EUROPEAN JOURNAL OF ENTOMOLOGY
ISSN (online): 1802-8829
http://www.eje.cz
Eur. J. Entomol. **122**: 302–307, 2025
doi: 10.14411/eje.2025.034
ORIGINAL ARTICLE

Temporal and spatial variation of *Xylosandrus germanus* (Coleoptera: Curculionidae: Scolytinae) captures in lowland forests: Positive effect of tree species diversity on the abundance of an invasive ambrosia beetle

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Key words. Black stem borer, Xyleborini, invasive species, flight activity, ethanol, Slovakia

Abstract. Invasive ambrosia beetles, such as the black stem borer (*Xylosandrus germanus*), pose serious ecological and economic threats to various natural, semi-natural and artificial ecosystems with suitable host plants. This study investigates the temporal and spatial variation in *X. germanus* abundance within lowland, mostly oak-dominated forests of the West Carpathians, focusing on the influence of tree species diversity, altitude, and forest stand age. Our findings reveal a strong positive correlation between tree diversity and *X. germanus* abundance, suggesting that diverse forests provide favourable conditions for beetle establishment. Altitude also exhibited a significant positive effect, likely due to increasing humidity and more suitable microclimatic conditions at higher elevations. In contrast, forest age had a small but significant negative effect, potentially due to reduced availability of stressed host trees in older stands. Beetle activity peaked in early to mid-June, in agreement with previous observations of phenology of this species in Central Europe. These findings contribute to our understanding of the ecological factors shaping *X. germanus* populations and provide valuable insights for forest management strategies aimed at mitigating the spread of invasive ambrosia beetles.

INTRODUCTION

Many bark and ambrosia beetle (Coleoptera: Curculionidae: Scolytinae) species pose a significant threat to forests and various types of agroecosystems worldwide (Ploetz et al., 2013; Biedermann et al., 2019). Unlike "typical" bark beetles, which are phloephagous, roughly half of all members of Scolytinae are xylomycetophagous – they bore into the wood of host trees where they cultivate symbiotic (ambrosia) fungi as a source of nutrition for both larvae and adults (Batra, 1963; Biedermann & Taborsky, 2011; Bussler et al., 2011; Dzurenko & Hulcr, 2022). Fungus-cultivating Scolytinae, also called ambrosia beetles, are becoming increasingly problematic as invasive pests. The most successful and widespread ambrosia beetle invaders comprise the clade Xyleborini (Smith & Hulcr, 2015; Hulcr & Stelinski, 2017; Gomez et al., 2018). Apart from the cryptic lifestyle and fungal mutualism characteristic of all ambrosia beetles, xyleborines have a curious breeding system (haplodiploidy and extreme inbreeding) which facilitates their spread and establishment in invaded areas (Kirkendall, 1983; Jordal et al., 2001; Peer & Taborsky, 2005). Thus, some non-native xyleborines have become economically important, and in a few cases, even destructive, pests in forests, tree nurseries, plantations, orchards, and timber yards (e.g., Oliver & Mannion, 2001; Hulcr & Dunn, 2011; Kendra et al., 2013; Ploetz et al., 2013; Galko et al., 2015; Ranger et al., 2016)

Habitat structure, host resources, climate, management, and antagonists (Park & Reid, 2007; Bussler et al., 2011; Marini et al., 2011; Watanabe et al., 2014; Rassati et al., 2016; Galko et al., 2019; Gossner et al., 2019) are among the principal factors that influence the distribution and abundance of invasive xyleborine populations. In Slovakia, two species of non-native xyleborines have become well-established thus far – *Xyleborinus attenuatus* (Blandford, 1894) (Knížek, 1988; Björklund & Boberg, 2017) and *Xylosandrus germanus* (Blandford, 1894) (Galko, 2013; Galko et al., 2019). However, it has been recently suggested that *X. attenuatus* may in fact represent a native species with a wide Palaearctic distribution (Fiala & Holuša, 2023). The black stem borer, *X. germanus*, is a xyleborine native to Eastern Asia and currently established in most of Europe and North America (Gomez et al., 2018; Galko et al., 2019). Genetic evidence indicates that its non-native populations are of Japanese origin (Dzurenko et al., 2021). *Xylosandrus germanus* is a highly polyphagous generalist, attacking over 200 species of woody plants, however, deciduous trees are preferred as hosts (Weber & McPherson, 1983, Ranger et al., 2010). Several recent studies carried out in Central European forests have shown that *X. germanus* is significantly more abundant at low and medium elevations in forest ecosystems dominated by oak and beech compared to montane areas dominated by spruce and fir, which are presumably less suitable for the species due to low temperatures (Galko et al., 2019, Hauptman et al., 2019, Fiala et al., 2020).

Although *X. germanus* has been established in Slovakia for over a decade, the influence of tree species diversity on its distribution and abundance within Central Europe has not been investigated. In Italy, it has been shown that forest composition had a clear effect on the activity-density of *X. germanus* (Rassati et al., 2016). We thus hypothesized that tree species diversity would significantly impact *X. germanus* numbers. Since most xyleborines, including *X. germanus*, may be effectively captured in large numbers by traps baited with ethanol, which is the primary volatile cue aiding the beetles in host recognition and colonisation (Ranger et al., 2010, 2021), we tested our hypothesis by deploying ethanol-baited traps in 24 lowland closed-canopy forests in the West Carpathians of Slovakia.

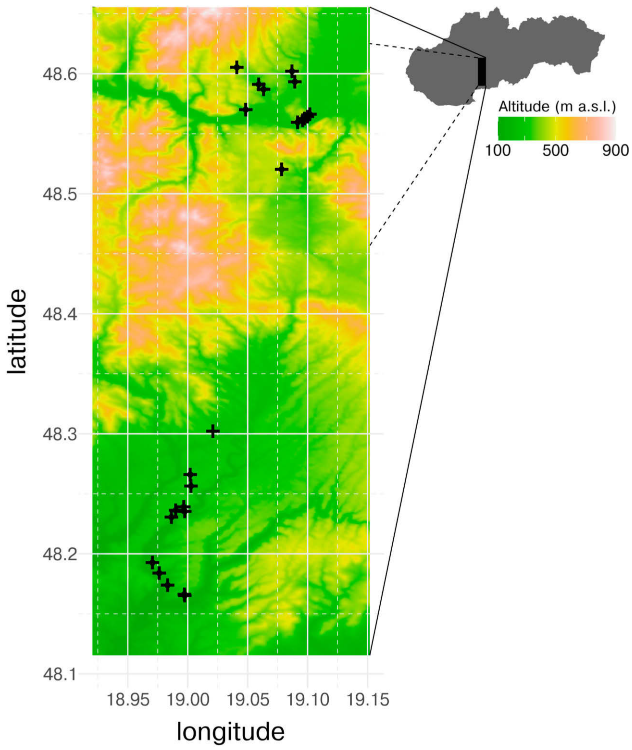

Fig. 1. Sites of the 24 forest stands where traps were deployed.

MATERIAL AND METHODS

Research area

Field research took place in lowland, managed, even-aged, and closed-canopy forest stands with the majority dominated by oak (*Quercus* spp.) with an admixture of hornbeam (*Carpinus betulus*), European beech (*Fagus sylvatica*), maple (*Acer* spp.), lime (*Tilia* spp.), black locust (*Robinia pseudoacacia*), wild cherry (*Prunus avium*), Scots pine (*Pinus sylvestris*), rowan (*Sorbus aucuparia*), and European aspen (*Populus tremula*). The forest stands were situated in two areas in central and southern Slovakia within an altitudinal gradient between 171 and 450 m a.s.l. (Fig. 1). See Table S1 for stand characteristics.

Trapping

Simple home-made traps were manufactured from 1.5 L plastic bottles with a cutout window (10 × 20 cm) after Steininger et al. (2015). Each bottle was inverted and baited with 85% aqueous solution of absolute ethanol (Galvex, LLC) contained in a 100 ml plastic container suspended within the bottle on a metal wire. Four circular openings (diameter 2.5 mm) were drilled evenly along the circumference in the upper part of the container to permit ethanol emission. Each container was filled with 75 ml of absolute ethanol with a measured release rate of 0.73 ± 0.09 g per day (n = 10) at 19 °C. The preservation solution (aqueous NaCl) was contained within the bottle neck.

Traps were deployed at 24 forest stands within the two areas (12 traps in central Slovakia and 12 in southern Slovakia) to capture *Xylosandrus germanus* females during peak flight activity from April to August in 2016 and 2017. Part of the 2017 dataset (trap captures only) was also used in a separate study (Dzurenko et al., 2022), which focused on the effect of unusually cold winter temperatures on the abundance of *X. germanus*. That publication did not analyse any of the ecological predictors examined in the present study (tree species diversity, altitude, or stand age). This ensures transparency and avoids duplication of analyses. The traps were attached with a metal wire to the lower branches of oak trees at 1.5–1.8 m above the ground. To ensure independence of captures, each trap was placed at a minimum distance of 100 m from the others. Traps were inspected and beetles collected at approximately two-week intervals. Trapped beetles were stored in 40% ethanol and subsequently counted in the laboratory. To characterise tree species composition, trees were counted and identified to the species level within a circle around the trap with a 30 m diameter at each site. Shannon index was used as a combined indicator of tree species richness and evenness.

Statistical analysis

Prior to analysis, the dataset was examined for data structure and potential collinearity among predictor variables. Beetle abundance, the response variable, was modeled using generalized linear mixed models (GLMMs; Bolker et al., 2009) with a negative binomial error distribution to account for overdispersion, as detected in an initial Poisson GLMM via the overdispersion test in the performance package (Lüdecke et al., 2021). The predictors included the number of tree host species, diversity of tree hosts (Shannon index), altitude, forest age, and sampling period. Sampling period was treated as a continuous variable to allow for a seasonal trend in beetle abundance. The random effect structure was optimised by sequentially removing random effects with near-zero variance, evaluated through changes in Akaike Information Criterion (AIC; Akaike, 1974). Initial models included year, area, and forest site as random intercepts. The variance estimates of year were negligible, and its removal resulted in an AIC decrease. Area also exhibited low variance and was subsequently removed, with model selection based on the lowest AIC. The final model retained forest site as the only random effect, reflecting the repeated sampling of specific locations across sampling periods.

Given the expectation of a nonlinear seasonal trend in beetle abundance, different transformations of sampling period were tested. Polynomial terms were incorporated into the models using orthogonal polynomials via the poly() function in R, comparing

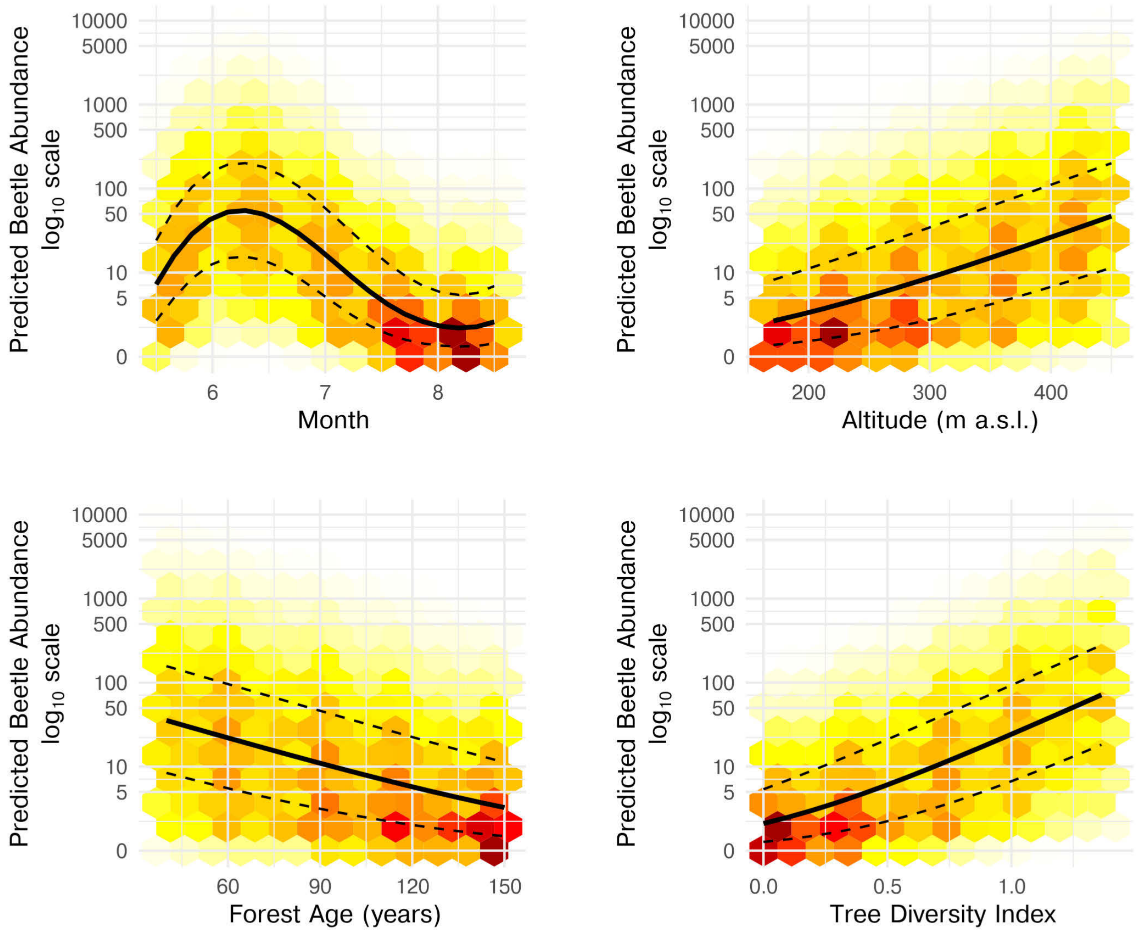

Fig. 2. Effect of sampling period (month), altitude, forest age, and tree diversity index on captures of *Xylosandrus germanus*.

quadratic and cubic representations. Model selection was based on AIC values, with the cubic polynomial providing the best balance between fit and interpretability. Although higher-degree polynomials further reduced AIC, they were not considered due to the risk of overfitting, as sampling period had only five unique values. The final model retained a cubic polynomial for sampling period, which adequately captured seasonal variation.

Similar transformations were explored for tree diversity, altitude, and forest age to assess potential nonlinear effects. However, incorporating polynomial terms for these variables did not consistently improve model fit, and in all cases, the second-order term was not statistically significant. Given these results, linear effects were retained for tree diversity, altitude, and forest age, while a cubic polynomial was used exclusively for sampling period.

Collinearity among fixed effects was assessed using the check_collinearity() function from the performance package, ensuring that all variance inflation factors (VIF) remained below five (Zuur et al., 2010). Model fit was evaluated using marginal and conditional R^2, where marginal R^2 represents variance explained by fixed effects and conditional R^2 includes variance explained by both fixed and random effects (Nakagawa & Schielzeth, 2013). The assumptions of the final model were verified using DHARMa residual diagnostics to check for normality, dispersion, and homoscedasticity of residuals (Hartig, 2022). The overdispersion test indicated that the dispersion parameter was not significantly different from expectation (dispersion = 0.092, $p = 0.344$), suggesting no overdispersion in the model. The zero-inflation test showed that the observed ratio of zeros was consistent with model expectations (ratioObsSim = 0.952, $p = 0.856$), confirming that a zero-inflated model was not necessary. Homoscedasticity was evaluated using the Kolmogorov-Smirnov test, which indicated no significant deviation from uniformity in the residuals ($D = 0.062$, $p = 0.324$). These results confirm that the model meets the necessary assumptions for valid inference.

Predictions from the final model were generated to examine the effects of tree diversity (Shannon index), altitude, sampling period, and forest age on beetle abundance. To obtain model-based predictions, a new dataset was created where each predictor was systematically varied over its observed range while keeping the number of tree host species constant at its mean value. Additionally, predictions were made for all forest sampling locations, allowing for the incorporation of random effect variability. The predicted values were then averaged across all sampling locations to derive an overall expected beetle abundance for each unique combination of predictor values.

All statistical analyses were conducted in R (R Core Team, 2023) using the packages glmmTMB (Brooks et al., 2017) for fitting generalized linear mixed models, lme4 (Bates et al., 2015) for additional mixed-model functionality, and mgcv (Wood, 2017) for smoothing splines and generalized additive models. Model diagnostics, including checks for overdispersion, collinearity, and residual patterns, were performed using the performance package (Lüdecke et al., 2021), while residual validation was conducted with DHARMa (Hartig, 2022). Model predictions were visualised using ggplot2 (Wickham, 2016) to illustrate the effects of key predictors on beetle abundance.

Table 1. Summary of the negative binomial GLMM predicting beetle abundance.

Predictor	Estimate (β)	SE	z-value	p-value
Intercept	–0.802	1.530	–0.524	0.600
Number of tree host species	–0.237	0.439	–0.539	0.590
Tree diversity (Shannon index)	3.047	1.227	2.484	0.013*
Altitude (m a.s.l.)	0.0119	0.0025	4.834	<0.001***
Forest age (years)	–0.0248	0.0117	–2.112	0.0346*
Sampling period	–13.932	1.265	–11.016	<0.001***
Sampling period ^2	–10.511	1.255	–8.376	<0.001***
Sampling period ^3	11.406	1.096	10.405	<0.001***

RESULTS

A total of 23,782 specimens of *Xylosandrus germanus* were captured during trapping conducted in the 24 selected forest stands in the West Carpathians of Slovakia. *Xylosandrus germanus* was, by far (>95% of all captured specimens), the most numerous ambrosia beetle species captured. Other species of ambrosia beetles captured during trapping included *Anisandrus dispar* (Fabricius, 1792), *Platypus cylindrus* (Fabricius, 1792), *Trypodendron domesticum* (L.), *T. signatum* (Fabricius, 1792), *Xyleborus dryographus* (Ratzeburg, 1837), *X. monographus* (Fabricius, 1792), and *Xyleborinus saxesenii* (Ratzeburg, 1837). These other species were captured in much lower numbers and were not considered in our analysis. See Table S1 for details on trap captures.

The final GLMM included tree diversity (Shannon index), altitude, sampling period, and forest age as fixed effects, while accounting for repeated sampling across locations by incorporating forest spot as a random effect. The variance estimate for the random effect of forest spot was 0.93, with a standard deviation of 0.96, indicating moderate variation among sampling locations.

Among the fixed effects, tree diversity had a significant positive effect on beetle abundance ($z = 2.484$, $p = 0.013$). Altitude also showed a significant positive relationship with beetle abundance ($z = 4.834$, $p < 0.001$). Forest age had a small but significant negative effect ($z = –2.112$, $p = 0.0346$). A third-degree polynomial term was used to model the effect of sampling period, capturing nonlinearity in seasonal patterns. All three polynomial terms were highly significant (all $p < 0.001$; Table 1).

Beetle abundance increased with tree diversity and altitude, while it declined with increasing forest age. The seasonal trend showed a non-monotonic pattern, with beetle abundance peaking around the first half of June and declining toward the later months. These trends were further visualised using quartile-based summaries, which provided additional insight into the distribution of predicted values across environmental gradients (Fig. 2).

DISCUSSION

Our study examined spatial and temporal patterns in the abundance of the invasive ambrosia beetle, *Xylosandrus germanus*, within oak-dominated forests of the Western Carpathians, highlighting the role of tree species diversity and environmental gradients. Supporting our initial hypothesis, we found a significant positive relationship between tree diversity, measured by the Shannon diversity index, and *X. germanus* abundance. This finding suggests that more diverse forest stands provide either a greater availability of suitable host trees or more favourable environmental conditions for beetle establishment and proliferation.

Our results are consistent with earlier research by Rassati et al. (2016), who also reported increased activity-density of *X. germanus* and related ambrosia beetles in more diverse forest stands. While *X. germanus* is highly polyphagous, its preference for certain host species may be influenced by variations in the growth conditions for its fungal symbionts within different host trees (Castrillo et al., 2012). Thus, increased tree species diversity within a forest stand may elevate the probability of suitable host availability, thereby promoting reproductive success and higher beetle densities.

Altitude emerged as another significant positive predictor of beetle abundance. Previous studies conducted in Central Europe have documented the highest abundances of *X. germanus* occurring in mid-elevation, beech-dominated forests, typically around 450–700 m a.s.l. (Galko et al., 2019; Hauptman et al., 2019). Our investigation, set at lower elevations within oak-dominated ecosystems, aligns with these findings by demonstrating an increase in beetle abundance along the elevational gradient, presumably reflecting a convergence toward the optimal environmental conditions found at mid-altitudes. The observed lower abundances at lower elevations could be attributable to the drier microclimatic conditions prevalent in these stands, given the dependence of ambrosia beetles on relatively high moisture levels to cultivate their fungal symbionts (Holuša et al., 2021). *Xylosandrus germanus* abundance in Central European forests plateaus within the mid-elevation, beech-dominated optimum and decreases with both decreasing and increasing altitude. Above this optimum, *X. germanus* is probably limited by low temperatures, since it is only rarely found in spruce-dominated montane forests above 1,000 m a.s.l. (Galko et al., 2019).

Forest age showed a modest yet statistically significant negative correlation with *X. germanus* abundance. Although *X. germanus* can colonise host materials of varying thickness (Zach et al., 2001; Henin & Verstein, 2004), evidence indicates a preference for thinner stems, generally less than 10 cm in diameter (Bruge, 1995; Reed et al., 2015; Ranger et al., 2016). Younger forests often experience intense inter-tree competition, leading to higher mortality rates and increased availability of smaller-diameter woody debris (Lutz & Halpern, 2006), particularly in even-aged stands (Westoby, 1984). Such conditions presumably provide more abundant and suitable breeding substrates for *X. germanus*, thus explaining their higher abundance in younger forests. Conversely, older stands might harbour increased populations of natural predators or competitors that contribute to suppressing beetle populations.

Our analysis further identified distinct seasonal activity patterns for *X. germanus*, with abundance peaking in early to mid-June and subsequently declining. This seasonal trend is consistent with documented phenological patterns of *X. germanus* flight activity in Central Europe (Galko et al., 2014; Fiala et al., 2020). The inclusion of a cubic polynomial term effectively captured this non-monotonic pattern, providing robust predictive power and clarity regarding seasonal fluctuations.

Overall, our findings underscore the importance of tree species diversity, altitude, and forest age in shaping the abundance patterns of *X. germanus* in oak-dominated forests of the Western Carpathians. The positive relationship with tree diversity highlights the ecological role forest composition plays in mediating invasive species dynamics, while the impacts of altitude and stand age illustrate the complex interactions among microclimatic conditions, habitat availability, and host suitability. An improved understanding of these ecological drivers is crucial for accurately predicting future spread and informing forest management strategies aimed at mitigating the impacts of *X. germanus* invasions. Future research should further investigate the underlying ecological mechanisms and consider longitudinal studies to better inform conservation and pest management practices.

ACKNOWLEDGEMENTS. This research was financially supported by the Scientific Grant Agency of the Ministry of Education of the Slovak Republic, grant project No. VEGA 2/0022/23 and the Ministry of Agriculture and Rural Development of the Slovak Republic, grant project No. 08V0301 [PROMOLES]. This study is dedicated to the memory of our co-author, P. Zach, whose expertise, enthusiasm, and friendship greatly enriched this work. His contribution to forest entomology and his support as a colleague and mentor will be fondly remembered.

REFERENCES

Akaike H. 1974: A new look at the statistical model identification. — *IEEE Trans. Autom. Control* **19**: 716–723.

Bates D., Mächler M., Bolker B. & Walker S. 2015: Fitting linear mixed-effects models using lme4. — *J. Stat. Softw.* **67**: 1–48.

Batra L.R. 1963: Ecology of ambrosia fungi and their dissemination by beetles. — *Trans. Kans. Acad. Sci.* **66**: 213–236.

Biedermann P.H. & Taborsky M. 2011: Larval helpers and age polyethism in ambrosia beetles. — *Proc. Natl. Acad. Sci. U.S.A.* **108**: 17064–17069.

Biedermann P.H., Müller J., Grégoire J.C., Gruppe A., Hagge J., Hammerbacher A. Hofstetter R.W., Kandasamy D., Kolarik M., Kostovcik M. et al. 2019: Bark beetle population dynamics in the Anthropocene: challenges and solutions. — *Trends Ecol. Evol.* **34**: 914–924.

Björklund N. & Boberg J. 2017: *Rapid Pest Risk Analysis Xyleborinus attenuatus.* Swedish University of Agricultural Sciences, Upsala, 17 pp.

Bolker B.M., Brooks M.E., Clark C.J., Geange S.W., Poulsen J.R., Stevens M.H.H. & White J.S.S. 2009: Generalized linear mixed models: a practical guide for ecology and evolution. — *Trends Ecol. Evol.* **24**: 127–135.

Brooks M.E., Kristensen K., van Benthem K.J., Magnusson A., Berg C.W., Nielsen A., Skaug H.J., Mächler M. & Bolker B.M. 2017: glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. — *R Journal* **9**: 378–400.

Bruge H. 1995: *Xylosandrus germanus* (Blandford, 1894) (Belg. sp. nov.) (Coleoptera: Scolytidae). — *Bull. Ann. Soc. R. Belg. Entomol.* **131**: 249–264.

Bussler H., Bouget C., Brustel H., Brändle M., Riedinger V., Brandl R. & Müller J. 2011: Abundance and pest classification of scolytid species (Coleoptera: Curculionidae, Scolytinae) follow different patterns. — *For. Ecol. Manag.* **262**: 1887–1894.

Castrillo L.A., Griggs M.H. & Vandenberg J.D. 2012: Brood production by *Xylosandrus germanus* (Coleoptera: Curculionidae) and growth of its fungal symbiont on artificial diet based on sawdust of different tree species. — *Environ. Entomol.* **41**: 822–827.

Dzurenko M. & Hulcr J. 2022: Ambrosia beetles. — *Curr. Biol.* **32**: R61–R62.

Dzurenko M., Ranger C.M., Hulcr J., Galko J. & Kaňuch P. 2021: Origin of non-native *Xylosandrus germanus*, an invasive pest ambrosia beetle in Europe and North America. — *J. Pest Sci.* **94**: 553–562.

Dzurenko M., Galko J., Kulfan J., Váľka J., Holec J., Saniga M., Zúbrik M., Vakula J., Ranger C.M., Skuhrovec J., Jauschová T. & Zach P. 2022: Can the invasive ambrosia beetle *Xylosandrus germanus* withstand an unusually cold winter in the West Carpathian forest in Central Europe? — *Folia Oecol.* **49**: 1–8.

Fiala T. & Holuša J. 2023: Distribution of the invasive ambrosia beetles *Xyleborinus attenuatus* Blandford, 1894 (Coleoptera: Curculionidae: Scolytinae) in the Czech Republic (Central Europe). — *Cent. Eur. For. J.* **70**: 34–40.

Fiala T., Holuša J., Procházka J., Čížek L., Dzurenko M., Foit J., Galko J., Kašák J., Kulfan J. & Lakatos F. 2020: *Xylosandrus germanus* in Central Europe: Spread into and within the Czech Republic. — *J. Appl. Entomol.* **144**: 423–433.

Galko J. 2013: First record of the ambrosia beetle, *Xylosandrus germanus* (Blandford, 1894) (Coleoptera: Curculionidae, Scolytinae) in Slovakia. — *Forestry J.* **58**: 279.

Galko J., Nikolov C., Kimoto T., Kunca A., Gubka A., Vakula J., Zúbrik M. & Ostrihoň M. 2014: Attraction of ambrosia beetles to ethanol baited traps in a Slovakian oak forest. — *Biologia* **69**: 1376–1383.

Galko J., Kunca A., Rell S., Zúbrik M., Nikolov C., Gubka A. & Vakula J. 2015: The black wood borer (*Xylosandrus germanus*) as a new technical wood pest in Slovakia. In Kunca A. (ed.): *Current Issues in Forest Protection. Proceedings of 24th Annual International Conference, January 29 and 30, 2015, Nový Smokovec.* National Forestry Center, Zvolen, pp. 35–40 [in Slovak].

Galko J., Dzurenko M., Ranger C.M., Kulfan J., Kula E., Nikolov C., Zúbrik M. & Zach P. 2019: Distribution, habitat preference, and management of the invasive ambrosia beetle *Xylosandrus germanus* (Coleoptera: Curculionidae, Scolytinae) in European forests with an emphasis on the West Carpathians. — *Forests* **10**: 10, 18 pp.

Gomez D.F., Rabaglia R.J., Fairbanks K.E.O. & Hulcr J. 2018: North American Xyleborini north of Mexico: a review and key to genera and species (Coleoptera, Curculionidae, Scolytinae). — *ZooKeys* **768**: 19–68.

Gossner M.M., Falck K. & Weisser W.W. 2019: Effects of management on ambrosia beetles and their antagonists in European beech forests. — *For. Ecol. Manag.* **437**: 126–133.

Hartig F. 2022: DHARMa: *Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R Package Version 0.4.6.* URL: https://CRAN.R-project.org/package=DHARMa

Hauptman T., Pavlin R., Grošelj P. & Jurc M. 2019: Distribution and abundance of the alien *Xylosandrus germanus* and other ambrosia beetles (Coleoptera: Curculionidae, Scolytinae) in different forest stands in central Slovenia. — *iForest* **12**: 451–458.

Henin J.M. & Versteirt V. 2004: Abundance and distribution of *Xylosandrus germanus* (Blandford 1894) (Coleoptera, Scolytidae) in Belgium: new observations and an attempt to outline its range. — *J. Pest Sci.* **77**: 57–63.

Holuša J., Fiala T. & Foit J. 2021: Ambrosia beetles prefer closed canopies: a case study in oak forests in Central Europe. — *Forests* **12**: 1223, 16 pp.

Hulcr J. & Dunn R. 2011: The sudden emergence of pathogenicity in insect-fungus symbioses threatens naive forest ecosystems. — *Proc. R. Soc. (B)* **278**: 2866–2873.

Hulcr J. & Stelinski L.L. 2017: The ambrosia symbiosis: from evolutionary ecology to practical management. — *Annu. Rev. Entomol.* **62**: 285–303.

Jordal B.H., Beaver R.A. & Kirkendall L.R. 2001: Breaking taboos in the tropics: incest promotes colonization by woodboring beetles. — *Glob. Ecol. Biogeogr.* **10**: 345–357.

Kendra P.E., Montgomery W.S., Niogret J. & Epsky N.D. 2013: An uncertain future for American Lauraceae: a lethal threat from redbay ambrosia beetle and laurel wilt disease (a review). — *For. Ecol. Manag.* **291**: 9–17.

Kirkendall L.R. 1983: The evolution of mating systems in bark and ambrosia beetles (Coleoptera: Scolytidae and Platypodidae). — *Zool. J. Linn. Soc.* **77**: 293–352.

Knížek M. 1988: Faunistic records from Czechoslovakia. Coleoptera, Scolytidae: *Xyleborus alni* Niijima, 1909. — *Acta Entomol. Bohemoslov.* **85**: 396.

Lüdecke D., Ben-Shachar M.S., Patil I., Waggoner P. & Makowski D. 2021: Performance: An R package for assessment, comparison, and testing of statistical models. — *J. Open Source Softw.* **6**: 3139, 8 pp.

Lutz J.A. & Halpern C.B. 2006: Tree mortality during early forest development: a long-term study of rates, causes, and consequences. — *Ecol. Monogr*. **76**: 257–275.

Nakagawa S. & Schielzeth H. 2013: A general and simple method for obtaining R^2 from generalized linear mixed-effects models. — *Methods Ecol. Evol.* **4**: 133–142.

Marini L., Haack R.A., Rabaglia R.J., Toffolo E.P., Battisti A. & Faccoli M. 2011: Exploring associations between international trade and environmental factors with establishment patterns of exotic Scolytinae. — *Biol. Invas.* **13**: 2275–2288.

Oliver J.B. & Mannion C.M. 2001: Ambrosia beetle (Coleoptera: Scolytidae) species attacking chestnut and captured in ethanol-baited traps in middle Tennessee. — *Environ. Entomol.* **30**: 909–918.

Park J. & Reid M.L. 2007: Distribution of a bark beetle, *Trypodendron lineatum*, in a harvested landscape. — *For. Ecol. Manag*. **242**: 236–242.

Peer K. & Taborsky M. 2005: Outbreeding depression, but no inbreeding depression in haplodiploid ambrosia beetles with regular sibling mating. — *Evolution* **59**: 317–323.

Ploetz R.C., Hulcr J., Wingfield M.J. & De Beer Z.W. 2013: Destructive tree diseases associated with ambrosia and bark beetles: black swan events in tree pathology? — *Plant Dis.* **97**: 856–872.

R Core Team 2023: R: *A Language and Environment for Statistical Computing.* R Foundation for Statistical Computing, Vienna, URL: https://www.R-project.org/

Ranger C.M., Reding M.E., Persad A.B. & Herms D.A. 2010: Ability of stress-related volatiles to attract and induce attacks by *Xylosandrus germanus* and other ambrosia beetles. — *Agric. For. Entomol.* **12**: 177–185.

Ranger C.M., Reding M.E., Schultz P.B., Oliver J.B., Frank S.D., Addesso K.M., Chong J.H., Sampson B., Werle C., Gill S. & Krause C. 2016: Biology, ecology, and management of nonnative ambrosia beetles (Coleoptera: Curculionidae: Scolytinae) in ornamental plant nurseries. — *J. Integr. Pest Manag.* **7**: 1–23.

Ranger C.M., Reding M.E., Addesso K., Ginzel M. & Rassati D. 2021: Semiochemical-mediated host selection by *Xylosandrus* spp. ambrosia beetles (Coleoptera: Curculionidae) attacking horticultural tree crops: a review of basic and applied science. — *Can. Entomol.* **153**: 103–120.

Rassati D., Faccoli M., Battisti A. & Marini L. 2016: Habitat and climatic preferences drive invasions of non-native ambrosia beetles in deciduous temperate forests. — *Biol. Invas.* **18**: 2809–2821.

Reed S.E., Juzwik J., English J.T. & Ginzel M.D. 2015: Colonization of artificially stressed black walnut trees by ambrosia beetle, bark beetle, and other weevil species (Coleoptera: Curculionidae) in Indiana and Missouri. — *Environ. Entomol.* **44**: 1455–1464.

Smith S.M. & Hulcr J. 2015: *Scolytus* and other economically important bark and ambrosia beetles. In Vega F.E. & Hofstetter R.W. (eds): *Bark Beetles. Biology and Ecology of Native and Invasive Species. 1st ed.* Elsevier Academic Press, Amsterdam, pp. 495–531.

Steininger M.S., Hulcr J., Šigut M. & Lucky A. 2015: Simple and efficient trap for bark and ambrosia beetles (Coleoptera: Curculionidae) to facilitate invasive species monitoring and citizen involvement. — *J. Econ. Entomol.* **108**: 1115–1123.

Watanabe K., Murakami M., Hirao T. & Kamata N. 2014: Species diversity estimation of ambrosia and bark beetles in temperate mixed forests in Japan based on host phylogeny and specificity. — *Ecol. Res.* **29**: 299–307.

Weber B.C. & McPherson J.E. 1983: Life history of the ambrosia beetle *Xylosandrus germanus* (Coleoptera: Scolytidae). — *Ann. Entomol. Soc. Am.* **76**: 455–462.

Westoby M. 1984: The self-thinning rule. — *Adv. Ecol. Res.* **14**: 167–225.

Wickham H. 2016: *ggplot2: Elegant Graphics for Data Analysis.* Springer, New York, 260 pp. URL: https://ggplot2.tidyverse.org

Wood S. 2017: *Generalized Additive Models: An Introduction with R. 2nd ed.* Chapman and Hall/CRC, New York, 496 pp.

Zach P., Topp W. & Kulfan J. 2001: Colonization of two alien ambrosia species (Coleoptera, Scolytidae) on debarked spruce logs. — *Biologia* **56**: 175–181.

Zuur A.F., Ieno E.N. & Elphick C.S. 2010: A protocol for data exploration to avoid common statistical problems. — *Methods Ecol. Evol.* **1**: 3–14.

Received June 3, 2025; revised and accepted September 19, 2025
Published online November 10, 2025

Online Supplement S1 (http://www.eje.cz/2025/034/S01.xlsx):

Table S1. Total captures of ambrosia beetles per stand.