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ORIGINAL ARTICLE

Exploring the relationship between characteristics of forest stands and the behaviour of *Lymantria dispar* (Lepidoptera: Erebidae) from a temporal and spatial perspective

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Key words. Defoliation, insect outbreaks, forest pests, reproduction, population dynamics

Abstract. In the context of ongoing threats to forest ecosystems, this study investigates the temporal and spatial dynamics of *Lymantria dispar* defoliation intensity over a period of three years. We analysed the relationship between the insects' reproductive and feeding behaviours and forest stand characteristics, exploring the key factors that shape this behaviour. The results revealed a dynamic pattern, with a significant escalation of defoliation starting from the second year and peaking in the third. The analysis highlighted that, among several forest stand characteristics, woody species abundance and specific forest composition significantly influence population density and defoliation intensity. Sporadic outbreaks of the insects were associated with stand features, posing major challenges to forest health. These findings make a significant contribution to understanding the population dynamics of *L. dispar* and provide essential insights for forest managers in efficiently managing this defoliator. By highlighting the complex interactions between the insect and its environment, this study lays the groundwork for conservation and protection strategies for forest ecosystems.

INTRODUCTION

Ecosystems dominated by oak trees hold significant economic importance due to the quality of their wood and derived products, as well as their ecological significance concerning climate, hydrology, and biodiversity effects (Oszako, 1997). In Europe, the 20 oak species contribute to 9% of the total growing stock and represent 27% of deciduous species (Oszako, 1997). However, these ecosystems face threats from the decline of oak species, first observed in Europe since the early 1900s (Falck, 1918; Day, 1927; Oszako, 1997). The decline results from a combination of abiotic and biotic factors (Manion, 1981; Shigo, 1986; Manion & LaChance, 1992). Sinclair (1967) classified the factors contributing to tree decline into three categories: (i) predisposing factors that weaken trees physiologically; (ii) inciting factors and (iii) contributing factors. Predisposing factors are often related to abiotic factors, such as local edaphic and climatic conditions (Sinclair, 1965, 1967). Inciting factors are responsible for the initial symptoms of decline and are linked to both abiotic factors, such as severe drought or extreme winter temperatures, and biotic factors, including viruses and defoliating insects (Sinclair, 1965). Contributing factors, which amplify the oak decline phenomenon, are primarily linked to the influence of biotic factors, such as pathogens (fungi) or secondary bark beetles (Sinclair, 1965). Therefore, it can be argued that eliminating one of the controllable factors in this logical chain, such as inciting factors, largely represented by defoliators, could prevent the success of the decline phenomenon.

Our study focuses on inciting factors such as defoliating insects, exemplified by *Lymantria dispar* Linnaeus 1758 (Lepidoptera: Erebidae). This insect species is recognised as one of the most prolific defoliators of oak forests (Elkinton & Liebhold, 1990; Tomescu et al., 2010; Milanović et al., 2014). This reputation stems from its voracious appetite in the larval stage (Prade & Coyle, 2023) and eruptive outbreaks that occur at variable intervals (Neţoiu et al., 2016). Although a polyphagous species, the defoliator exhibits a pronounced preference for oak species, as their leaves provide a more favourable environment for the insect's development (Liebhold, 1995; Milanović et al., 2014). Numerous studies have highlighted that defoliation caused by *L. dispar* has significant effects, including the impairment of radial growth (Davidson et al., 1999; Muzika & Liebhold,



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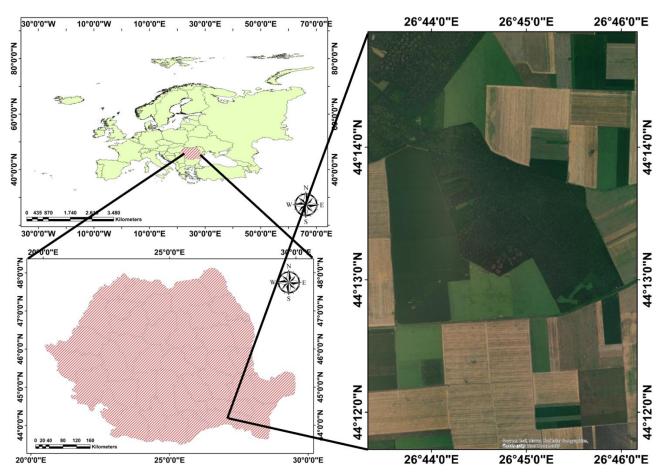


Fig. 1. Location of the study area (Esri, Maxar, GeoEye, Earthstar Geographics, and the GIS User Community).

1999, 2000; Netoiu, 2000; Naidoo & Lechowicz, 2001; Fajvan et al., 2008; Milanović et al., 2014), reduced ability to produce acorns (Gottschalk, 1989; Davidson et al., 1999), the creation of conditions conducive to outbreaks of secondary insects (Fratian, 1973; Netoiu, 1998), and, in the case of repeated severe defoliation, partial or complete tree dieback (Marcu, 1966; Davidson et al., 1999). In Europe, significant outbreaks have been recorded in Germany (Wulf & Graser, 1996), Italy (Luciano & Prota, 1995; Camerini, 2009), the Netherlands (Moraal, 1996), Austria (Hoch et al., 2001), Portugal (Sousa, 1995), Spain (Roy et al.,1995), France (Hérard et al., 1996), Croatia (Hrašovec et al., 2008), Slovakia (Zúbrik & Novotný, 1996), Russia (Savotikov et al., 1995), Ukraine (Meshkova, 1999), Serbia (Tabaković-Tošić, 2005; Tabaković-Tošić et al., 2015), and Hungary (Csoka, 1996; McManus & Csóka, 2007). In the United States, it is estimated that over a century (1920– 2020), it defoliated nearly 40 million hectares (Prade & Coyle, 2023), with an annual economic impact of over 250 million dollars (Aukema et al., 2011; Paini et al., 2018).

The decline of oaks has been reported in Romania since the 1930s, and in research conducted in the 1960s, defoliation caused by *L. dispar* was identified as a key factor in tree decline (Marcu, 1966). In past decades, *L. dispar* has exhibited notable outbreaks in Romanian oak forests, particularly during the periods of 1954–1957 and 1986–1989, with intermittent infestations occurring between these pe-

riods on smaller scales (Simionescu et al., 2000; Tomescu & Neţoiu, 2006). The oak forests in Romania, particularly those in the southern part of the country, are characterised by a continental climate, with periods of drought and reduced rainfall, conditions favourable for the outbreak development of the defoliator (Tomescu & Neţoiu, 2006; Neţoiu et al., 2016; Zúbrik et al., 2016). In addition to climatic factors, these forests have been impacted by anthropogenic factors, such as intensive logging and grazing, which create favourable conditions for an outbreak of defoliating insects such as *Tortrix viridana* Linnaeus 1758, a species of winter moth, *L. dispar, Malacosoma neustria* Linnaeus 1758, and others (Simionescu et al., 2000; Neţoiu et al., 2016).

Typically, population dynamics can be positively or negatively influenced by biotic factors such as food abundance and quality, the number of predators/parasites, and competition for food, as well as abiotic factors like climate and soil (Capinera & Barbosa, 1977; Berryman, 1986; Neţoiu et al., 2016). In addition to these factors, several studies indicate that stand characteristics, such as age, composition, and canopy coverage, may play an important role in the behaviour of insects triggering outbreak phenomena (Doane & McManus, 1981; Muzika et al., 1998; Davidson et al., 2001; Ilyinykh et al., 2011; Neţoiu et al., 2016).

This study aims to investigate the temporal and spatial dynamics of defoliation intensity over a three-year period

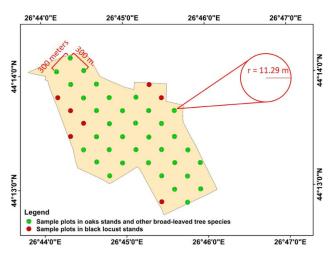


Fig. 2. Representation of the study's network of sample plots.

and address the following questions: (i) Is there a relationship between the insects' reproduction and feeding behaviour, and stand characteristics? (ii) Which stand characteristics can be considered key factors in shaping insect behaviour? We hypothesised that population density and defoliation intensity may be influenced by factors such as woody species abundance, specific composition of the forest, canopy density, and stand age.

MATERIAL AND METHODS

Study site and data collection

The research was conducted in Tatina Forest, located in Călărași County, Romania (Fig. 1). This forest is managed by Mitreni Forest District and is predominantly composed of Quercus pedunculiflora K. Koch, in association with other deciduous tree species as Quercus cerris L., Ulmus minor Mill., Tilia tomentosa Moench., Fraxinus excelsior L. and Gleditschia triacanthos L.

To investigate the relationship between insect behaviour and stand structure characteristics, we conducted a comprehensive collection of data focusing on two main aspects:

- Stand characteristics (predictors of population density and defoliation intensity);
- · Insect reproduction and feeding behaviour

To collect the data, we implemented a network with 42 sample plots, distributed on a grid at intervals of 300 m (Fig. 2, Table S1). Each sample plot was defined as the centre of a circle with a radius of approximately 11.29 m, covering an area of about 400 m². Since, regardless of the degree of infestation and outbreak phase, no visible defoliation occurs in *Robinia pseudoacacia* forests, indicating that black locust is an unsuitable food source for

L. dispar (Simionescu et al., 2000), we excluded sample plots that fell within black locust stands from the data collection process. In total, 35 sample plots were inventoried, representing an area of 1400 ha, consisting of 504 trees. The data collection process took place over a period of three years, from 2021 to 2023.

The stand characteristics (predictors) considered for each sample plot are listed in Table 1.

Regarding the reproduction and feeding behaviour of the insects, two types of information were gathered:

- Population density, expressed by the number of egg masses per sample plot;
- Defoliation intensity, expressed by the degree of defoliation caused by larvae at the end of the feeding period.

Population density was determined by direct counting in the field (without collecting) in January of each year, assessing the egg masses on each tree within the sample plots. The term "egg masses" strictly refers to the number of egg layings, without considering the size or number of eggs in each. Therefore, each egg mass was counted equally, regardless of the fecundity of each. They were recorded for each tree (regardless of species) and subsequently either the average number of egg masses per tree (see Fig. 6) or the total number of egg masses per plot sample was calculated (see Fig. 4).

Defoliation intensity was assessed in the field in June, after the completion of larval feeding. For each sample plot, average defoliation was estimated based on assessments of all trees within the plot, considering the degree of defoliation for each tree. Each tree in the sample plots was inventoried (regardless of species), and the level of defoliation – expressed as a deviation from normal crown integrity – was quantified by percentage intervals of 5 (Buzatu et al., 2023), ranging from 0 (undefoliated) to 100 (completely defoliated).

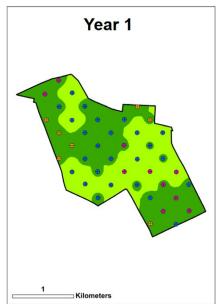
Mapping defoliation produced by Lymantria dispar

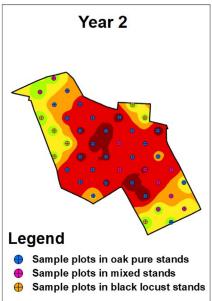
The data regarding insect-induced damage were interpreted both statistically and graphically through image analysis, and the generation of thematic maps based on the intensity of defoliation. This graphic processing provides an overall picture of the temporal and spatial dynamics of defoliation intensity during the study period.

Thematic maps were obtained with ArcMap 10.5 software (ESRI), employing ArcToolbox-Special Analyst Tools-Interpolation-IDW to generate a raster dataset. We selected this method based on the assumption that the calculated average intensity at each sample plot has a local influence that diminishes with distance, with values measured closest to the location having a greater impact on the predicted values than those farther away. To render the raster dataset, the 'classified' method with a single-band raster layer was used. To highlight the differences between sample plots in terms of inflicted damage, we opted for the 'manual classified' method, allowing us to set the class breaks at

Table 1. Analysis of stand characteristics.

Stand characteristics	Assessment indicators	Categories	Sample plot structure Low abundance Medium abundance High abundance	
Woody species abundance	Number of tree species present in sample plot	1 species 2 species 3 species		
Specific composition	Proportion of oak in forest composition	100% oak Oak + other tree species	Pure stand Mixed stand	
Canopy density	Ratio between canopy projection area and stand area	0.7–0.9 0.4–0.6	Almost closed canopy Open canopy	
Stand age	e The average age of the component trees		Young stand Mature stand	





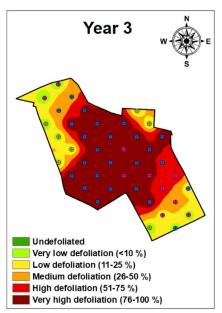


Fig. 3. Spatial patterns of Lymantria dispar defoliation over the three-year study period.

threshold values according to the established standards for insect defoliation (Simionescu et al., 2000) (Table 2).

Data analysis

In the initial phase of statistical analysis, Shapiro-Wilk and Levene's tests were applied to assess normality and homoscedasticity of variances. Since the data passed both tests, we proceeded to the second stage, applying a parametric approach. We conducted a two-way ANOVA (analysis of variance) to examine the effects of stand characteristics as independent variables on the population density and defoliation intensity as dependent variables.

Data analyses were conducted using STATISTICA 8.0 software (StatSoft Inc., 2007).

RESULTS

Temporal evolution of defoliation produced by *Lymantria dispar*: A cartographic analysis

Visual analysis of the data indicates that in the first year of research, no significant damage caused by *L. dispar* was recorded. However, from the second year, defoliations intensified (with the exception of black locust stands), reaching a peak in the third year, marked by the most significant defoliations (Fig. 3). A preliminary review of the cartographic analysis from each year reveals that the insect exhibited a preference for defoliating pure oak stands over mixed stands.

Table 2. Threshold values for defoliation ranges used in thematic mapping.

Defoliation range	The degree of defoliation	Colour ramp
< 1%	Undefoliated	
1–10%	Very low	
10.1-25%	Low	
25.1-50%	Medium	
50.1-75%	High	
>75%	Very high	

Exploring the relationship between reproduction and feeding behaviour of *Lymantria dispar* and stand characteristics

The relationship between insect population density and stand characteristics

Data analyses indicate that in the first two years of the study, the population density, expressed by the number of egg masses, was not significantly affected (p > 0.05) by any of the stand characteristics. In the third year, a significant increase in population density was observed in stands consisting of only one (p = 0.024) or two (p < 0.001) tree species compared to those consisting of three species (Fig. 4A), and additionally in stands composed solely of oak compared to those in which oak was mixed with other tree species (p = 0.013) (Fig. 4B). Canopy density and stand age had no significant influence (p > 0.05) on population density expressed by the number of egg masses (Fig. 4C, D).

The relationship between defoliation intensity and stand characteristics

Results indicate that in the first year of the study, when both the insect population and defoliation levels were low, defoliation intensity was not significantly influenced (p > 0.05) by any of the stand characteristics. From the second year, both woody species abundance and specific forest composition began to play a significant role in the level of defoliation, confirming the cartographic analysis. Defoliation intensity increased notably in stands consisting of only one (p < 0.001) or two (p < 0.001) species compared to those consisting of three species (Fig. 5A) and in pure oak stands compared to mixed stands (p < 0.001) (Fig. 5B). Furthermore, canopy density (Fig. 5C) and stand age (Fig. 5D) continued to have no significant influence (p > 0.05) on defoliation intensity.

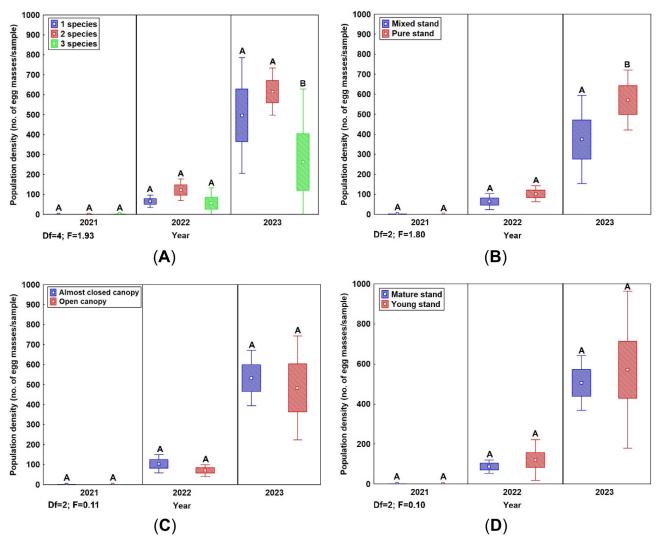


Fig. 4. Temporal analysis of the relationship between insect population density and forest stand characteristics: (A) Woody species abundance; (B) Specific composition; (C) Canopy density; (D) Stand age. Differences between the means marked with different letters were statistically significant (*p* < 0.05) according to two-way ANOVA.

The feeding and oviposition preferences of *Lymantria dispar* across tree species

In the second year of the study, a distinct preference for Q. pedunculiflora was observed in terms of reproduction behaviour (Fig. 6A). On average, L. dispar deposited significantly more egg masses on Q. pedunculiflora in comparison with Q. cerris (p < 0.001), T. tomentosa (p < 0.001), and other broad-leaved tree species, but not significantly more than U. minor (p > 0.05). This preference persisted throughout the third year, with L. dispar continuing to deposit significantly more egg masses on Q. pedunculiflora than on all other species, including Q. cerris (p < 0.001), U. minor (p = 0.002), T. tomentosa (p < 0.001), and other broad-leaved tree species (p < 0.001).

As for feeding preference, in the second year, *L. dispar* exhibited a distinct preference for *Q. pedunculiflora*, with significantly higher defoliation intensity compared to *Q. cerris* (p < 0.001), *U. minor* (p < 0.001), *T. tomentosa* (p < 0.001), and other broad-leaved tree species, which showed no defoliation (p < 0.001). In the third year, as the insect population increased, defoliation continued to be highest

on *Q. pedunculiflora*, significantly higher than on *Q. cerris* (p < 0.001), *T. tomentosa* (p < 0.001), and other broadleaved tree species (p < 0.001). However, the difference in defoliation intensity between *Q. pedunculiflora* and *U. minor* was not statistically significant (p > 0.05).

DISCUSSION

The results obtained in this study provide a detailed perspective on the behaviour of *L. dispar* in relation to the characteristics of the forest stand. The analysis not only revealed dynamic and effervescent temporal and spatial patterns, but also identified the stand characteristics that played a decisive role in this phenomenon. For forest managers, understanding the reproduction and feeding behaviour of insect pests and identifying key factors in such phenomena are essential, as sporadic outbreaks of such insects pose a significant threat to forest health in many countries, leading to substantial losses and environmental resource degradation (Boukouvala et al., 2022).

The rapid spread of infestations – from very weak defoliation in the first year to strong in the second, and pre-

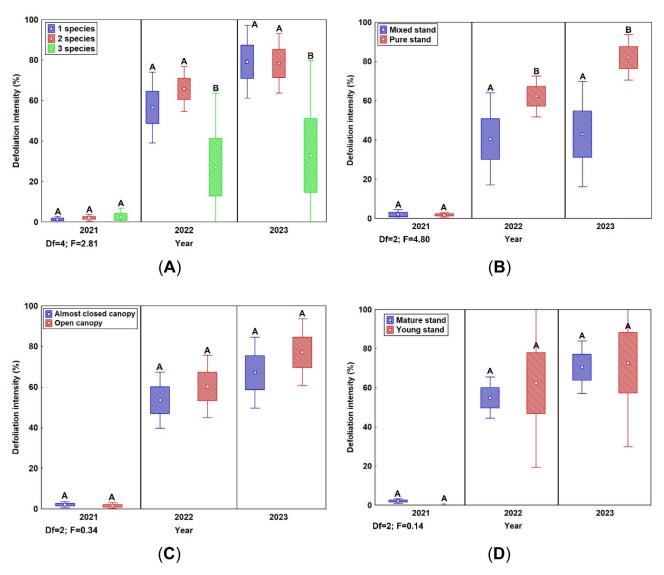


Fig. 5. Temporal analysis of the relationship between defoliation intensity and forest stand characteristics: (A) Woody species abundance; (B) Specific composition; (C) Canopy density; (D) Stand age. Differences between the means marked with different letters were statistically significant (p < 0.05) according to two-way ANOVA.

dominantly very strong by the third year - can be explained by the natural population cycle, a common phenomenon in many species of forest Lepidoptera (Berryman, 1995; Myers & Cory, 2013). L. dispar is one of the Lepidoptera species that exhibit a cyclic population dynamic (Johnson et al., 2005; McManus & Csóka, 2007; Hlásny et al., 2016; Inoue et al., 2019). The rapid population growth observed in this study, from barely detectable to very strong defoliation in just two years could be attributed to a rapid increase in population density over a few generations. At times, densities can reach levels sufficient to defoliate trees with more than 5000 egg masses per hectare (Liebhold et al., 2000). Moreover, another factor contributing to this increase could be the type of outbreak produced by this eruptive-pulsator pest with variable cyclicality, depending on the phytogeographic zone, seasonal conditions, and characteristics of the stands (Netoiu et al., 2016).

Regarding the indicators of insect behaviour, mixed stands (characterised by higher woody species abundance and oak in composition with other species) were associated with both lower levels of defoliation and a reduced number of egg masses, when compared to pure stands. This highlights the influential impact of tree species abundance on the reproduction and feeding behaviour of this insect species. However, deeper analysis revealed that in mixed forests, the number of woody species plays a crucial role in significantly influencing these indicators. Specifically, only in stands with three species was the defoliation and population density significantly lower compared to stands with one or two species. Davidson (2001) showed that defoliation intensity increases as the proportion of host species increases. There are studies indicating that a certain tree species is less affected by herbivorous insects when grown in mixed stands than in monocultures, a phenomenon known as associational resistance (Jactel & Brockerhoff, 2007; Castagneyrol et al., 2014; Jactel et al., 2017). This may be due to the fact that, in addition to its own resistance to herbivores, a plant species may experience associational resistance to herbivores when in close proximity to other plant species (Tahvanainen & Root, 1972). In a Europe-

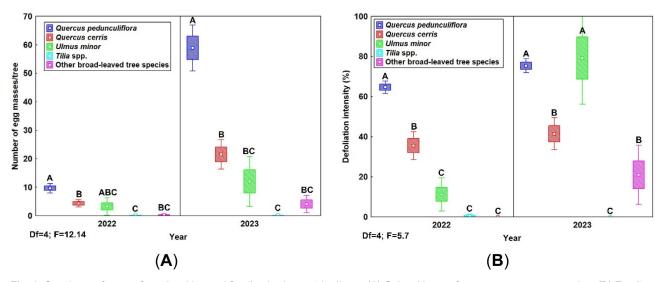


Fig. 6. Species preference for oviposition and feeding by *Lymantria dispar*. (A) Oviposition preferences across tree species; (B) Feeding preferences across tree species. Differences between the means marked with different letters were statistically significant (p < 0.05) according to two-way ANOVA.

an study (Guyot et al., 2016), a positive relationship was found between tree species richness and their resistance to insects, with leaf damage significantly decreasing with the number of species in the forest. This resistance may be based on the preference of herbivores to stay where the host plant is abundant (Root, 1973). Additionally, this phenomenon can be explained by the fact that natural enemies are more abundant in mixed forests than in monocultures (Elton, 1958; Root, 1973). However, there are also studies that refute the influence of diversity on herbivore attacks (Vehviläinen et al., 2007). Nevertheless, another study suggests that even if forest diversity and management did not influence forest resistance to defoliation by L. dispar, these factors can significantly contribute to the recovery after a disturbance event (Blanco-Rodríguez & Espelta, 2022). In any case, studies indicate that higher diversity indices of tree species in a forest can have positive implications for the ecosystem's resilience and adaptability to climate change, enhancing their capacity to provide various ecosystem services (Leca et al., 2023). Regarding canopy density and the presence of shrubs, we did not identify any significant differences that could prove these factors influence the behaviour of L. dispar. However, a study conducted at a distance of approximately 200 km (Netoiu et al., 2016) indicates that forest stands with a low crown density and a high percentage of land covered with shrubs are unfavourable for infestations by L. dispar. Additionally, Tomescu et al. (2010) showed that the development of L. dispar outbreaks can be influenced by stand properties, including tree density. Furthermore, it is suggested that in the context of canopy defoliation, thinning can exacerbate damage (Marini et al., 2022). Thus, thinned forests are shown to favour phenomena such as the density of sawfly larvae (Ostaff et al., 2006), the percentage of trees attacked by the pine processionary moth (Régolini et al., 2014) and the growth performance of spruce budworm caterpillars (Fuentealba & Bauce, 2012).

Moreover, stand age is a stand characteristic that has been demonstrated not to influence the behaviour of *L. dispar* in our study. In contrast, a study that tracked infestations caused by *L. dispar* in beech forests (Tomescu et al., 2010) indicated that forest stand age significantly determined the level of insect infestations.

Regarding the preferences of L. dispar, our findings highlight a consistent preference of the insect for Q. pedunculiflora, both in terms of feeding and reproduction behaviour. However, in the final year of the study, when the population grew significantly, our results indicate that the insect fed on U. minor leaves to the same extent as those of Q. pedunculiflora. This phenomenon could be explained by the fact that, with the population increase, the available food resources became limited, and L. dispar was forced to adapt to other tree species to ensure its survival. Additionally, it was observed that both in the second and third years, the insect clearly preferred O. pedunculiflora over Q. cerris, further complementing the results of previous studies. Milanović et al. (2014) investigated the preference and performance of the insect on three species of European oaks, concluding that Q. cerris was the most preferred and suitable host. Furthermore, Foss & Rieske (2003) indicated that Quercus palustris Münchh. leaves were the most suitable among the five oak species studied on which L. dispar larvae experimentally grew.

Over three years, our study allowed for a detailed analysis of insect behaviour, while the dense network of sample plots ensured extensive coverage of the study area. However, it is important to note that the study is limited to a single geographical area (Tatina Forest, Călărași County), and the inclusion of other external factors, such as climatic, edaphic, or seasonal conditions from multiple study areas, was not possible. Therefore, the exclusion of these factors from the analysis represents a significant limitation in assessing the environmental factors' impact on the defoliator's behaviour and may prevent the application of results to other forest regions. In conclusion, this research has

made significant contributions to understanding the temporal and spatial dynamics of defoliation intensity by *L. dispar* in Tatina Forest. These results provide forest managers with a solid foundation for adapting management strategies, considering the impact of spatial and temporal variations in defoliator behaviour.

AUTHOR CONTRIBUTIONS. F.B: Conceptualization; data curation; formal analysis; investigation; methodology; resources; writing – original draft; writing – review and editing. D.T.: Conceptualization; data curation; formal analysis; investigation; methodology; resources; writing – original draft; writing – review and editing. C.N.: Conceptualization; funding acquisition; methodology; project administration; resources; supervision; writing–review and editing.

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CONFLICT OF INTEREST STATEMENT. The authors declare no conflicts of interest.

DATA AVAILABILITY. The original data is available on request from the author.

REFERENCES

- AUKEMA J.E., LEUNG B., KOVACS K., CHIVERS C., BRITTON K.O., ENGLIN J., FRANKEL S.J., HAIGHT R.G., HOLMES T.P., LIEBHOLD A.M. ET AL. 2011: Economic impacts of non-native forest insects in the continental United States. *PLoS ONE* 6: e24587, 7 pp.
- Berryman A.A. 1986: Forest Insects: Principles and Practice of Population Management. Plenum, New York, 279 pp.
- BERRYMAN A.A. 1995: Population cycles: a critique of the maternal and allometric hypotheses. *J. Anim. Ecol.* **64**: 290–293.
- Blanco-Rodríguez M.Á. & Espelta J.M. 2022: Tree species composition and management influence short-term resilience to defoliation by *Lymantria dispar* L. in oak forests. *For. Ecol. Manag.* **520**: 120399, 13 pp.
- BOUKOUVALA M.C., KAVALLIERATOS N.G., SKOURTI A., PONS X., ALONSO C.L., EIZAGUIRRE M., FERNANDEZ E.B., SOLERA E.D., FITA S. & BOHING T. 2022: *Lymantria dispar* (L.) (Lepidoptera: Erebidae): Current status of biology, ecology, and management in Europe with notes from North America. *Insects* 13: 854, 35 pp.
- BUZATU A., NEţOIU C., APOSTOL B. & BADEA O. 2023: The use of remote sensing indices derived from Sentinel 2 satellite images for the defoliation damage assessment of *Lymantria dispar*. *Ann. For. Res.* **66**: 123–138.
- CAMERINI G. 2009: Factors affecting *Lymantria dispar* mortality in a willow wood in northern Italy. *Bull. Insectol.* **62**: 21–25.
- Capinera J.L. & Barbosa P. 1977: Influence of natural diets and larval density on gypsy moth, *Lymantria dispar* (Lepidoptera: Orgyiidae), egg mass characteristics. *Can. Entomol.* **109**: 1313–1318.
- CASTAGNEYROL B., JACTEL H., VACHER C., BROCKERHOFF E.G. & KORICHEVA J. 2014: Effects of plant phylogenetic diversity on herbivory depend on herbivore specialization. *J. Appl. Ecol.* 51: 134–141.
- CSOKA G. 1996: Aszályos évek-fokozódó rovarkárok erdeinkben. [Years of drought-increasing damage by forest insects.] *Növényvédelem* **32**: 545–551 [in Hungarian].

- DAVIDSON C.B., GOTTSCHALK K.W. & JOHNSON J.E. 1999: Tree mortality following defoliation by the European gypsy moth (*Lymantria dispar* L.) in the United States: a review. *Forest Sci.* 45: 74–84.
- DAVIDSON C.B., JOHNSON J.E., GOTTSCHALK K.W. & AMATEIS R.L. 2001: Prediction of stand susceptibility and gypsy moth defoliation in Coastal Plain mixed pine hardwoods. *Can. J. For. Res.* 31: 1914–1921.
- DAY W.R. 1927: The oak mildew *Microsphaera quercina* (Schw.) Burrill and *Armillaria mellea* (Vahl) Quel. in relation to the dying back of oak. *Forestry* 1: 108–112.
- DOANE C.C. & McManus M.L. (EDS) 1981: The Gypsy Moth: Research Toward Integrated Pest Management. USDA, Washington D.C., 757 pp.
- ELKINTON J.S. & LIEBHOLD A.M. 1990: Population dynamics of gypsy moth in North America. *Annu. Rev. Entomol.* **35**: 571–596.
- ELTON C.S. 1958: The Ecology of Invasions by Animals and Plants. Springer, Cham, xxi + 261 pp.
- Fajvan M.A., Rentch J. & Gottschalk K. 2008: The effects of thinning and gypsy moth defoliation on wood volume growth in oaks. *Trees* 22: 257–268.
- FALCK R. 1918: Oak decline in Lödderitz forest district and in Westphalia. Z. Forst. Jagdw. 50: 123–132.
- Foss L.K. & RIESKE L.K. 2003: Species-specific differences in oak foliage affect preference and performance of gypsy moth caterpillars. *Entomol. Exp. Appl.* **108**: 87–93.
- Fratian A. 1973: Influența defolierilor produse de insecte asupra productivității pădurilor. [The Influence of Insect Defoliation on Forest Productivity.] Ceres, Bucuresti, 197 pp. [in Romanian].
- FUENTEALBA A. & BAUCE É. 2012: Soil drainage class, host tree species, and thinning influence host tree resistance to the spruce budworm. *Can. J. For. Res.* 42: 1771–1783.
- GOTTSCHALK K.W. 1989: Gypsy moth effects on mast production. In McGee C.E. (ed.): *Proceedings of the Workshop Southern Appalachian Mast Management, August 14–16, 1989, University of Tennessee, Knoxville.* pp. 42–50.
- GUYOT V., CASTAGNEYROL B., VIALATTE A., DECONCHAT M. & JACTEL H. 2016: Tree diversity reduces pest damage in mature forests across Europe. *Biol. Lett.* **12**: 20151037, 5 pp.
- HÉRARD F., CHEN K. & CAMERON E.A. 1996: Natural enemy impact on gypsy moth in Alsace, France, during 1995. In Fosbroke S.L.C. & Gottschalk K.W. (eds): Proceedings of the U.S. Department of Agriculture Interagency Gypsy Moth Research Forum 1996, January 16–19, 1996, Annapolis, MD. Gen. Tech. Rep. NE-230, USDA, Forest Service, NE Experiment Station, Radnor, PA, p. 39.
- HLÁSNY T., TROMBIK J., HOLUŠA J., LUKÁŠOVÁ K., GRENDÁR M., TURČÁNI M., ZÚBRIK M., TABAKOVIĆ-TOŠIĆ M., HIRKA A., BUKSHA I. ET AL. 2016: Multi-decade patterns of gypsy moth fluctuations in the Carpathian Mountains and options for outbreak forecasting. *J. Pest Sci.* **89**: 413–425.
- HOCH G., ZUBRIK M., NOVOTNY J. & SCHOPF A. 2001: The natural enemy complex of the gypsy moth, *Lymantria dispar* (Lep., Lymantriidae) in different phases of its population dynamics in eastern Austria and Slovakia a comparative study. *J. Appl. Entomol.* **125**: 217–227.
- HRAŠOVEC B., PERNEK M. & MATOŠEVIĆ D. 2008: Spruce, fir and pine bark beetle outbreak development and gypsy moth situation in Croatia in 2007. — Forstschutz Aktuell 44: 12–13.
- ILYINYKH A.V., KURENSHCHIKOV D.K., BABURIN A.A. & IMRANO-VA E.L. 2011: Factors influencing the duration of gypsy moth (*Lymantria dispar* L.) population outbreaks. — *Russ. J. Ecol.* **42**: 236–240.

- INOUE M.N., SUZUKI-OHNO Y., HAGA Y., AARAI H., SANO T., MARTEMYANOV V.V. & KUNIMI Y. 2019: Population dynamics and geographical distribution of the gypsy moth, *Lymantria dispar*, in Japan. *For. Ecol. Manag.* 434: 154–164.
- Jactel H. & Brockerhoff E.G. 2007: Tree diversity reduces herbivory by forest insects. *Ecol. Lett.* **10**: 835–848.
- Jactel H., Bauhus J., Boberg J., Bonal D., Castagneyrol B., Gardiner B., Gonzalez-Olabarria J.R., Koricheva J., Meurisse N. & Brockerhoff E.G. 2017: Tree diversity drives forest stand resistance to natural disturbances. *Curr. For. Rep.* **3**: 223–243.
- JOHNSON D.M., LIEBHOLD A.M., BJØRNSTAD O.N. & McManus M.L. 2005: Circumpolar variation in periodicity and synchrony among gypsy moth populations. — J. Anim. Ecol. 74: 882–892.
- Leca Ş., Popa I., Chivulescu Ş., Popa A., Pitar D., Dobre A.-C., Pascu I.-S., Apostol B. & Badea O. 2023: Structure and diversity in a periurban forest of Bucharest, Romania. *Ann. For. Res.* **66**: 139–153.
- LIEBHOLD A.M., GOTTSCHALK K.W., MUZIKA R.-M., MONTGOMERY M.E., YOUNG R., O'DAY K.. KELLEY B. 1995: Suitability of North American Tree Species to Gypsy Moth: A Summary of Field and Laboratory Tests. Gen. Tech. Rep. NE-211. USDA, Forest Service, NE Forest Experiment Station, Radnor, PA, 34 pp.
- LIEBHOLD A., ELKINTON J., WILLIAMS D. & MUZIKA R. 2000: What causes outbreaks of the gypsy moth in North America? *Popul. Ecol.* **42**: 257–266.
- LUCIANO P. & PROTA R. 1995: Insect pests in Sardinian cork-oak forests. *IOBC/WPRS Bull.* **18**: 1–7.
- Manion P.D. 1981: *Tree Disease Concepts*. Prentice-Hall, Englewood Cliffs, NJ, 399 pp.
- MANION P.D. & LACHANCE D. (EDS) 1992: Forest Decline Concepts. APS Press, St. Paul, MN, 249 pp.
- MARCU G. 1966: Studiul cauzelor și al metodelor de prevenire și combatere a uscării stejarului. [Study of the Causes and Methods of Preventing and Combating Oak Drying.] Centrul de Documentare Tehnică pentru Economia Forestieră, Bucharest, 582 pp. [in Romanian].
- MARINI L., AYRES M.P. & JACTEL H. 2022: Impact of stand and landscape management on forest pest damage. *Annu. Rev. Entomol.* 67: 181–199.
- McManus M. & Csóκa G. 2007: History and impact of gypsy moth in North America and comparison to the recent outbreaks in Europe. *Acta Silvat. Lignar. Hungar.* **3**: 47–64.
- MESHKOVA V.L. 1999: Forest pests outbreaks prognosis on the base of climatic factors analysis. In Forster B., Knížek M. & Grodzki W. (eds): *Methodology of Forest Insect and Disease Survey in Central Europe. Proceedings of the Second Workshop of the IUFRO Working Party 7.03.10 April 20–23, 1999, Sion-Chateauneuf, Switzerland.* Swiss Federal Institute for Forest, Snow and Landscape Research, Birmensdorf, pp. 74–79.
- MILANOVIĆ S., LAZAREVIĆ J., POPOVIĆ Z., MILETIĆ Z., KOSTIĆ M., RADULOVIĆ Z., KARADŽIĆ D. & VULETA A. 2014: Preference and performance of the larvae of *Lymantria dispar* (Lepidoptera: Lymantriidae) on three species of European oaks. *Eur. J. Entomol.* 111: 371–378.
- MORAAL L.G. 1996: 50 jaar monitoring van insectenplagen op bomen en struiken: In bossen, natuurgebieden en wegbeplantingen. [50 years of monitoring insect pests on trees and shrubs: in forests, nature reserves and road plantings.] *Nederlands Bosbouw Tijdschr.* 68: 194–203 [in Dutch].
- MUZIKA R.M. & LIEBHOLD A.M. 1999: Changes in radial increment of host and nonhost tree species with gypsy moth defoliation. Can. J. For. Res. 29: 1365–1373.

- MUZIKA R.M. & LIEBHOLD A.M. 2000: A critique of silvicultural approaches to managing defoliating insects in North America.

 Agric. For. Entomol. 2: 97–105.
- MUZIKA R.M., LIEBHOLD A.M. & GOTTSCHALK K.W. 1998: Effects of silvicultural management on gypsy moth dynamics and impact: an eight year study. In McManus M.L. & Liebhold A.M. (eds): Proceedings: Population Dynamics, Impacts, and Integrated Management of Forest Defoliating Insects, Banska Stiavnica, Slovak Republic, August 18–23, 1996. Gen. Tech. Rep. NE-247, USDA, Forest Service, NE Experiment Station, Radnor, PA, pp. 261–268.
- MYERS J.H. & CORY J.S. 2013: Population cycles in forest Lepidoptera revisited. — Annu. Rev. Ecol. Evol. Syst. 44: 565–592.
- NAIDOO R. & LECHOWICZ M.J. 2001: Effects of gypsy moth on radial growth of deciduous trees. *For. Sci.* 47: 338–348.
- NEȚOIU C. 1998: Cercetări asupra evoluției proceselor fiziologice de bază sub influnța defolierilor la stejarul pedunculat și gârniță. [Research on the Evolution of Basic Physiological Processes under the Influence of Defoliation in Pedunculate Oaks.] PhD thesis, Academia de Științe Agricole și Silvice Gheorghe Ionescu-Sisești, Bucharest, 62 pp. [in Romanian].
- Neţoiu C. 2000: Influence of the defoliation on physiological processes on the trees. In Simionescu A., Mihalache G., Mihalciuc V., Ciornei C., Chira D., Olenici N., Lupu D., Neţoiu C., Vlăduleasa A., Iliescu M. et al. (eds): *Forest Protection*. Editura Muşatinii, Suceava, pp. 675–683.
- Neţoiu C., Tomescu R. & Buzatu A. 2016: The basic environment and *Lymantria dispar* L. (Lepidoptera, Erebidae) infestations. *Oltenia / Studii și Comunicări Științele Naturii* 32: 71–78.
- OSTAFF D.P., PIENE H., QUIRING D.T., MOREAU G., FARRELL J.C.G. & SCARR T. 2006: Influence of pre-commercial thinning of balsam fir on defoliation by the balsam fir sawfly. *For. Ecol. Manag.* 223: 342–348.
- OSZAKO T. 1997: Oak decline in European forests. In Turok J., Kremer A. & de Vries S.M.G. (eds): First EUFORGEN Meeting on Social Broadleaves. Bordeaux, France, 23–25 October 1997. International Plant Genetic Resources Institute, Rome, pp. 145–151.
- Paini D.R., Mwebaze P., Kuhnert P.M. & Kriticos D.J. 2018: Global establishment threat from a major forest pest via international shipping: *Lymantria dispar*. *Sci. Rep.* 8: 13723, 7 pp.
- PRADE P. & COYLE D.R. 2023: Insect pests of forest trees. In Asiegbu F.O. & Kovalchuk A. (eds): Forest Microbiology. Vol. 3. Tree Diseases and Pests. Elsevier, Amsterdam, pp. 195–211.
- RÉGOLINI M., CASTAGNEYROL B., DULAURENT-MERCADAL A.-M., PIOU D., SAMALENS J.-C. & JACTEL H. 2014: Effect of host tree density and apparency on the probability of attack by the pine processionary moth. *For. Ecol. Manag.* **334**: 185–192.
- Root R.B. 1973: Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecol. Monogr.* **43**: 95–124.
- ROY A.S., McNamara D.G. & Smith I.M. 1995: Situation of *Lymantria dispar* in Europe. *EPPO Bull.* **25**: 611–616.
- SAVOTIKOV I.F., SMETNIK A.I. & ORLINSKII A.D. 1995: Situation of the Asian form of gypsy moth (*Lymantria dispar*) in Russia and in the world. *EPPO Bull.* **25**: 617–622.
- SHIGO A.L. 1986: A New Tree Biology Dictionary: Terms, Topics, and Treatments for Trees and their Problems and Proper Care. Shigo and Trees Associates, Durham, NH, 132 pp.
- Simionescu A., Mihalache G., Mihalciuc V., Ciornei C., Chira D., Olenici N., Lupu D., Neţoiu C., Vladuleasa A., Iliescu M. et al. 2000: *Protecția pădurilor.* [Forest Protection.] Editura Musatinii, Suceava, 867 pp. [in Romanian].

- SINCLAIR W.A. 1965: Comparisons of recent declines of white ash, oaks, and sugar maple in northeastern woodlands. *Cornell Plantat.* **20**: 62–67.
- SINCLAIR W.A. 1967: Decline of hardwoods: possible causes. In: *Proceedings of the 42th International Shade Tree Conference, Urbana, IL, Aug. 1966.* pp. 17–32.
- Sousa E.M.R. 1995: Les principaux ravageurs du chêne-liège au Portugal. Leurs relations avec le déclin des peuplements. *IOBC/WPRS Bull.* **18**: 18–23.
- Tabaković-Tošić M. 2005: A new gypsy moth outbreak in Serbia. *Biljni Lekar* **33**: 44–50.
- Tabaković-Tošić M., Marković M. & Milosavljević M. 2015: Gypsy moth outbreaks in forest complexes of Jablanica Region (Southern Serbia) in the period 1996–2014. *For. Ideas* 21: 285–292.
- Tahvanainen J.O. & Root R.B. 1972: The influence of vegetational diversity on the population ecology of a specialized herbivore, *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae). *Oecologia* 10: 321–346.
- Tomescu R. & Neţoiu C. 2006: Control of the broad leave's mains defoliators in Romania in 2005. In: *Proceedings of the Workshop on "Methodology of Forest Insect and Disease Survey in Central Europe" Sept. 11th–14th, 2006.* Federal Research and Training Centre for Forests, Natural Hazards and Landscape Forest Training Centre Ort, Gmunden, pp. 263–270.
- Tomescu R., Neţoru C. & Tăut I. 2010: The analysis of favourable mass multiplication conditions of defoliator *Lymantria dispar* in beech forests from Romania. *ProEnvironment* 3: 9–16.
- VEHVILÄINEN H., KORICHEVA J. & RUOHOMÄKI K. 2007: Tree species diversity influences herbivore abundance and damage: meta-analysis of long-term forest experiments. *Oecologia* 152: 287–298.
- WULF A. & GRASER E. 1996: Gypsy moth outbreaks in Germany and neighboring countries. — *Nachr. Dtsch. Pflanzensch.* 48: 265–269.
- ZÚBRIK M. & NOVOTNÝ J. 1996: The complex of gypsy moth (*Lymantria dispar* L.) parasitoids in Slovakia and other Central European countries. In Fosbroke S.L.C. & Gottschalk K.W. (eds): *Proceeding of the U.S. Department of Agriculture Interagency Research Forum 1996, January 16–19, Annapolis, MD.* U.S. Department of Agriculture Forest Service, Northeastern Forest Experiment Station General Technical Report NE-230, Radnor, PA, pp. 83–88.
- ZÚBRIK M., HAJEK A., PILARSKA D., ŠPILDA I., GEORGIEV G., HRAŠOVEC B., HIRKA A., GOERTZ D., HOCH G. & BARTA M. 2016: The potential for *Entomophaga maimaiga* to regulate gypsy moth *Lymantria dispar* (L.) (Lepidoptera: Erebidae) in Europe. *J. Appl. Entomol.* **140**: 565–579.

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Table S1. Detailed description of monitoring points network.

	01. D	Ctaned desc	Tiption of monitoring points her	
	۸	A I I		Species
Plot		Analyzed	Specific forest composition	proportion
	(m²)	trees		in plot
				samples
1	400	40	Tillia tomentosa	78%
			Quercus pedunculiflora	22%
			Tillia tomentosa	59%
2	400	29	Quercus pedunculiflora	27%
			Quercus cerris	14%
3			lyzed (<i>Robinia pseudoacacia</i> L	
4	400	18	Quercus pedunculiflora	100%
_ 5	400	5	Quercus pedunculiflora	100%
6			lyzed (<i>Robinia pseudoacacia</i> L	
7	400	18	Quercus pedunculiflora	100%
8	400	7	Quercus pedunculiflora	100%
9			lyzed (<i>Robinia pseudoacacia</i> L	
_10		Not ana	lyzed (<i>Robinia pseudoacacia</i> L	.)
_11	400	11	Quercus pedunculiflora	100%
12	400	8	Quercus pedunculiflora	100%
13	400	10	Quercus pedunculiflora	100%
14	400	10	Quercus pedunculiflora	100%
15	400	24	Quercus pedunculiflora	100%
16	400	18	Quercus pedunculiflora	100%
17	400	8	Quercus pedunculiflora	100%
18		Not ana	lyzed (<i>Robinia pseudoacacia</i> L	.)
19	400	7	Quercus pedunculiflora	100%
20	400	8	Quercus pedunculiflora	100%
21	400	14	Quercus pedunculiflora	100%
			Quercus pedunculiflora	71%
22	400	6	Ulmus minor	29%
23	400	10	Quercus pedunculiflora	100%
24	700		lyzed (<i>Robinia pseudoacacia</i> L	
25	400	1	Quercus pedunculiflora	100%
26	400	16	Quercus pedunculiflora	100%
	700	10	Quercus pedunculiflora	60%
27	400	20	Ulmus minor	40%
28	400	13	Quercus pedunculiflora	100%
29	400	10	Quercus pedunculiflora	100%
30	400	11	Quercus pedunculiflora	100%
31	400	11	Quercus pedunculiflora	100%
	400	- !!	Quercus pedunculiflora	86%
32	400	15	Prunus mahaleb	7%
32	400	13	Ulmus minor	7%
33	400	5	Quercus pedunculiflora	100%
34	400	 11	Quercus pedunculiflora	100%
	400	- ''		
35	400	20	Quercus pedunculiflora	85% 15%
			Prunus mahaleb	
36	400	19	Quercus pedunculiflora	89%
		NI4	Acer platanoides	11%
_37		inot ana	lyzed (Robinia pseudoacacia L	
20	400	20	Quercus pedunculiflora	55%
38	400	20	Prunus mahaleb	30%
			Acer platanoides	15%
39	400	21	Quercus pedunculiflora	95%
			Acer platanoides	5%
40	400	18	Quercus cerris	100%
41	400	30	Quercus cerris	100%
40	400	40	Quercus cerris	58%
42	400	12	Quercus pedunculiflora	25%
-	4.400-		Ulmus minor	17%
Iotal	14000	504		