SEEFOR SOUTH-EAST EUROPEAN FORESTRY
OPEN ACCESS
ISSN 1847-6481
eISSN 1849-0891

ORIGINAL SCIENTIFIC PAPER

DOI: https://doi.org/10.15177/seefor.25-16

Phenological Study of the Spruce Bark Beetles *Ips typographus* (L.) and *Pityogenes chalcographus* (L.) (Coleoptera: Curculionidae) on Tara Mountain, Serbia

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Citation: Milosavljević M, Taraković-Tošić M, Stajić S, Češljar G, Mitrović S, 2025. Phenological Study of the Spruce Bark Beetles *Ips typographus* (L.) and *Pityogenes chalcographus* (L.) (Coleoptera: Curculionidae) on Tara Mountain, Serbia. *South-east Eur for* 16(2): early view. https://doi.org/10.15177/seefor.25-16.
Received: 29 Jul 2025; **Revised:** 26 Aug 2025; **Accepted:** 27 Aug 2025; **Published online:** 17 Nov 2025

ABSTRACT

This study presents a detailed phenological analysis of two important spruce bark beetle species, *Ips typographus* (L.) and *Pityogenes chalcographus* (L.) (Coleoptera: Curculionidae), in the region of Tara Mountain in western Serbia, conducted over a period of three years (2016–2018). Field observations were complemented by growth degree days (GDD) calculations to determine thermal thresholds for development under local climatic conditions. Both species were found to be univoltine, with the potential for a sister generation. Timing of life stages, particularly adult emergence, was closely linked to accumulated thermal units, with developmental thresholds of 557 GDD reached between early and mid-July each year. The results highlight the influence of microclimate and temperature variability on bark beetle development and illustrate the potential for phenological shifts under future climate scenarios. These findings provide a regional framework for predicting outbreaks and improving forest pest control strategies in the face of ongoing climate change.

Keywords: voltinism; European spruce bark beetles; growing degree days (GDD); climate change; western Serbia

INTRODUCTION

Climate change is increasingly recognised as one of the main causes of changes in the biology, ecology and population dynamics of insects. Rising global temperatures, changing precipitation regimes, and more frequent extreme events have accelerated insect evolution, shifted phenologies, expanded geographic ranges and disrupted ecological interactions (Harvey et al. 2020). Many insect species now exhibit multivoltinism — producing more generations per year — while others, particularly cold-adapted pollinators, are experiencing range contractions and population declines due to thermal stress and phenological imbalances (Bellard et al. 2012, Bhagarathi and Maharaj 2023). Warmer winters reduce overwintering mortality and allow insects to expand into previously unsuitable habitats, while climate-induced droughts weaken host plant defences and increase their susceptibility to herbivory and infestation (Bellard et al. 2012, Lehmann et al. 2020). These changes not only threaten biodiversity and food security, but also disrupt important ecosystem services such as pollination, natural pest regulation and nutrient cycles.

Among the most affected insect groups are bark beetles (Curculionidae: Scolytinae), in particular *Ips typographus* L. (eight-toothed spruce bark beetle) and *Pityogenes chalcographus* L. (six-toothed spruce bark beetle), both of which play an important role in the dynamics of spruce forests across Europe. Global warming has led to a shorter development time, greater reproductive success and higher survival rates for these species, increasing the frequency and severity of outbreaks (Wermelinger and Seifert 1999, Jönsson et al. 2007, Mezei et al. 2017, Wermelinger et al. 2021). Drought-stressed trees with limited resin production are more susceptible to colonisation, while warmer conditions often allow the development of more generations per year (Raffa et al. 2015, Netherer et al. 2024). Simulation modelling suggests that even a modest 4°C rise in temperature could cause beetle-infested regions to expand by over 265%, while the average size of individual outbreak patches could grow more than 18-fold (over 1,800%) (Guillaume et al. 2024). These outbreaks further disrupt forest carbon and water cycles, reduce biodiversity and alter successional pathways in temperate ecosystems (Biedermann et al. 2019, Singh et al. 2024).

In Serbia, particularly in Tara National Park, the combination of increased temperatures and recurrent drought has contributed to increased beetle activity, increased deadwood volume and widespread spruce mortality (Tomić and Bezarević 2014, Tabaković-Tošić and Milosavljević 2015, 2016, Karaklić 2021, Češljar et al. 2022, 2024).

Despite the increasing importance of these species under changing climatic conditions, the biological and ecological data for *I. typographus* and *P. chalcographus* in Serbia come mainly from Central European studies, often without validation for the local environmental context. However, the local climate, altitude and forest composition can significantly influence the timing of development, life cycle duration and voltinism. At altitudes below 700 m, *I. typographus* can go through several generations per year, while at higher altitudes (above 1000 m), typically only one generation is observed (Annila 1969, Zahradník 2007, Kasumović 2016). In warmer regions, up to three generations can occur, provided they are not interrupted by a photoperiodic diapause (Doležal and Sehnal 2007).

Developmental thresholds are often assessed using growing degree days (GDD), which quantify the heat required to complete the life cycle. In *I. typographus*, approximately 557 GDD are required for full development, at a baseline temperature of 8.3°C (Wermelinger and Seifert 1998). However, other studies use lower thresholds such as 5°C, resulting in GDD estimates between 557 and 770 (Annila 1969, Jönsson et al. 2007, Baier et al. 2009, Faccoli 2009).

Considering these knowledge gaps, one of the main objectives of this study was to determine the biological, phenological and ecological characteristics of *Ips typographus* and *Pityogenes chalcographus* under the specific climatic conditions of Tara Mountain in western Serbia. In addition to detailed phenological observations, the study included the calculation of growing degree days (GDD) to determine the local thermal requirements for development. This integrative approach enables a regionally relevant understanding of beetle dynamics and provides insight into their potential response to future climate scenarios.

MATERIALS AND METHODS

The study was conducted in the region of Tara Mountain in western Serbia (43°55′N, 19°30′E), within the boundaries of Tara National Park. Established in 1981, the park covers 19,175 hectares and is part of the Dinaric Alps (Medarević 2005). It has significant geological diversity dating back to the Palaeozoic era (Gajić et al. 1992) and is known for its rich biodiversity. Around a third of Serbia's flora can be found on Tara Mountain (Radović et al., 2005). The area is mostly forested, with natural forest stands making up about 80% of the area. The predominant species are silver fir (*Abies alba* Mill., 43.3%), European beech (*Fagus sylvatica* L., 30.2%) and spruce (*Picea abies* (L.) H. Karst., 15.3%). These three species together form the *Piceto-Abieti-Fagetum* Čolić 1965 community, which occupies 85% of the forest area and is thus the most widespread forest phytocoenosis in Tara National Park (Gajić et al. 1992, Cvjetićanin and Novaković 2010, Jovanović et al. 2022). The climate of Tara Mountain is described as a continental mountain range with subalpine characteristics (Gajić et al. 1992). It is characterised by cool to mild summers and cold winters, with moderate annual fluctuations in air temperature. The average annual precipitation is 977.3 mm, with a maximum in July (104.0 mm) and a minimum in January (56.5 mm). The average annual air temperature in the wider Tara area is 7.9°C, with the lowest monthly average in January (-3.5°C) and the highest in August (17.3°C), which corresponds to an annual amplitude of 20.8°C. The meteorological data collected by the newly established station in Mitrovac (in operation since 2015) confirms a clear warming trend. Between 2015 and 2020, the mean annual air temperature rose to 7.0°C, an increase of 1.9°C compared to previous records. During the growing season, the average temperature reached 14.4°C, 2.0°C above the original values. The insect species studied are the spruce bark beetles *Ips typographus* L. and *Pityogenes chalcographus* L. *I. typographus* is widespread in Europe and Asia Minor. The adults are 4.0–5.5 mm long, cylindrical, and dark brown to black. It is polygamous, with females laying 25–60 eggs in longitudinal galleries under the bark; development takes about 2.5 months, and swarming begins in spring at 16–20°C (Pfeffer 1952, 1995, Annila 1969, Botterweg 1982, Wermelinger 2004). *P. chalcographus* is distributed from Central and Eastern Europe to the Far East; it is smaller (1.6–3.0 mm), and develops mainly under spruce bark, with one to two generations per year depending on conditions (Pfeffer 1995, Hedgren 2004, Zahradník 2007).

From 2016 to 2018, phenological studies were conducted on Tara Mountain located within the Tara forest management unit, which comprises twenty permanent observation plots (Figure 1).

At each site, felled spruce trees, also known as trap trees, were set up to observe the development of the beetles. Inspections were carried out every 15 days from April to September. At the end of each season, the bark was removed to prevent an outbreak of beetles (Figure 2).

As part of the studies on the phenology of spruce bark beetles on Tara Mountain, the accumulated growing degree days (GDD) were calculated in order to compare the values obtained with the developmental stages observed in the field. The accumulated growing degree days (GDD) were calculated based on the daily maximum and minimum air temperature (Ta) in relation to the minimum biological temperature (Tb) for each day of the study period (Prentice et al. 1992, Lalić et al. 2021). A biological minimum temperature of 8.3°C was used for the spruce bark beetles (Wermelinger and Seifert 1998).

RESULTS

The developmental stages of spruce bark beetles consist of the egg, three larval instars, the pupa and the adult (Sauvard 2004). The egg stage usually lasts about a week but

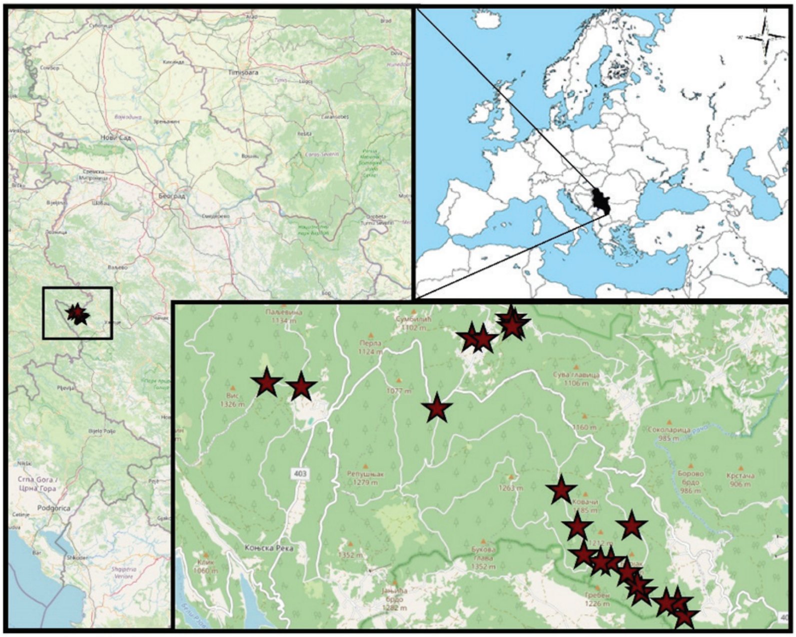

Figure 1. Location of spruce trap trees established for phenological monitoring of *Ips typographus* and *Pityogenes chalcographus* in Tara National Park.

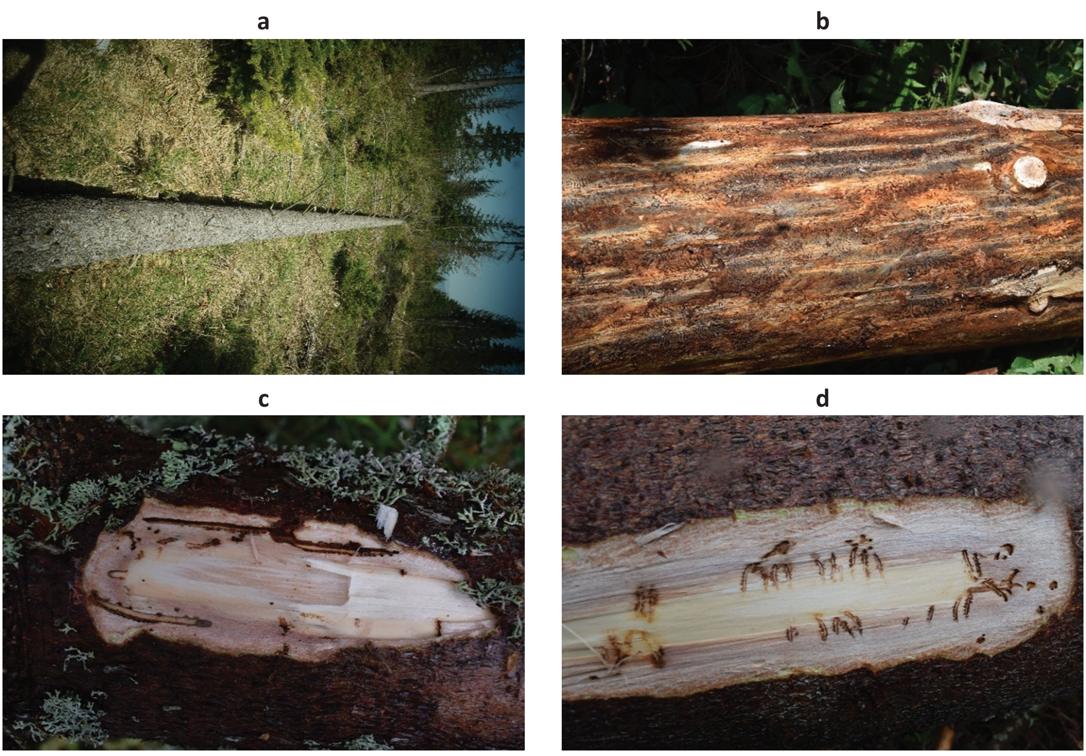

Figure 2. Monitoring bark beetle phenology: **(a)** felled spruce for monitoring bark beetle phenology; **(b)** debarked tree at the end of the research season; **(c)** oviposition of *Ips typographus*; **(d)** oviposition of *Pityogenes chalcographus*.

can range from 3.5 days at 24°C to 12 days at 14°C (Annila 1969, Zahradník 2007, Vakula et al. 2014). The larval period varies between 9 and 31 days, typically lasting three to four weeks depending on temperature. Pupation generally takes up to two weeks. Overall, the complete development cycle of *I. typographus* takes about 50 to 70 days, while *P. chalcographus* requires about 50 to 84 days at higher altitudes. Based on the field data, development thresholds of 557 growing degree days (GDD) were established for the completion of a full life cycle, which took place on 15 July 2016, 12 July 2017 and 4 July 2018 (Supplementary Table 1). The results of the three-year phenological study of the two spruce bark beetle species in the Tara Mountain region are shown in Figures 3–6.

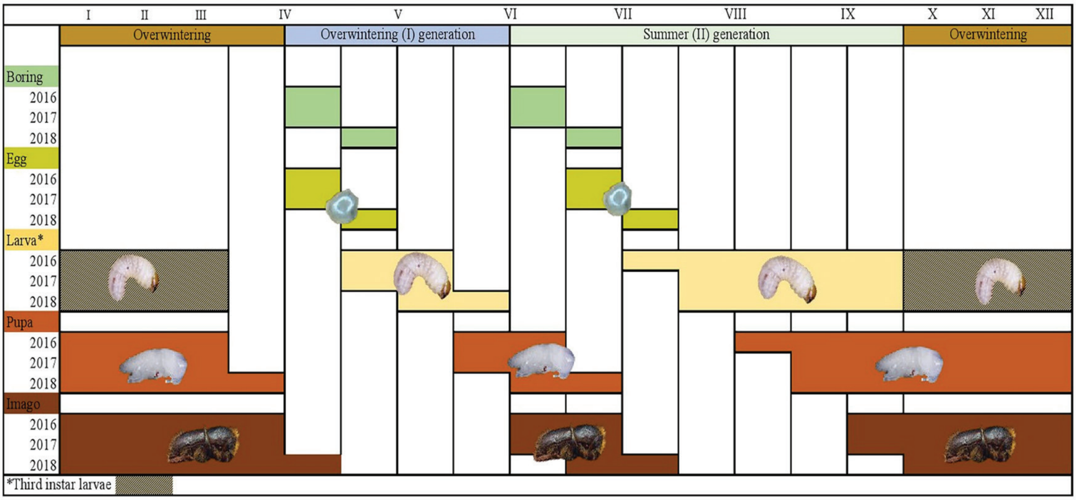

Figure 3. Phenology of *Ips typographus* L. in the Tara Mountain region in the period 2016–2018.

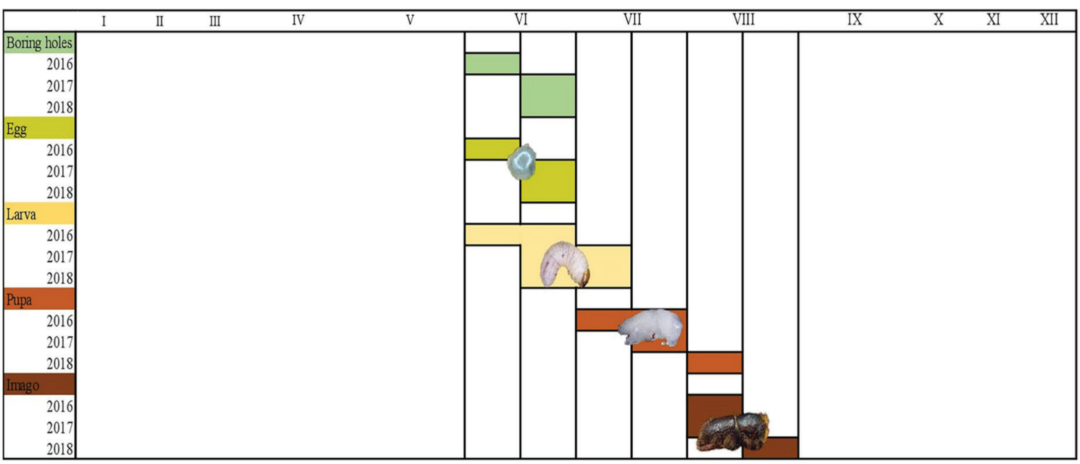

Figure 4. Phenology of the *I. typographus* sister brood generation in the Tara Mountain region in the period 2016–2018.

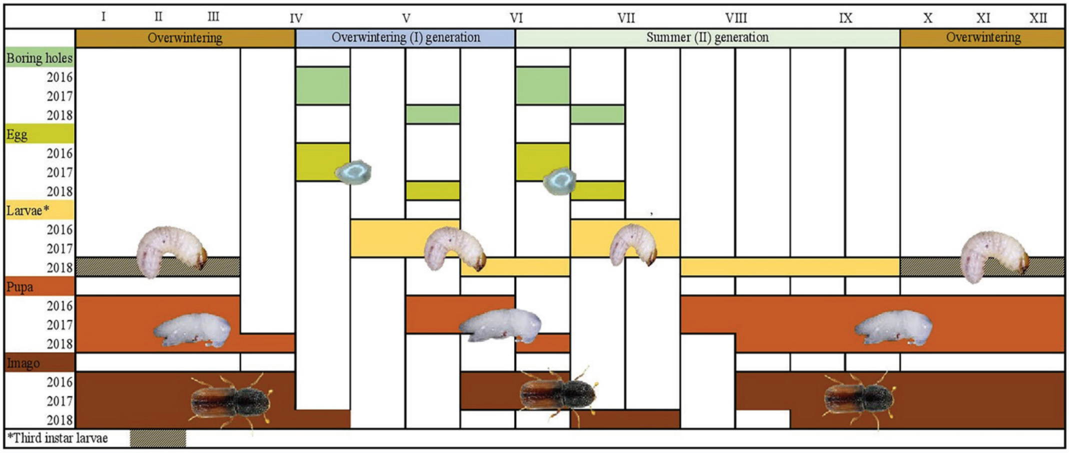

Figure 5. Phenology of *Pityogenes chalcographus* L. in the Tara Mountain region in the period 2016–2018.

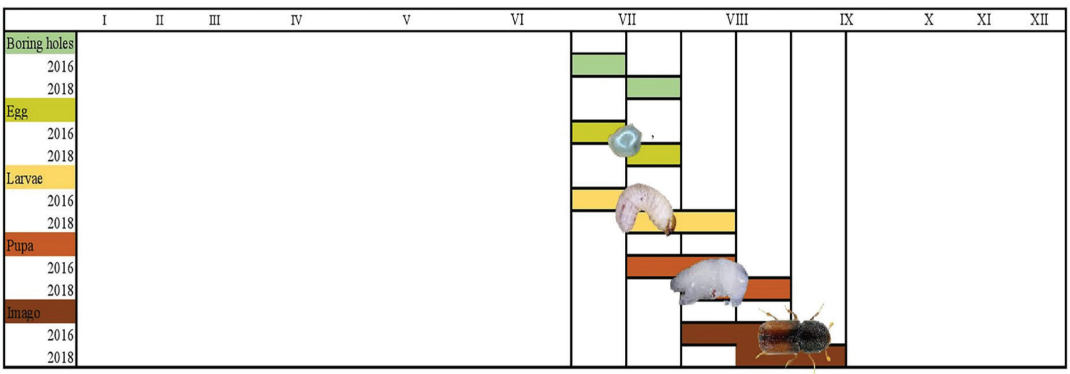

Figure 6. Phenology of the *P. chalcographus* L. sister brood generation in the Tara Mountain region in the period 2016–2018.

DISCUSSION

The phenological patterns of *Ips typographus* L. and *Pityogenes chalcographus* L., observed on Tara Mountain during the period 2016–2018 provide a detailed temporal framework for understanding their development under local climatic conditions. Our results confirmed that both species are univoltine under current environmental conditions, with the possibility of partial sister generations in warmer years. These results are consistent with previous research in central and south-eastern Europe, where these species are typically univoltine at higher altitudes, but can initiate a second, incomplete generation when thermal conditions allow (Annila 1969, Botterweg 1982, Hedgren 2004, Jönsson et al. 2007, Schroeder 2013, Kasumović 2016, Demirović et al. 2016). In *I. typographus*, swarming and oviposition began in late April (Figure 3), with eggs developing shortly thereafter, followed by larval activity in May and pupation in mid to late June. Adults hatched between late June and early July and completed the development cycle in 62–74 days, coinciding with the accumulation of approximately 557 growing degree days (GDD). As can be seen in Figure 4, a sister brood was initiated in mid to late July, but its development was generally halted before completion due to falling temperatures and shortened photoperiods, which is an indication of the climatic limitations of multivoltinism at higher altitudes. *P. chalcographus* followed a similar seasonal pattern, with swarming and oviposition also beginning in late April (Figure 5). However, its development took slightly longer, completing the life cycle in 78–84 days, with adults hatching in mid-July. This longer duration likely reflects species-specific thermal requirements or microhabitat variability within the bark. It is noteworthy that a sister brood of *P. chalcographus* was only observed in 2016 and 2018 (Figure 6). Its absence in 2017 could be due to unfavorable microclimatic conditions, the lack of suitable brood material or a general suppression of sister brood development regardless of host availability. These observations highlight the value — and inherent limitations — of phenological models such as PHENIPS and the Jönsson model, which use non-linear heat accumulation and bark temperature to estimate developmental thresholds (Baier et al. 2007, Jönsson et al. 2007). A recent study by Webb et al. (2025) in south-east England has shown how adapted versions of the PHENIPS model — using air temperature as a proxy for bark temperature — can more accurately capture swarming and generation timing at the start of the season. This suggests that these tools could also be used effectively to predict and manage bark beetle populations in Serbian forest ecosystems if calibrated to local conditions. Looking to the future, the Tara Mountain region, where the average temperature in the growing season has already risen by 2°C, may be approaching a critical climate threshold. If temperatures rise by 2–3°C by 2100, as predicted (Jönsson et al. 2011, Guillaume et al. 2024), the completion of two full generations per season could become common, even at altitudes previously considered safe from multivoltinism. This scenario would significantly increase pest pressure and the vulnerability of forests.

These predictions are also confirmed by the recent work of Potterf et al. (2025), which showed that hotter droughts — a combination of extreme heat and low water availability — have accelerated bark beetle phenology, shortened generation times and increased populations across Europe. Their results suggest that while high temperatures immediately accelerate physiological development, the effects of drought are delayed, reducing host tree defences and promoting beetle success in subsequent years. For example, the 2018–2020 drought period led to earlier and more intense swarming and facilitated large-scale regional synchronisation of the *I. typographus* population. These composite climate dynamics have direct implications for Tara Mountain, where both thermal stress and drought are becoming more frequent. If these trends continue, multivoltinism could become the norm, especially at mid and lower elevations, increasing the risk of widespread outbreaks.

CONCLUSIONS

Phenological studies of *Ips typographus* and *Pityogenes chalcographus* on Tara Mountain confirmed both species are univoltine and capable of producing one sister generation under current conditions. *I. typographus* completes its life cycle between late April and early July (62–74 days), while *P. chalcographus* extends its cycle until mid-July (78–84 days).

Expanded Conclusion: These findings provide valuable insight into the local phenology of economically significant bark beetles in Serbia. They highlight the importance of monitoring developmental stages in relation to altitude, temperature, and microhabitat conditions. As temperatures continue to rise due to climate change, shifts in phenology may lead to additional generations, increased beetle populations, and potentially more severe outbreaks. Effective pest management strategies must therefore incorporate local data and predictive models to mitigate future risks. This research underscores the need for continued observation and the integration of environmental data into forestry practices. Emphasis should also be placed on biological control methods and integrated pest management strategies that leverage natural enemies and adaptive models to protect forest health sustainably in the face of climate uncertainty.

Author Contributions

Conceptualization, MM and MT-T; methodology, MM, and MT-T; investigation, MM, SS, and GČ; resources, MM and MT-T; data curation, MM and SM; writing the original draft preparation, MM; original draft editing, MM, MT-T, and SM; visualization, MM All authors have read and agreed to the published version of the manuscript.

Funding

The work of MM was supported by a grant from the European Community's Program Interreg Czech-Austria BIPC, reg. no. ATCZ00189. Also, the work of MT-T, SS, GČ, and SM, was supported by the Ministry of Science, Technological Development and Innovation of the Republic of Serbia (No. No. 451-03-136/2025-03/200027

Acknowledgments

The authors would like to thank the public company "Tara National Park" for providing the experimental site and human resources.

Conflicts of Interest

The authors declare no conflict of interest. The funders had no role neither in the design of the study, in the collection, analyses, or interpretation of data, nor in the writing of the manuscript and in the decision to publish the results.

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