterized as follows: phloeophagous species developing under the bark, colonizing mainly dying or dead lower parts of both coniferous and broadleaf trees (particular species are usually oligophagous), they are polygamous and are not pests of economic significance (Pfeffer, 1955; Smith & Hulcr, 2015). Only the species *Dryocoetes confusus* Swaine, 1912, with its associated pathogenic fungi, has been reported to cause dieback of living trees (*Abies* spp.) in considerable numbers (Garbutt, 1992; Smith & Hulcr, 2015). The current state of knowledge on DH bionomy suggests that the species represents an exception among other species of the genus *Dryocoetes*; and it may possess higher aggressivity, similar to *D.confusus*. Hence, along with presumably increased physiological stress of trees associated with ongoing climate change (Allen et al., 2010), DH might exhibit as an important pest of walnut trees in the future.

Having a good knowledge of DH distribution and its life history (habitat requirement, phenology, population dynamics, antagonists, etc.) is a necessary prerequisite for decisive risk assessment associated with DH, as well as for specification of effective measures for the pest's control. Unfortunately, except for some very basic information (Barnouin et al., 2020; Foit et al., 2017), detailed knowledge of DH bionomy is missing. Thus, the present study aimed to bring first systematic research of DH distribution and bionomy, dealing with following issues:

- (i) Current distribution of DH in the Czech Republic.
- (ii) Phenology of DH emergence.
- (iii) Tree level habitat requirements of DH.
- (iv) Assessment of DH impact on walnut dieback.

## 2 | METHODS

### 2.1 | Mapping the current distribution of DH in the Czech Republic

Various resources were compiled to obtain a database of known localities of DH occurrence in the Czech Republic. Based on that, the current distribution of the species was visualized in a map (Figure 1).

As a first step, already published records of the species from the Czech Republic were excerpted: first accidental records published by Knížek (2011); later another locality of the species published by Foit et al. (2017) and Procházka et al. (2018) published several new localities where the species was captured in flight-intercept and light traps; and finally Knížek and Kopecký (2021) for first time reported the species from the Bohemian part of the Czech Republic. Additionally, some data on DH distribution were gathered from unpublished results of saproxylic beetle surveys using flight-intercept traps (for author names of these records see Appendix S1). Furthermore, within the present study, known localities with declining BW and CW trees were actively visited and checked for the presence of DH.

### 2.2 | Phenology of DH emergence

To further specify knowledge on DH distribution and mainly to describe its emergence phenology, we selected 15 localities with possible occurrence of DH across South and Central Moravia, Czech Republic, and checked for the presence of the species using trap trees during 2017–2022 (Appendix S1). All the selected localities were forest stands with dominance of BW (>90%), but two different types of forest sites were represented: (i) lowland floodplain sites

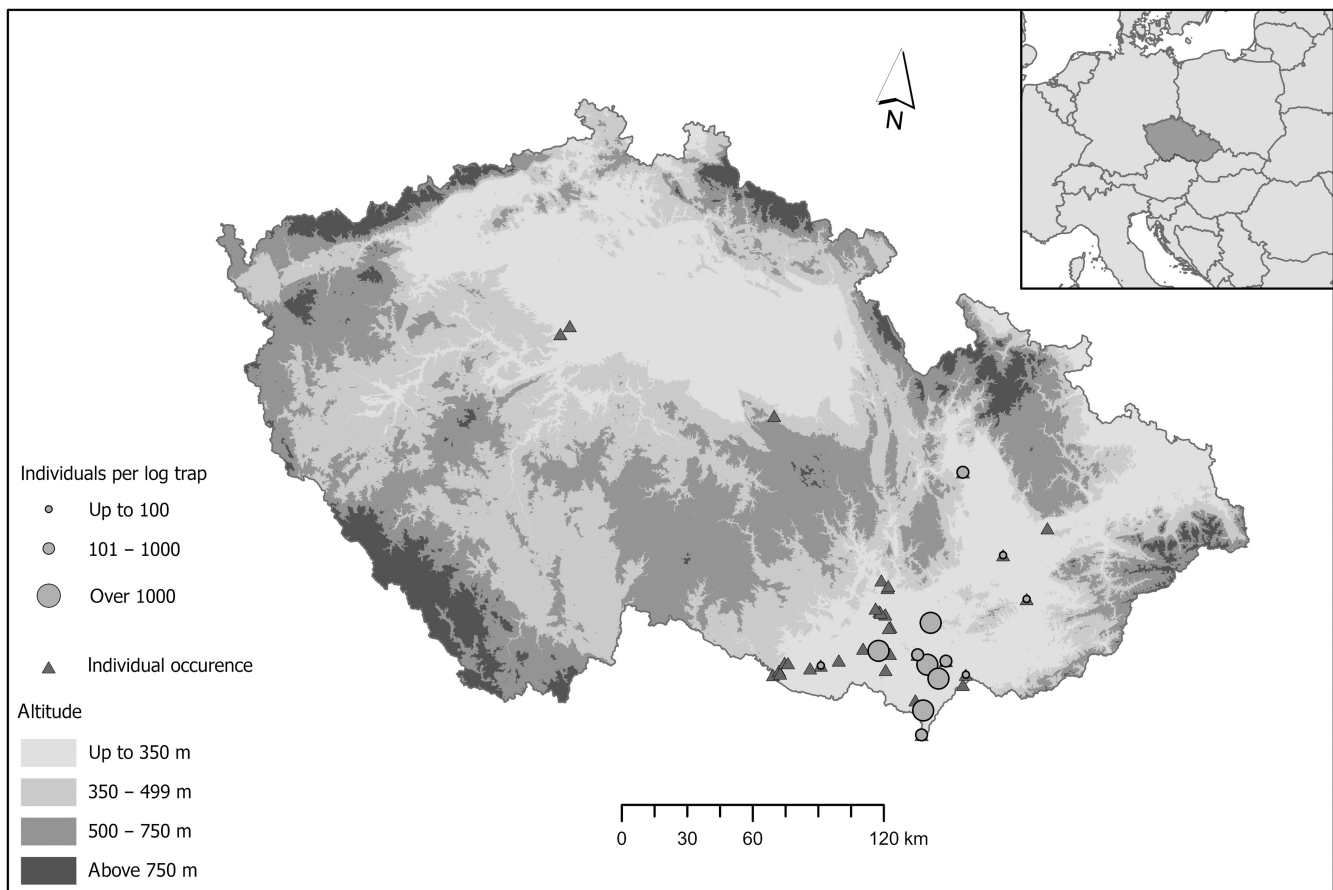


FIGURE 1 Map of known occurrence of the bark beetle *Dryocoetes himalayensis* in the Czech Republic in years 2009–2022.

(170–250 m.a.s.l.) and (ii) mesic sites on hilly terrain (190–310 m.a.s.l.). Two (or three) trap trees were felled at each locality (in total, 36 trap trees were felled). Trap trees were exposed from April to September. Subsequently (during October and November), one-metre-long logs were sampled from each trap tree and put into photoelectors located outdoors under a roof in shady conditions. Logs were sampled from three different parts of trap trees: (i) trunk base (diameter = 20–25 cm), (ii) the middle part of the trunk (diameter = 7–15 cm), and (iii) trunk in crown and branches (diameter = 2–7 cm). As a result, three photoelectors were gained from each locality, i.e., one photoelector per sampled tree part. During the following approx. 12 months (until the following October), emerging beetles were captured in jars with 70% ethanol as conservation liquid; the jars were emptied and renewed every 10–14 days. All the captured beetles were subsequently identified and counted. Counts of logs placed in each photoelector and their diameters were recorded. In total, 50 photoelectors were employed for rearing DH.

### 2.3 | Tree level habitat requirement of DH

To study tree level habitat requirements of DH, two study stands (Blučina for BW and CW, and Břežany for CW; Appendix S1) were investigated in South Moravia (Czech Republic) during June and July 2021. Both localities represent isolated patches of woodland with an area of approx. 25 ha in an intensive agricultural landscape. The stands are situated in zones of mesic oak woodlands at an altitude of 250–300 m.a.s.l. Both study stands are mature mixed broadleaf forests with closed canopy of diverse tree species composition represented by oaks (*Quercus* spp.), ashes (*Fraxinus* spp.), limes (*Tilia* spp.) and also invasive species such as black locust (*Robinia pseudacacia* L.) and boxelder maple (*Acer negundo* L.). Of course, BW and CW have a remarkable representation in the Blučina and Břežany localities, respectively. However, the main canopy of the stands, an even-aged understorey composed of shrubs (mainly *Prunus spinosa* L. and *Sambucus nigra* L.) and young trees, is noticeably developed. Forest stands in the area are traditionally managed in a clear-cutting system and prevailing artificial regeneration.

In each study stand, every second walnut tree with diameter in breast height (dbh) > 5 cm was examined for the presence of DH and characterized by a set of parameters, i.e., approximately half of the present sufficiently-grown walnut trees were sampled. In total, 246 walnut trees (180 BW and 66 CW) were sampled. The presence of DH was examined based on the presence of its galleries and adults at the trunk base up to 2.5 m above ground. Dbh was measured for each sampled tree. The tree position in stand (edge/interior) and its social status (dominant tree/co-dominant tree/suppressed tree) were recorded. Furthermore, any decline in the tree's vitality (hereinafter, "tree vitality") was evaluated by distinguishing among five degrees: (0) highly vital tree; (1) tree with slightly reduced vitality (growth stagnation, dieback of peripheral branches); (2) tree with significantly reduced vitality (tree crown recession, dieback of terminal part of crown); (3) tree with residual vitality (most of the crown

dead); and (4) dead tree. Presence of breakage of the trunk or primary branch with diameter  $\geq 1/3$  of the tree's breast height diameter ("breakage") was recorded. Further parameters were recorded only for the basal part of the trunk (to 2.5 m above ground): sun exposure; bark roughness; tree damage; trunk blaze; other species galleries; and dark oozing. Sun exposure was evaluated on a 4-point scale according to the estimated percentage of trunk circumference exposed to the sun: completely in shade (0%–25%); mostly in shade (25%–50%); half-exposed to sun (50%–75%); and completely exposed to sun (75%–100%). Bark roughness was estimated on a 3-point scale (smooth; medium – grooves under 1.5 cm of depth; rough – grooves deeper than 1.5 cm). Other trunk damages were evaluated on a 3-point scale according to presence and extent of checks, cracks, callus, etc. (none; moderate – affected surface area < 100 cm<sup>2</sup>; serious – affected surface area > 100 cm<sup>2</sup>). Trunk blaze was measured as total surface area of the trunk parts without bark (with a precision of 25 cm<sup>2</sup>). Additionally, the presence or absence of other species galleries (i.e., presence of galleries of other bark and wood-boring insects) and dark oozing from the bark (only dark oozing not associated with DH infestation was recorded).

### 2.4 | DH – Assessment of pest importance

Finally, we tried to summarize the available knowledge on DH (distribution and ecology) to evaluate to what extent the species might be a threat for walnut trees in the Czech Republic (or its European invasive range). In order to get additional data on the species contribution to walnut decline, a case study was conducted at the Blučina locality on BW trees. The same set of BW trees (180 trees) that was used within a habitat requirement study realized in 2021 (see above) was resampled for presence of DH and tree vitality 1 year later in 2022 (162 resampled, 18 trees not found). To minimize bias in tree vitality estimation, the sampling was done by the same person and in the same part of the vegetation period (July–August).

To assess whether DH might be a threat also for broadleaf tree species other than walnuts, we selected one locality with a documented abundant occurrence of DH (Rajhrad – see Appendix S1) and set two BW and two oak (*Quercus robur* L.) trap trees next to each other. The trap trees were of similar size (dbh around 25 cm) and exposed for colonization from April to October. Furthermore, these trees were put into photoelectors and examined for emerging beetles in the same way as described above (Phenology of DH emergence).

### 2.5 | Statistical analysis

The importance of explanatory variables within the studies of Phenology of DH emergence and Tree level habitat requirement of DH was evaluated by implementing a random forest algorithm utilizing conditional inference trees as base learners provided in the party package (function `cforest`, 10,000 trees generated) in R 4.0.2

software. This method was used because it is a highly effective method of evaluating the importance of explanatory variables: it can manage different types of variables, and is robust to the multicollinearity of variables (Strobl et al., 2008). Since certain tested explanatory variables exhibited multicollinearity in our dataset, a conditional computation of the importance was performed (option `conditional=TRUE`). In addition, an unbiased random forest model was constructed (option `control=cforest_unbiased()`) because the tested predictors were both quantitative and categorical variables. Subsequently, the statistical significance ( $\alpha=0.05$ ) of the explanatory variables was evaluated using the permutation-based attribute selection algorithm provided in the *Boruta* package. In the case of the phenology study, the response variable entering the model was represented by the number of DH in particular samples (sample=catch of particular photoelector during one capture interval, i.e., 10–14 days; see above). In the case of the tree level habitat requirement study, the response variable was just the presence/absence of DH on the sampled trees. Subsequently, effects of significant explanatory variables were illustrated by separate figures. For categorical variables, simple mean values of the species abundance or frequency of the species occurrence  $\pm$  standard errors (SE) were shown; for numerical variables, scatter plots showing the original data were accompanied by regression curves with marked 95% confidence interval. Regression curves were fitted using generalized linear models (GLM) with Poisson distribution for count data in the study of phenology, and binomial distribution for the presence/absence data in the habitat requirement study. GLM analyses and construction of plots were also performed in R 4.0.2 software.

### 3 | RESULTS

#### 3.1 | Mapping the current distribution of DH in the Czech Republic

To date, DH has been confirmed to occur at 42 localities in the Czech Republic (Figure 1). All the known localities are below 500 m a.s.l., most of them (81%) lower than 300 m (Appendix S1). Present localities with DH occurrence are scattered over an extensive part of Moravia and in Central Bohemia. The species has not been recorded in Northern Moravia nor the major part of Bohemia yet. Warm parts of Southern Moravia, with 86% of the known DH occurrences in the Czech Republic, represent the centre of its occurrence. DH has been found to occur across different habitats, including various forest habitats (12 localities in floodplain forests, 11 localities in mesic forests, and 10 localities in xeric forests), and urban habitats in both cities and villages (nine localities in urban parks, tree lines, gardens, etc.). Forest localities were mostly associated with the occurrence of DH on BW (BW trees attacked by DH were documented only in forest habitats). In contrast, CW was more frequently attacked by the species in urban habitats, less frequently in forests. Higher densities of the species

as represented by considerable numbers of colonized trees were documented in floodplain and mesic forests, where about 10 or in one case even more than 100 colonized trees could be found in a single stand. Only individual colonized trees were found in xeric forests and urban habitats (Appendix S1).

#### 3.2 | Phenology of DH emergence

During the study based on rearing DH from sample logs of BW, the presence of the species was confirmed at 13 of 15 sampled localities, with 14,711 DH individuals in total. In positive localities, the number of reared DH individuals ranged from 1 to 6493 (Appendix S1). All the tested variables exhibited significant effect on the number of the species' individuals emerging from the logs (Figure 2a). Locality was found to have by far the biggest explanatory power. Also, a profound effect of the calendar month was observed. However, the species was emerging throughout the vegetation period (March–October), with remarkable unimodal distribution of its abundance reaching the peak in June (Figure 2b). The diameter of the sampled logs affected abundance of the species less remarkably but still significantly (Figure 2a), and rather weak effects were found in the case of calendar year and area of the sample logs' mantle (Figure 2a). While the species was found to develop also in twigs of only 2 cm diameter in two cases, its abundance was obviously higher in thicker logs (Figure 2c).

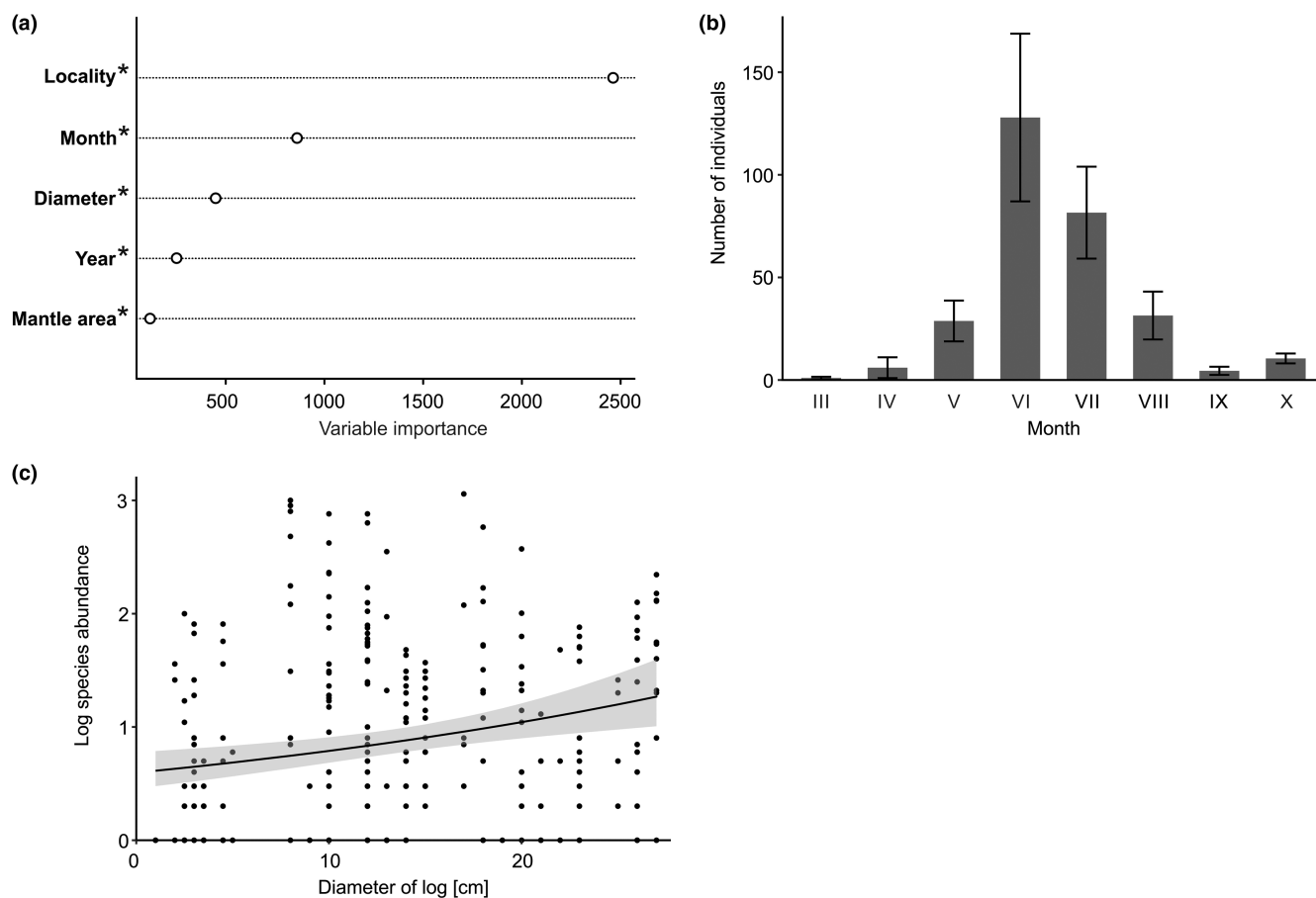
#### 3.3 | Tree level habitat requirement of DH

Within investigation of tree level habitat requirement of DH, 100 of 180 (56%) sampled BW, and 20 of 66 (30%) sampled CW were infested by DH. In the case of BW, the presence of DH (i.e., infestation of trees by the species) was significantly affected only by trunk diameter (Figure 3a) and considerably higher probability of species occurrence was observed on trees of bigger diameter (Figure 3b). Other tested predictors, including tree vitality, were virtually of no importance in BW. In the case of CW, probability of tree infestation by DH was affected mainly by tree vitality (Figure 4a), and probability of tree infestation increased with declining tree vitality (Figure 4b). While almost all the sampled freshly dead trees and trees with only residual vitality were occupied by the species, in more vital trees (categories 0–2) the mean frequency of occupancy was below 22%. Similarly, as in BW, probability of CW trees infestation by DH was also significantly affected by trunk diameter with probability increasing with bigger diameter (Figure 4c). Finally, infestation of CW by DH was slightly but still significantly associated with more serious trunk damage (Figure 4d).

#### 3.4 | DH – Assessment of pest importance

In the BW study stand, where the habitat requirements of DH were investigated, we confirmed significant year-on-year increase in the





**FIGURE 2** Results of random forest regression of numbers of *Dryocoetes himalayensis* individuals emerging from black walnut logs: (a) variable importance plot (based on the decrease of mean model accuracy with omission of the variable) showing the importance of particular variables for the presence of *D. himalayensis*. Variables with a significant effect ( $p < 0.05$ ) are highlighted with asterisk characters and particular effects of these variables on number of emerging species' individuals are shown on figures (b) and (c). (b) Mean values of counts of emerging individual  $\pm$  standard errors (SE) in particular calendar months are shown; (c) scatter plot of association between diameter of the log and log<sub>10</sub>-transformed number of emerging species' individuals accompanied by a regression curve with marked 95% confidence interval.

proportion of trees infected by the species, from 56% in 2021 to 85% in 2022 (McNemar's chi-squared = 39.024,  $df = 1$ ,  $p < 0.001$ ), and also successive decline in the vitality of the sampled trees, with mean tree vitality value 1.4 in 2021 and 1.6 in 2022 (Wilcoxon signed rank test with continuity correction:  $V = 180$ ,  $p < 0.001$ ).

In the experiment testing attractivity of other broadleaf tree species for DH, the species densely colonized BW trap trees but no individual of DH was found to colonize neighbouring oak trap trees.

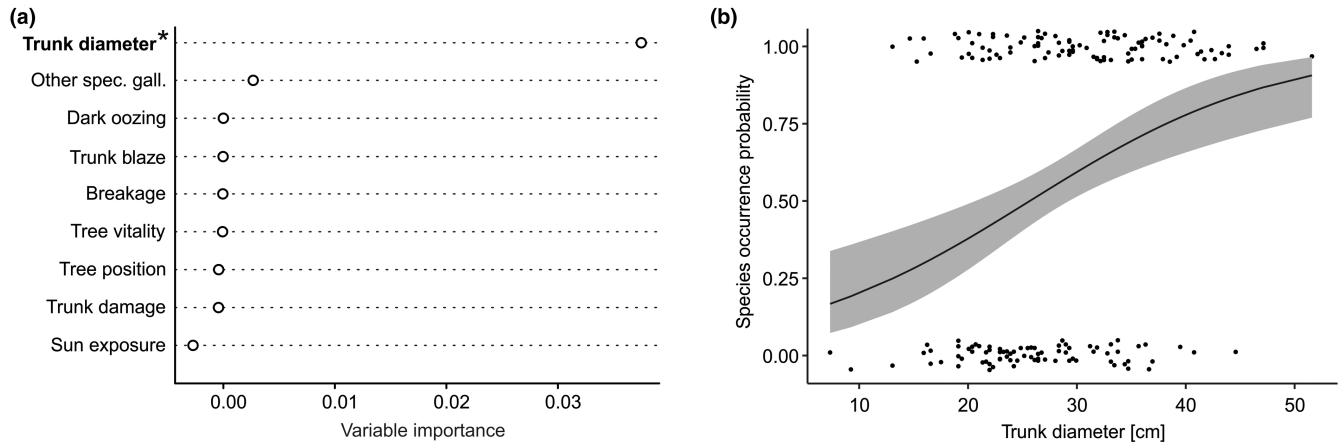
## 4 | DISCUSSION

The present study documented that DH is distributed over a substantial part of the Czech Republic, but its occurrence largely bound to regions in lower altitudes with warmer climate. We found that both BW and CW trees growing in forest or urban habitats might be attacked by DH. Adult DH beetles were documented to emerge throughout the whole vegetation period (March–October) with a considerable peak in June. Although even thin trees (dbh = 6 cm) can

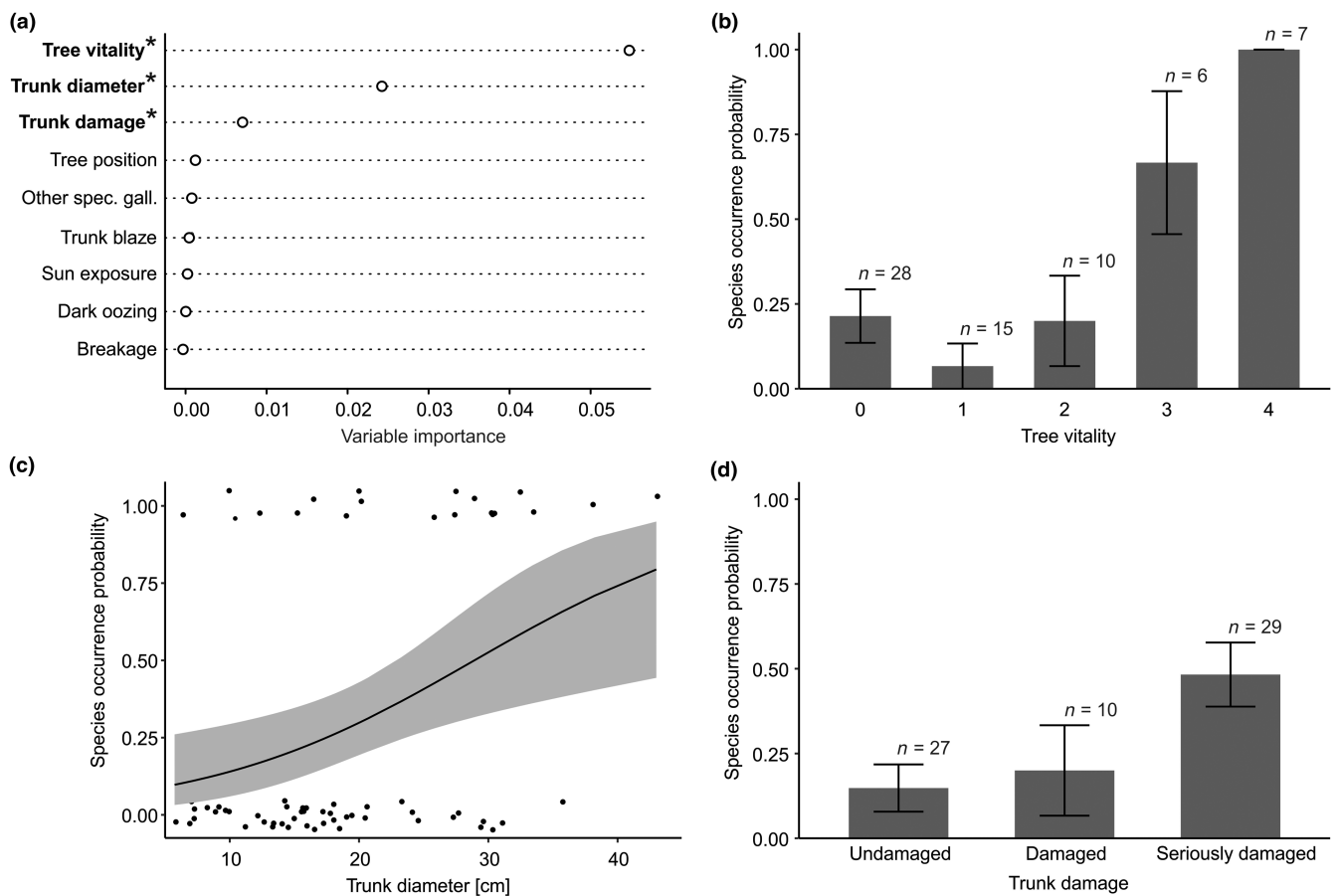
be attacked by DH, trees with bigger dbh are preferred. While dbh was the only factor found to affect probability of BW tree colonization by DH, trees with decreased vitality and trunk injuries were significantly preferred in the case of CW. This suggests more efficient defence/repellent mechanisms against DH in the case of CW that might have been obtained during coevolution of these species (CW is an indigenous DH host tree). In general, results of the present study point out that DH might become a pest of significant importance and hence the need for additional studies.

### 4.1 | Current distribution of DH in the Czech Republic, type of habitat

DH, an alien and invasive species in Europe, is already known to be present in several European countries, but our knowledge on the distribution of this species is mostly based on individual captures (Procházka et al., 2018). Surprisingly, the present study documented the species is rather widespread and numerous in certain areas of



**FIGURE 3** Results of random forest regression of occurrence of *Dryocoetes himalayensis* on black walnut trees: (a) variable importance plot (based on the decrease of mean model accuracy with omission of the variable) showing the importance of particular variables for the presence of *D. himalayensis*. Variables with a significant effect ( $p < 0.05$ ) are highlighted with asterisk characters. The significant effect of tree diameter (figure b) is illustrated by a scatter plot showing the original presence/absence data accompanied by a regression curve with marked 95% confidence interval.



**FIGURE 4** Results of random forest regression of occurrence of *Dryocoetes himalayensis* on common walnut trees: (a) variable importance plot (based on the decrease of mean model accuracy with omission of the variable) showing the importance of particular variables for the presence of *D. himalayensis*. Variables with a significant effect ( $p < 0.05$ ) are highlighted with asterisk characters, and particular effects of these variables on the probability of the species' occurrence are shown (b–d). For categorical variables (b, d), mean values of frequency of the species' occurrence  $\pm$  standard errors (SE) and number of samples are shown for particular categories. For tree diameter (c), a scatter plot showing original presence/absence data accompanied by a regression curve with marked 95% confidence interval is used.

the Czech Republic. The species seems to be distributed mainly in lower altitudes of warmer regions (below 500 m a.s.l.), which corresponds more or less to the altitude range of walnut planting in the Czech Republic, which is mostly below 600 m a.s.l. Thus, in Central Europe, DH is probably associated with warmer regions of lower altitude; in Southern Europe with its generally warmer climate, it has been recorded also at higher altitudes, such as the foothills of the Alps in France (Barnouin et al., 2020). The preference of DH for climatically warmer areas corresponds to the humid subtropical to moderate mountain climate in its original range in the Himalayan regions of India (Utar Pradesh) (Wood & Bright, 1992). In correspondence with the humid climate in DH's original range, the results of the present study suggest DH rather avoids xeric habitats, and the species was found to be the most numerous in floodplain forests. Generally, species of *Dryocoetes* genus are known to prefer very humid subcortical space, as has been reported in the case of the North American species *D. betulae* (Furniss & Kegley, 2006) and *D. confusus* (Negron & Popp, 2009) as well as the European species *D. autographus* (Pfeffer, 1955). Overall, invasive range expansion through Southern Europe and lowlands corresponds well to patterns of invasion of many other invasive bark beetles in Europe (Kirkendall & Faccoli, 2010).

Within its European invasive range, DH has been documented to develop in BW and CW (Barnouin et al., 2020; Foit et al., 2017). Within the present study, DH developed in CW mainly in urban habitats and much less frequently in forests; in contrast, development in BW was found only in forests. This rather distinctive pattern simply reflects distribution of these walnut species among habitats in the Czech Republic, where CW is planted mostly in gardens, parks, orchards, and tree lines for its nuts; whereas BW is planted mainly in forest stands for high-quality wood and only exceptionally as an ornamental tree in several parks.

## 4.2 | Phenology of DH emergence

The phenology of the DH life cycle has remained largely unknown; the knowledge to date could be summarized that in Central Europe, imagoes of the species occur during the summer period (Barnouin et al., 2020; Foit et al., 2017; Procházka et al., 2018). Thus, the present study, reporting the first systematic data on the species phenology, documented that DH emerges throughout the whole vegetation period, i.e., from March to October, reaching the peak of abundance in June. These findings indicate that the species has likely one generation per year, and the development is not apparently synchronized. Also records of DH imagoes under bark throughout the year (authors' observations) are in line with this. A similarly long period of emergence has been documented also in North American *D. betulae* (Furniss & Kegley, 2006) and *D. confusus* (Negron & Popp, 2009). In the case of *D. betulae*, the long emergence period is associated with successive colonization of a particular tree stem by several generations without dispersal (Furniss & Kegley, 2006). According to our observations, this might

be the case of DH as well. In the case of *D. confusus*, a two-year development of the part of population was claimed to underlie the observed prolonged period of emergence (Negron & Popp, 2009). However, patterns of DH emergence from the trap logs in the present study suggest this is not the case.

## 4.3 | Tree level habitat requirement of DH

Characteristics of a particular tree individual such as age, size, vitality, sun-exposure, injury, etc., are known to affect the probability of colonization and success of development of any saproxylic insect (Albert et al., 2012; Åström et al., 2013; Foit et al., 2016). The present study examined characteristics of host trees that affect the probability of being colonized by DH. Surprisingly, our study revealed that such characteristics differed considerably between the two host tree species, despite both being members of the same genus, *Juglans*. Whereas in the case of CW, the probability of its colonization was affected by the tree vitality, diameter, and damage; for BW, diameter was the only significant variable.

In the present study, the probability of colonization of trees by DH increased with higher dbh in both studied host tree species. Correspondingly, within the BW trap log experiment, higher numbers of individuals emerged from trunk sections with higher diameter, although even thin stems and branches (diameter  $\geq 2$  cm) were colonized. However, in the case of trap logs, higher numbers of individual emerging from thicker stems could rather reflect its bigger mantle (i.e., subcortical space for development) than preference for thicker material. Overall, DH exhibits a certain level of preference for bigger diameter and likely more rough bark, which is in line with the known bionomy of other members of the genus *Dryocoetes* that are known to colonize mainly lower, thicker parts of trunks with coarse bark (Furniss & Kegley, 2006; Negron & Popp, 2009; Pfeffer, 1955).

In contrast to BW, the probability of CW colonization by DH was most strongly affected by the tree vitality. Although the species strongly preferred host trees with residual vitality or freshly dead trees, vital trees were colonized in some cases as well. This pattern of preference for host tree vitality fits into a common strategy of secondary "facultative parasites" that usually develop in weakened and dying trees but are capable of colonizing even vital trees if reaching high population densities (Lieutier et al., 2009; Raffa, 1993). Furthermore, the probability of occurrence of DH on CW was higher on trees with trunk damage. Such injuries might promote tree colonization by DH through associated overall decline in tree vitality or by formation of a locally preferable subcortical microhabitat adjacent to the injury. It has been documented that some specific microhabitats of saproxylic beetles are often associated with injuries such as bark scratch, breakage, or cut branches (Kašák & Foit, 2018; Šebek et al., 2013). In the present study, the majority of trunk damage were wounds after cuts of thick branches.

As mentioned above, CW with trunk damage and decreased vitality were preferably colonized by DH in our study, whereas BW



were attacked by the species regardless of vitality or damage. Since the majority of saproxylic insects within their host selection seem not to distinguish among closely related host trees from the same genus, our finding is surprising (Milberg et al., 2014; Sláma, 1998). On the other hand, in some saproxylic beetles, a significant preference for certain host tree species within a genus was documented (Plátek et al., 2019). This is the case of the European longhorn beetle *Cerambyx cerdo* which develops in oak species (*Quercus* sp.) native to Europe more often than in the introduced American species (Oleksa & Klejdysz, 2017). The different patterns of host selection by DH that have been observed in the case of BW and CW in the present study might arise from the coevolution of DH with CW. Native ranges of CW and DH overlap, and CW is known to serve as a host tree in the DH native range (Wood & Bright, 1992). Thus, CW defence mechanisms as well as host selection mechanisms of DH might have adapted during their coevolutionary interactions (Gossner et al., 2009; Ulyshen et al., 2018). In contrast, North American BW, without a coevolutionary history with DH, can exhibit as evolutionary naive without effective defence mechanisms against the Asian bark beetle, and DH might struggle to distinguish precisely tree vitality or injuries in BW at the same time (Cudmore et al., 2010). Similarly, new host species in the invasive range of some other saproxylic beetles were documented to be evolutionary naive, performing weak defence reactions (Cudmore et al., 2010; Fiala et al., 2020; Jendek et al., 2018).

## 5 | CONCLUSION, ASSESSMENT OF THE PEST'S IMPORTANCE

According to the observed pattern of DH selection for the vitality of its native host tree (CW), DH should be considered as a relatively aggressive secondary pest, i.e., a "facultative parasite" to "near obligate parasite" according to Raffa (1993). Such pest species might become especially significant threats to trees if the insects reach high population density or host trees are weakened by drought, defoliators, pathogens, etc. (Lieutier, 2004). DH might represent a threat especially to BW, because this host tree species was colonized by DH regardless of its vitality in the present study.

Within our study, DH presence was associated with dark brown (almost black) fluid oozing from entrance holes and the gallery systems were usually surrounded by dark brown to black necrotic areas, which are assumed to be caused by an associated fungus. A variety of fungi are known to be associated with bark beetles with various kinds and tightness of mutual relations (Kirisits, 2004; Six, 2012). Several species of bark beetles were documented to be associated with pathogenic ophiostomatoid fungi that help the beetles to overwhelm tree defence mechanisms (Kirisits, 2004; Lieutier et al., 2009). Even within the *Dryocoetes* genus, a species *D. confusus* was reported to use associated fungus in a process of overcoming tree defences (Negron & Popp, 2009). Thus, DH is likely associated with an ophiostomatoid fungus as well, which might contribute to the capability of DH to colonize more vital trees.

Within the present study, we surveyed year-on-year changes in the case of a BW stand with occurrence of DH. There was a significant increase in the portion of trees colonized by DH (by 26%) and the vitality of trees already colonized slightly declined. Hence, DH is likely capable of successively colonizing almost all available host trees in a forest stand, but the process of dieback of the trees colonized by DH is slow (taking up to several years). This is in contrast to the majority of tree-killing bark beetle species such as members of the *Ips* or *Dendroctonus* genus, which achieve successful colonization of host trees by overwhelming host tree defences via an aggregated massive attack, leading to quick tree death within weeks or months (Lieutier et al., 2009). The impact of DH attack on walnut trees rather resembles the progression of infestation of these trees by *P.juglandis* associated with the fungus *G.morbida*, where trees withstand several years before dieback (Bracalini et al., 2023). Thus, rather than the aforementioned strategy of overwhelming tree defences by aggregated attack, DH might use the strategy of avoiding host defences, which is typical of "true parasites" (e.g. *Dendroctonus micans* [Kugelann, 1794]; Lieutier et al., 2009; Raffa, 1993).

The observed slow decline of walnut trees that are colonized by DH is in line with our observations of its slow, successive, and scattered pattern of colonization of the tree trunks. A similar pattern of tree colonization was described in the North American relative species *D.betulae*, where several successive generations colonize host tree trunk without flight dispersal, and thus most of the available subcortical space is exploited step-by-step within a few years (Furniss & Kegley, 2006). DH might use the same strategy of source utilization, which would well correspond to its unsynchronised emergence, with imagoes emerging throughout the whole vegetation period.

It is not yet clear if DH can also attack tree species other than walnuts. Before DH development in walnuts was evidenced (Foit et al., 2017), its host tree species in the European invasive range had been unknown. Since DH was most frequently recorded in oak woodlands, its development in oaks was presumed (Knížek, 2011). As there are no reliably documented records of DH development in oaks and no DH individuals were found to colonize oak trap trees in our experiment, we consider development of DH in oaks to be highly improbable. Quite frequent captures of DH in oak forests thus represent individuals just dispersing from nearby walnut trees (dispersed walnut trees can be found in most oakwood localities with recorded occurrence of DH; Procházka et al., 2018). Thus, DH most likely does not represent a threat for oaks and probably neither for any other tree species than walnuts in Europe.

In conclusion, DH can be designated as a considerable pest of walnut trees, which might become of significant importance in its European invasive range in the future with BW, a North American walnut tree species, being especially susceptible. Although striking damage known in conventional tree-killing bark beetles (extensive outbreaks causing large infestation patches and fast dieback of whole stands) is improbable, DH can cause (or contribute to) a slow and gradual but possibly extensive dieback of walnuts. However, the degree to which DH is really able to cause damage to a vital walnut

tree is questionable, and should be investigated in future studies in detail. Said future studies should also focus on the species' associates, above all fungi.

## AUTHOR CONTRIBUTIONS

**Kašák Josef:** Data curation; investigation; writing – original draft preparation; writing – review and editing; methodology; supervision. **Holuša Otakar:** Data curation; conceptualization; writing – review and editing; funding acquisition; investigation; methodology; project administration. **Foit Jiří:** Methodology; data curation; writing – original draft; writing – review and editing; formal analysis; investigation; visualization.

## ACKNOWLEDGEMENTS

The data of this paper was gathered within the framework of the research project of the Grant Agency of Forests of the Czech Republic, a state enterprise: “Pests and diseases of the black walnut (*Juglans nigra* L.) and possibilities of its cultivation in the Czech Republic”. We are grateful to L. Floková for map creation, M. Stražil for substantial help in the field, J. Holuša and T. Fiala for provided data and last but not least Matthew Sweney for English proofreading.

## FUNDING INFORMATION

Forests of the Czech Republic, a state enterprise (84).

## CONFLICT OF INTEREST STATEMENT

The authors declare they have no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Whole data for distribution is provided in Appendix S1. The dataset for studied species phenology, habitat requirement, and impact on trees is available on the following link: <https://zenodo.org/record/8113196>.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**How to cite this article:** Kašák, J., Holuša, O., & Foit, J. (2023). Invasive bark beetle *Dryocoetes himalayensis* (Coleoptera: Curculionidae: Scolytinae) – A threat for walnut trees (*Juglans* spp.) in Europe? *Journal of Applied Entomology*, *147*, 941–952. <https://doi.org/10.1111/jen.13190>