

## ARTICLE

# Trait-mediated responses of caterpillar communities to spongy moth outbreaks and subsequent tebufenozide treatments

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## Abstract

Outbreaks of the spongy moth *Lymantria dispar* can have devastating impacts on forest resources and ecosystems. Lepidoptera-specific insecticides, such as *Bacillus thuringiensis* var. *kurstaki* (BTK) and tebufenozide, are often deployed to prevent heavy defoliation of the forest canopy. While it has been suggested that using BTK poses less risk to non-target Lepidoptera than leaving an outbreak untreated, in situ testing of this assumption has been impeded by methodological challenges. The trade-offs between insecticide use and outbreaks have yet to be addressed for tebufenozide, which is believed to have stronger side effects than BTK. We investigated the short-term trade-offs between tebufenozide treatments and no-action strategies for the non-target herbivore community in forest canopies. Over 3 years, Lepidoptera and Symphyta larvae were sampled by

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canopy fogging in 48 oak stands in southeast Germany during and after a spongy moth outbreak. Half of the sites were treated with tebufenozide and changes in canopy cover were monitored. We contrasted the impacts of tebufenozide and defoliator outbreaks on the abundance, diversity, and functional structure of chewing herbivore communities. Tebufenozide treatments strongly reduced Lepidoptera up to 6 weeks after spraying. Populations gradually converged back to control levels after 2 years. Shelter-building species dominated caterpillar assemblages in treated plots in the post-spray weeks, while flight-dimorphic species were slow to recover and remained underrepresented in treated stands 2 years post-treatment. Spongy moth outbreaks had minor effects on leaf chewer communities. Summer Lepidoptera decreased only when severe defoliation occurred, whereas Symphyta declined 1 year after defoliation. Polyphagous species with only partial host plant overlap with the spongy moth were absent from heavily defoliated sites, suggesting greater sensitivity of generalists to defoliation-induced plant responses. These results demonstrate that both tebufenozide treatments and spongy moth outbreaks alter canopy herbivore communities. Tebufenozide had a stronger and longer lasting impact, but it was restricted to Lepidoptera, whereas the outbreak affected both Lepidoptera and Symphyta. These results are tied to the fact that only half of the outbreak sites experienced severe defoliation. This highlights the limited accuracy of current defoliation forecast methods, which are used as the basis for the decision to spray insecticides.

#### KEYWORDS

defoliation, DNA barcoding, Lepidoptera, *Lymantria dispar*, oak forest, pest control, Symphyta, tebufenozide

## INTRODUCTION

Since the publication of Rachel Carson's *Silent Spring* in 1962, the ecological damage caused by the widespread use of pesticides has been at the heart of a heightened public consciousness on environmental issues. Although increased regulatory scrutiny put an end to the DDT era (Whitney, 2012), pesticides have remained the linchpin of pest management strategies despite mounting evidence of their large-scale side effects (Goulson, 2013; Li et al., 2020; Morrissey et al., 2015) as well for their plausible role in the current trend of insect declines (Forister et al., 2019).

Against this backdrop, pesticide use in forestry is increasingly met with public outrage, as rising concerns about environmental impacts are added to the rooted perception that spraying presents substantial health risks to local populations (e.g., Möller, 2020). However, forestry's contribution to the global pesticide footprint is negligible as it accounts for only a very minor share of the global pesticide market (Thompson, 2011). Pesticide use strategies in forestry widely differ from those implemented in cropping systems. As ecosystems, forests are far more

resilient to herbivory, and timber production volumes are, unlike crop yields, not sensitive to endemic levels of damage. As a result, the economic thresholds for insecticide application are much higher in forestry than in agriculture (Letourneau, 2012; Thompson, 2011), and forests are only treated when a risk of total defoliation is anticipated. In temperate regions, a few species of moths (Lepidoptera) and sawflies (Symphyta) show periodic population outbreaks that can pose such a risk (Berryman, 1988), with potentially dire implications for the health of affected trees (Lobinger, 1999; MacLean, 2016). Among them, the spongy moth *Lymantria dispar* L. (Lepidoptera: Erebidæ) is considered the most critical defoliator of temperate hardwood forests, notably in Eastern North America where it has infested millions of acres since its introduction in the late 19th century (McManus & Csóka, 2007) and considerable resources are expended on slowing its westward expansion (Mayo et al., 2003). The species is also a serious pest in its native European range where several large-scale defoliation episodes have been recorded over the past three decades (Hlásny et al., 2016; Wulf & Graser, 1996; Zúbrik et al., 2021).

Only a few insecticides are approved to manage spongy moth outbreaks, with the bacterium *Bacillus thuringiensis* var. *kurstaki* (BTK) being the most widely used over the past four decades (Matyjaszczyk et al., 2019; USDA Forest Service, 2022; Villemant, 2010). The toxicity of BTK is restricted to the larval stages of Lepidoptera (henceforth caterpillars) but substantial differences in sensitivity among lepidopteran taxa have been recorded in both laboratory bioassays (Peacock et al., 1998) and field studies (e.g., Rastall et al., 2003; Wagner et al., 1996). The performance of BTK treatments can be somewhat erratic, notably due to its short persistence on foliage after application (van Frankenhuyzen, 2000), sometimes leading to treatment failure (e.g., Martin et al., 2002). The insect growth regulator tebufenozide emerged as a promising alternative to BTK due to its comparably narrow spectrum of action coupled with longer persistence on foliage (Holmes & MacQuarrie, 2016; Sundaram et al., 1996). Tebufenozide is often preferred in situations where BTK treatments are prone to fail (Eggen et al., 2022). Despite the elevated risks of lethal and sublethal exposure associated with its longer persistence (Sundaram et al., 1996), there is a lack of comprehensive exploration of its effects on non-target Lepidoptera. Tebufenozide toxicity records for non-pest species are scarce, and only three impact assessment studies have been published in the scientific literature thus far (Butler, Kondo, & Blue, 1997; Leroy et al., 2019; Westwood et al., 2019).

A debated concept in the field of forest protection posits that the economic thresholds for spraying insecticides are set so high that deciding not to implement management measures, thereby allowing an outbreak to run its course, could potentially have equally negative consequences for non-target organisms (Schweitzer, 2004; Scriber, 2004). Spongy moth outbreaks can be particularly detrimental to chewing herbivores with ecological niche overlap with the spongy moth. Besides the risk of starvation in situations of extreme defoliation (Luciano & Lentini, 1999), outbreaks expose canopy herbivores to elevated concentrations of plant defense compounds, increased hazards from natural enemies and pathogens (Redman & Scriber, 2000), as well as altered light, moisture, and nutrient regimes (Lovett et al., 2006). However, the ecological trade-offs between insecticide-based and “hands-off” management approaches have not been extensively investigated in practical settings. Indeed, only a few studies have simultaneously addressed the effects of spongy moth outbreaks and insecticides, all of them in the context of BTK applications (Luciano & Lentini, 1999; Manderino et al., 2014; Sample et al., 1996). No common conclusion can be drawn from these studies due to broad discrepancies in their objectives, design, and results. Specifically, the reported outbreak effects range from very minor alterations (Manderino et al., 2014; Sample

et al., 1996) to the near total suppression of the non-target assemblage (Luciano & Lentini, 1999). In the case of tebufenozide, the issue has yet to be addressed at all.

The lack of consensus on the issue of insecticide-outbreak trade-offs can be generally attributed to the complex methodological demands inherent in conducting suitable experiments. Namely, studies involving aerial spraying in forests are impeded by methodological shortcomings along multiple phases of the research process: (1) Practical limitations such as the need for intensive population surveys for site selection, complex logistics, or difficulties to secure official clearance for spraying within an appropriate timeframe, often constrained the use inadequately or insufficiently replicated experimental designs (Leroy et al., 2019); (2) Sampling canopy-dwelling insects is complicated by the challenge of accessing tree canopies (Ozanne, 2005), especially the upper crown which cannot be sampled by traditional branch-beating or clipping methods (e.g., Luciano & Lentini, 1999; Sample et al., 1996; Wagner et al., 1996). Besides, the large number of branches required to gather statistically meaningful sample sizes using such methods makes them prohibitively resource-intensive for large-scale applications (Wagner et al., 1996); (3) The identification of caterpillars by morphological examination is challenging, notably due to the frequency of morphological changes across larval instars in many species (Wagner & Hoyt, 2022). The common workaround of rearing adults from larval samples (e.g., Luciano & Lentini, 1999; Miller, 1990; Sample et al., 1996) is prone to failure and may introduce bias in the data due to inflated mortality in individuals sampled in treated areas (Miller, 1990); (4) During an outbreak, defoliation is rarely uniform across sites (Sample et al., 1996) and its effects on the canopy fauna are expected to vary with its magnitude. Nevertheless, defoliation effects have so far only been analyzed qualitatively (defoliated vs. non-defoliated; Luciano & Lentini, 1999; Sample et al., 1996; Timms & Smith, 2011; Work & McCullough, 2000). (5) Past studies suggested that species traits such as shelter-building behavior, dietary overlap with the pest species, dispersal ability, and voltinism mediate exposure and recovery dynamics for both insecticide and outbreak-associated disturbances (e.g., Manderino et al., 2014; Miller, 1990; Scriber, 2004). However, these hypotheses are generally speculative and have yet to be statistically evaluated at the community level.

In this study, we assessed the relative impacts of spongy moth outbreaks and their treatment with tebufenozide on the structure of leaf-chewing herbivore communities in tree canopies, using a two-factorial experimental design. We selected 48 oak stands for which either a high or low risk of defoliation was predicted

based on egg-mass surveys, and treated half of these stands with tebufenozide. We combined morphological examinations and individual-level DNA barcoding to identify more than 20,000 caterpillars and sawfly larvae sampled by canopy fogging over 3 years. We used satellite-borne remote sensing data to timely monitor changes in canopy cover throughout the outbreak and quantify defoliation in a standardized and precise way. We assessed the role of life history in mediating the short- and long-term response of different species to tebufenozide and competition by an outbreaking defoliator. Specifically, we tested the following hypotheses concerning the insecticide effects (Hypotheses 1–4) and the effect of the defoliator outbreak (Hypotheses 5 and 6):

**Hypothesis 1.** Tebufenozide treatments reduce the abundance and diversity of Lepidoptera but do not affect Symphyta due to the high target selectivity of tebufenozide.

**Hypothesis 2.** Shelter-building behavior mitigates the short-term effects of tebufenozide.

**Hypothesis 3.** Individual caterpillars sampled in the treatment year in treated plots are smaller than those sampled in control plots due to sublethal exposure to tebufenozide.

**Hypothesis 4.** The speed of post-disturbance recovery increases with species' mobility and the number of generations per year.

**Hypothesis 5.** High densities of spongy moth caterpillars and defoliation reduce the abundance and diversity of Lepidoptera and Symphyta proportionally to the intensity of the outbreak.

**Hypothesis 6.** Species with large dietary overlap with the spongy moth are more strongly impacted by defoliation than species capable of exploiting less preferred spongy moth hosts.

## MATERIALS AND METHODS

### Study design

The study was conducted in a 2400-km<sup>2</sup> area between the towns of Schweinfurt (North), Bamberg (East), Bad Windsheim (South), and Würzburg (West), in

northwestern Bavaria, Germany. The area includes a significant proportion of oak-dominated woodlands (deciduous oak *Quercus robur* L. and *Quercus petraea* Mattuschka) which suffered from a severe outbreak of the spongy moth *Lymantria dispar* L. (Lepidoptera: Erebidae) between 2018 and 2020. Complete information on site location, characteristics, and selection procedures is provided in Leroy, Lemme, et al. (2021). Briefly, study sites were selected based on the results of a large-scale monitoring program conducted by forest management authorities across the region to identify forest stands at risk of severe defoliation. Defoliation risk was estimated by calculating a risk index based on a threshold of spongy moth egg-mass density per oak stem, up- or downweighed by additional parameters, such as tree vitality and recent outbreak history. Within 12 blocks, we selected four forest stands, two at high and two at low risk of defoliation. All four sites within a block were structurally and compositionally comparable oak stands with a minimum size of 6.7 ha. Each stand within each defoliation risk class was randomly assigned to one of two management strategies: (1) suppression of spongy moth populations with tebufenozide, or (2) no intervention, leaving the spongy moth populations to develop and fluctuate naturally.

We used the insecticide tebufenozide which is the recommended active substance for the management of spongy moth outbreaks in Bavaria, Germany (Hahn et al., 2021). Tebufenozide kills Lepidoptera larvae by triggering a premature molt following ingestion of a lethal dose (Smagghe et al., 2012) and is also known to inhibit feeding and reduce fecundity at sublethal doses (Sundaram et al., 1996; van Frankenhuyzen & Régnière, 2017). Tebufenozide was applied by helicopter as Mimic<sup>®</sup> (Spiess-Urania Chemicals, Hamburg, Germany), from 3 to 23 May, 2019, at the legally defined concentration of 750 mL ha<sup>-1</sup> (i.e., 180 g AI/ha), as part of an operational treatment campaign conducted in northwestern Bavarian forests at high risk of defoliation. In each stand, we set up even-sized (ca. 4.5 ha) sampling areas around the site centroid. All focal data (i.e., vegetation composition, caterpillars, defoliation estimates) were collected within these sampling areas, subsequently referred to as plots.

### Vegetation assessment

We surveyed the vegetation to account for plot-level differences in plant species composition in the calculation of host range overlap between non-target species and the spongy moth. For the canopy layer, we identified 20 oaks and their five closest neighboring trees with a diameter at breast height (dbh) >7 cm at distances of 25, 50, 75, 100,

and 125 m from the plot center in four transects following the cardinal directions. The ground vegetation was surveyed in two 5 × 5-m-subplots located within 30 m of the plot centroid. All herbaceous and woody plants were identified to species level.

## Caterpillar sampling

### Caterpillar communities in oak stands

The chewing herbivore community in the canopy of deciduous oak *Q. robur* and *Q. petraea* is characterized by very strong seasonality, both in terms of biomass and species composition. In spring (late April to mid June), Lepidoptera larvae contribute to a large fraction of the total herbivore population (Brändle & Brandl, 2001; Southwood et al., 2004). This assemblage is dominated by several functional groups: winter-flying geometrid species with apterous females, shelter-builders such as leaf rollers, and large free-living noctuids (Raimondo et al., 2004; Sarvašová et al., 2020). Other leaf-chewing larvae, predominantly sawflies (Hymenoptera: Symphyta), are comparatively rare (Brändle & Brandl, 2001), and their life history remains poorly known for many species. However, they are an interesting group to include in the analysis given their ecological similarity to Lepidoptera but lack of sensitivity to tebufenozide.

In summer (late June to mid September), free-living caterpillars are far less abundant than in spring (Southwood et al., 2004). Only a few species with long larval stages can be found across both seasons, the most notable of which is the spongy moth itself. Spongy moth caterpillars hatch between late April and early May, and feed until early July, consuming particularly large quantities of leaves during their last instars (Leonard, 1981). During outbreak phases, severe defoliation therefore typically occurs in the early summer, from late June to early July.

### Arthropod sampling

We used canopy fogging to sample the crown-dwelling arthropod community. In each plot, three areas, representative in terms of vegetation composition and structure and centered around one mature oak tree (dbh >30 cm), were selected in April and May 2019. Within each area, four 3 × 5-m-tarpaulin sheets were laid on the forest floor to collect insects falling from the focal tree crowns. Insects were knocked down with a 2.5% oil-pyrethrum solution fogged into the canopy with SwingFog SN50 machines (Swingtec, Isny, Germany). Sampling was only conducted on dry and calm nights (i.e., wind speed under 2.5 m/s) for optimal

accuracy. One machine was operated continuously until the canopy area above the sheets was coated by the fog cloud (i.e., 2–25 min depending on atmospheric conditions). Arthropods were collected after 30 min and stored at –18°C. During the outbreak year, fogging was performed on three occasions: (1) “pre-treatment phase,” before insecticide application (25 April–8 May 2019;  $n = 38$ ), (2) “acute phase,” the period of highest toxicity (23 May–7 June 2019, i.e., 1–3 weeks post-spray;  $n = 48$ ), and (3) “peak defoliation phase” (1–4 July 2019;  $n = 48$ ). To examine community recovery following disturbance, fogging was repeated three times in the two post-outbreak years; (4) “acute phase–post-treatment year 1” (18–21 May 2020;  $n = 48$ ) and (5) “peak defoliation phase–post-treatment year 1” (7–12 July 2020;  $n = 48$ ), respectively; and (6) “acute phase–post-treatment year 2” (22–28 May 2021;  $n = 48$ ). To ensure the independence of repeated measures within plots, each repetition was performed in a different area within each plot in 2019, and sampling areas were switched between spring and summer in the following year.

### Species determination

All macro-arthropods (i.e., all arthropods excluding mites, springtails, and thrips) were sorted to order or sub-order and counted shortly after sampling, with holometabolous adults and juveniles being sorted separately. At this stage, larvae were further separated into two groups, (1) spongy moth caterpillars and (2) other species, and the body length of all individuals was measured. Non-spongy moth larvae were identified to species level following a two-step procedure involving (1) sorting into morphotypes (i.e., putative species) based on rapid examination and (2) individual-level DNA-barcoding. These two steps were necessary to maximize taxonomic resolution as not all species can be quickly identified morphologically, and DNA sequencing may fail on a fraction of the specimens.

#### Morphotyping

We designed a simplified morphological determination key by identifying specific characters (based on Patočka, 1980) to assign caterpillars to morphotypes or species (when the identity could be determined unambiguously). Due to the small size and young age of the caterpillars sampled in the pre-treatment (early May 2019) and peak defoliation (July 2019 and 2020) phases, we could not delimit accurate morphotypes for these sampling periods, such that this morphotyping was only conducted on samples from the acute phase in the treatment and post-treatments years (i.e., late May 2019, 2020, and 2021). Only caterpillars were morphotyped as we lacked sufficient taxonomic expertise to reliably separate sawfly larvae into putative species.

### DNA barcoding

Characterization of DNA barcodes was completed at the Centre for Biodiversity Genomics following the standard protocols for DNA extraction and polymerase chain reaction (PCR) (<https://ccdb.ca/resources/>), in combination with SMRT-sequencing of asymmetrically labeled cytochrome c oxidase subunit I (COI) amplicons (Hebert et al., 2018). To mitigate PCR inhibition with plant secondary compounds from the caterpillar's diet, the DNA extraction protocol for plants was applied to the caterpillar specimens (Ivanova et al., 2008). A standard aliquot of each lysate (50  $\mu$ L) was transferred from tube racks or vials into a 96-well microplate and underwent bind-wash-elute DNA extraction using deck robotic method on dual multichannel Biomek FXP liquid handler (Beckman Coulter). In each well, the lysate was mixed with 100  $\mu$ L of binding buffer (contains 5M GuSCN) and the entire well content was applied onto a 96-well 1  $\mu$ m glass-fiber filter plate (Pall Corporation) positioned on a vacuum manifold. DNA washes were completed with 180  $\mu$ L of binding mix (contains 3M GuSCN) followed by 750  $\mu$ L of wash buffer. After removing the residual buffers by centrifugation at 5000 g for 5 min after each step, the glass-fiber membranes were placed in the incubator at 56°C for 30 min in order to evaporate the remaining ethanol. DNA was eluted in 80  $\mu$ L of elution buffer and used as a template for PCR amplification. The full-length COI barcodes were generated with asymmetrically labeled fusion primers supplied by Integrated DNA Technologies. Each well contained a 1:1 mixture of two forward oligos (LepF1 and LCO1490) tailed with the same unique forward Unique Molecular Identifier (UMI), and a 1:1 mix of two reverse oligos (LepR1 and HCO2198) both tailed with the same unique reverse UMI. All oligos contained a five-nucleotide pad on the 5' end of the primer. All PCRs were completed in 6- $\mu$ L volume in 384-well format, and a total of 9216 uniquely labeled amplicons (including controls) were combined from 24,348-well microplates in a single amplicon pool. The pool was purified with AMPure beads and quantified on a Qubit Fluorimeter. SMRTbell libraries were prepared using standard PacBio protocol for short inserts with Express Template kit 2.0. SMRTbell library for each amplicon pool was sequenced on its own 8M SMRT cell on Sequel II with 10 h movie time and 150 pM on plate loading concentration. Post-sequencing analysis of circular consensus reads, including contig assembly and taxonomy assignments were completed on the mBRAVE platform (Ratnasingham, 2019).

### Species identity assignment

DNA barcodes were successfully obtained from 86% of the sequenced caterpillars. All barcodes were matched to

reference sequences on the BOLD database using a BLAST algorithm with a minimum sequence similarity threshold of 97%. The resultant taxonomic assignments were then compared with preliminary morphological determinations of the caterpillars to improve taxonomic resolution. Species identities assigned via DNA barcoding were preferred in cases of conflictual identification between methods and for individuals that could not be morphologically identified. Morphological assignments were kept for caterpillars for which no usable barcode was obtained, provided that both methods agreed for the majority of other specimens assigned to the same morphotype. In situations when this control could not be done (i.e., singletons), only high-confidence morphological assignments were kept.

### Life-history traits

Life-history traits were compiled from Hacker and Müller (2006), Patočka (1980), Potocký et al. (2018), and several online databases which assemble traits from primary sources (Biological Records Centre, 2022; Ellis, 2022; Jonko, 2022). We gathered data for the six following traits following our previously listed hypotheses.

1. **Shelter-building behavior.** Binary (0-Free-feeding species; 1-Shelter-building species, including leaf rolls and ties, silk cocoons or nests, and larval cases).
2. **Host range overlap.** Continuous (percentage of a species' host plant range used as preferred hosts by the spongy moth). Based on Wellenstein and Schwenke (1981) and Kraus and von der Dunk (1993), each tree genus was assigned a value depicting its use as a host plant by the spongy moth in our study region: 0-never used; 1-generally avoided; 2-secondary host; 3-primary host. Only plants in categories 2 and 3 were considered at risk of defoliation during outbreaks so they were included in the calculation of host range overlap. We calculated host-range overlap (HRO) for each species and plot based on the vegetation surveys (see *Vegetation assessment*) as:

$$\text{HRO} = \frac{\sum_{i=1}^n (\text{PA}_i \times \text{SMpref}_i \times \text{SPpref}_i)}{\sum_{i=1}^n (\text{PA}_i \times \text{SPpref}_i)}, \quad (1)$$

where  $\text{PA}_i$ ,  $\text{SMpref}_i$ , and  $\text{SPpref}_i$  are binary variables characterizing for each plant species  $i$  its presence in the focal plot (PA), its use as a host by the spongy moth (SMpref), and the focal species (SPpref). NA values (i.e., host absent or not used) were excluded from the calculations.

3. **Flight dimorphism.** Binary (0-Flight monomorphic species, i.e., both sexes can fly; 1-Flight dimorphic species, i.e., females are apterous or mostly flightless).
4. **Male wingspan.** Continuous (unit: mm). Wingspan data are readily available for many Lepidoptera species and were shown to be a satisfactory proxy for dispersal ability (Sekar, 2012). Here, we used the wingspan of adult males to account for sexual dimorphism and excluded flight-dimorphic species as their dispersal is not driven by flight.
5. **Voltinism.** Binary (0-Univoltine species, i.e., only one generation per year; 1-Multivoltine species, i.e., two or more generations per year).

To determine the importance of the focal traits in the spring and summer communities, we examined their distribution patterns as well as pairwise correlations between traits (Appendix S2). We found that shelter-building behavior and flight dimorphism mostly characterize the spring assemblage, while differences in voltinism are only relevant in summer, as most spring species are univoltine (Appendix S2: Figure S1). We calculated community-weighted means (i.e., abundance-weighted average trait value for each plot within sampling period; CWMs) to characterize the functional composition of the communities with regard to the traits relevant in each season.

### Quantification of insecticide and outbreak disturbances

We characterized the treatment status of each plot in a binary fashion as: 0-not treated; 1-treated with tebufenozide in 2019, and the outbreak disturbance with two different variables: (1) relative abundance of spongy moth caterpillars; and (2) canopy development as a measure of defoliation. Caterpillar abundance describes the outbreak disturbance in spring when defoliation intensity is low but the high density of caterpillars can affect other herbivores via host- or natural enemy-mediated competition (Kaplan & Denno, 2007). We divided the number of spongy moth larvae by the total number of macro-arthropods to avoid spurious correlations due to sampling effects. Canopy development describes the outbreak disturbance through spring and summer as spongy moth feeding intensifies along with caterpillar development. We monitored canopy development using Sentinel-1 C-band SAR data, following the method described in Bae et al. (2021). We downloaded all available level-1 ground-range-detected high-resolution (GRDH) products acquired from March to September 2019, 2020, and 2021 from the ESA Scientific Hub (<https://scihub.copernicus.eu/>). The GRDH products have two polarizations with a pixel spacing of 10 m: VV (vertically transmitted, vertically received radar pulse) and VH

(vertically transmitted, horizontally received radar pulse). The GRDH products were pre-processed using the Sentinel Application Platforms (SNAP) Sentinel-1 Toolbox software and converted to dB (detailed information on pre-processing procedures is provided in Bae et al., 2021). We calculated the mean  $\gamma_0$  values (i.e., backscatter coefficients measuring the reflective strength of the radar target) of both polarizations ( $\gamma_{VV}^0$  and  $\gamma_{VH}^0$ ) within each plot for each day. The canopy development index (CDI; unit: dB) was calculated for each sampling date  $t_n$  as:

$$CDI_{t_n} = \gamma_{VV}^0 - \gamma_{VH}^0 \tag{2}$$

To reduce noise and aid interpretability, we normalized CDI by the baseline CDI measured at leaf-off:

$$NCDI_{t_n} = \frac{CDI_{t_n} - CDI_{t_0}}{CDI_{t_0}} \tag{3}$$

The resultant normalized canopy development index  $NCDI_{t_n}$  can be coarsely interpreted as the relative increase in canopy cover at time  $t_n$  since leaf-off ( $t_0$ ).

### Statistical analyses

All analyses were conducted in R 4.1.2 ([www.r-project.org](http://www.r-project.org)). We applied generalized linear mixed models (GLMMs) with the package *glmmTMB* (Brooks et al., 2022) and generalized additive mixed models (GAMMs) with the package *mgcv* (Wood, 2022). Model diagnostics were performed with the package *DHARMA* (Hartig, 2022) and *mgcViz* (Fasiolo et al., 2021). All statistical inference was performed using Wald tests and reported effect sizes and confidence intervals (CIs) are based on estimated marginal means calculated with the package *emmeans* (Lenth et al., 2022). Species-treatment associations were quantified with the package *indicspecies* (Cáceres et al., 2022).

### Treatment efficacy and defoliation extent

Our hypotheses assume that tebufenozide treatments fulfilled their intended purpose, that is, reducing spongy moth populations and preventing defoliation. We performed a preliminary analysis which confirmed treatment efficacy in both aspects (methods and results are detailed in Appendix S3). The results showed that tebufenozide nearly suppressed all spongy moth caterpillars from treated plots (Appendix S3: Figure S1a). Defoliation measured at the peak defoliation period (July) was significantly greater in untreated outbreak plots than in other plot types but varied substantially

among outbreak plots (Appendix S3: Figure S1b). Severe defoliation (i.e., NCDI <0.15) was measured in six plots, two of which were completely defoliated (i.e., NCDI near 0). By contrast, four plots where severe defoliation was forecast during the site selection process experienced negligible defoliation (i.e., NCDI >0.2). Importantly, spongy moth abundances naturally collapsed in control plots after 2019 leading to no outstanding level of defoliation in any plot in 2020 (Appendix S3: Figure S1b), such that the outbreak turned out to be a single-year event. Therefore, we only used spongy moth relative abundance and NCDI measured in 2019 in subsequent models testing for outbreak effects over the 3 years of the study. For NCDI, we used values measured during the peak defoliation period (i.e., July 2019) to test for long-term effects in both spring and summer assemblages.

### Effects of tebufenozide and defoliator outbreaks on community structure

In the first analysis, we used generalized linear mixed models to compare the effects of the 2019 spongy moth outbreak with those of tebufenozide on the structure of the Lepidoptera community, using abundance, species richness, and CWMs of the selected traits as response variables, separately for the spring and summer assemblages. For the Symphyta, the analysis was restricted to abundance and species richness in the spring

assemblage, as they were too rare in summer for meaningful statistical analysis. In the spring models (model 1), the fixed terms tebufenozide treatment (TBF), spongy moth relative abundance (SM), and normalized canopy development index (NCDI) were nested into the four sampling periods (May 2019 pre- and post-spray, May 2020, and May 2021) to assess the change in disturbance effect over time. In the summer model (model 2), the fixed terms were nested into the two sampling periods in July 2019 and 2020. SM was dropped, as spongy moth caterpillars had already left the tree crowns to pupate in most plots at the time of sampling. Both models include a random effect for plot. The models were fitted with the glmmTMB function of the same-named package and specified as follows:

$$\text{(Model 1 — spring) response} \sim \text{period} \\ + \text{period:}(\text{TBF} + \text{SM}_{2019} + \text{NCDI}_{2019}) + (1|\text{plot}).$$

$$\text{(Model 2 — summer) response} \sim \text{period} \\ + \text{period:}(\text{TBF} + \text{NCDI}_{2019}) + (1|\text{plot}).$$

The notation  $x1:(x2)$  denotes that the fixed term  $x2$  is nested within  $x1$  (here the sampling period). The notation  $(1|z)$  is the glmmTMB syntax for modeling a random intercept for a grouping variable  $z$ . Additional parameters such as family distribution, zero inflation, and weights were adjusted individually for each response variable to best fit the data (Table 1). The models were fitted using maximum likelihood estimation.

**TABLE 1** Parameters for the different models.

Assemblage	Response	Family distribution	Link function	Additional parameter(s)
Model 1: Lepidoptera—Spring	Abundance	Negative binomial	Log	
	Species richness	Negative binomial	Log	
	CWM shelter-building	Beta <sup>a</sup>	Logit	$z_i = \sim 1$
	CWM flight dimorphism	Binomial	Logit	Weights = abundance
	CWM male wingspan	Gaussian	Identity	
	CWM host overlap	Gaussian	Identity	
Model 2: Lepidoptera—Summer	Abundance	Negative binomial	Log	
	Species richness	Poisson	Log	
	CWM male wingspan	Gaussian	Identity	
	CWM voltinism	Binomial	Logit	Weights = abundance
	CWM host overlap	Beta <sup>a</sup>	Logit	
Model 3: Symphyta	Abundance	Negative binomial	Log	
	Species richness	Poisson	Log	
Model 4: Body size versus tebufenozide	Body length	Gamma <sup>b</sup>	Log	

<sup>a</sup>Values of 1 were transformed to  $(1 + \max(y|y < 1))/2$  to fit a zero-inflated ( $z_i$ ) beta distribution.

<sup>b</sup>Family distribution is specified to fit the parametric component of the generalized additive mixed model.



We calculated variance inflation factors (VIF) for each predictor to detect potential collinearity issues. With VIF consistently below 2.7, all predictors could be included in subsequent analyses (Appendix S4: Table S1). CWM regressions are widely used in community ecology though they tend to have high type I error rates. We performed a row-column-based permutation test as defined by Peres-Neto et al. (2017) to address this issue. The procedure involves two sequential permutation tests: (1) row-based permutation test, where the environmental (here disturbance) variables are reshuffled; (2) column-based permutation test, where the trait variables are reshuffled before computing the CWMs. The maximum  $p$ -value is then kept. Row-based permutations were constrained within sampling period and retained the data's correlation structure among predictors (i.e., values of TBF,  $SM_{2019}$ , and  $NCDI_{2019}$  were grouped before shuffling). For both tests, 1000 permutations were performed, mixed models were fitted to each randomized dataset and  $p$ -values calculated as the fraction of Wald tests equal to or larger than the observed one for each model term.

### Individual species' responses

We performed an indicator species analysis to compare the acute response of species sampled in the post-application weeks in May and July 2019. Twenty-two species with at least 24 individuals ( $n/2$ ) were included in the analysis. We quantified the association between species and tebufenozide-treated sites as a point biserial correlation ( $r_{PB}$ ), which measures the strength of the association between a continuous variable (i.e., species abundance) and a binary variable (i.e., tebufenozide treatment). We estimated the uncertainty of the correlations by computing bootstrap confidence intervals (5000 replicates). We estimated the statistical significance of the species-treatment associations by computing permutation  $p$ -values (1000 permutations) that were subsequently corrected for multiple testing with the Šidák method.

### Effects of tebufenozide on caterpillar body size

We fitted a third model to test Hypothesis 3 addressing the presence of sublethal effects of tebufenozide in the form of differences in caterpillar body size between treated and control plots. We used a generalized additive mixed model (GAMM) because assumptions of linearity of residuals and homogeneity of variance could not be met in a linear model framework. We restricted the analysis to species sampled at least once in both control and treated plots in 2019 post-spray, which also included the spongy moth. Caterpillar body length was regressed against tebufenozide treatment (TBF) nested within year.

Adult male wingspan was added as a covariate to control for species-specific body size. To account for random variation in body size due to differences in sampling time, species phenology, and unmeasured environmental gradients, we included a smooth term for sampling date (in day-of-year) and random intercepts for species and plot. The model was fitted with the function `gam` of the package `mgcv` and specified as follows:

(Model 3 — Body size vs. tebufenozide)

$$\begin{aligned} \text{body length} \sim & \text{year} + \text{year}:(\text{male wingspan} + \text{TBF}) \\ & + s(\text{species}, \text{bs} = \text{"re"}) + s(\text{plot}, \text{bs} = \text{"re"}) \\ & + s(\text{sampling date}, \text{bs} = \text{"tp"}) + \end{aligned}$$

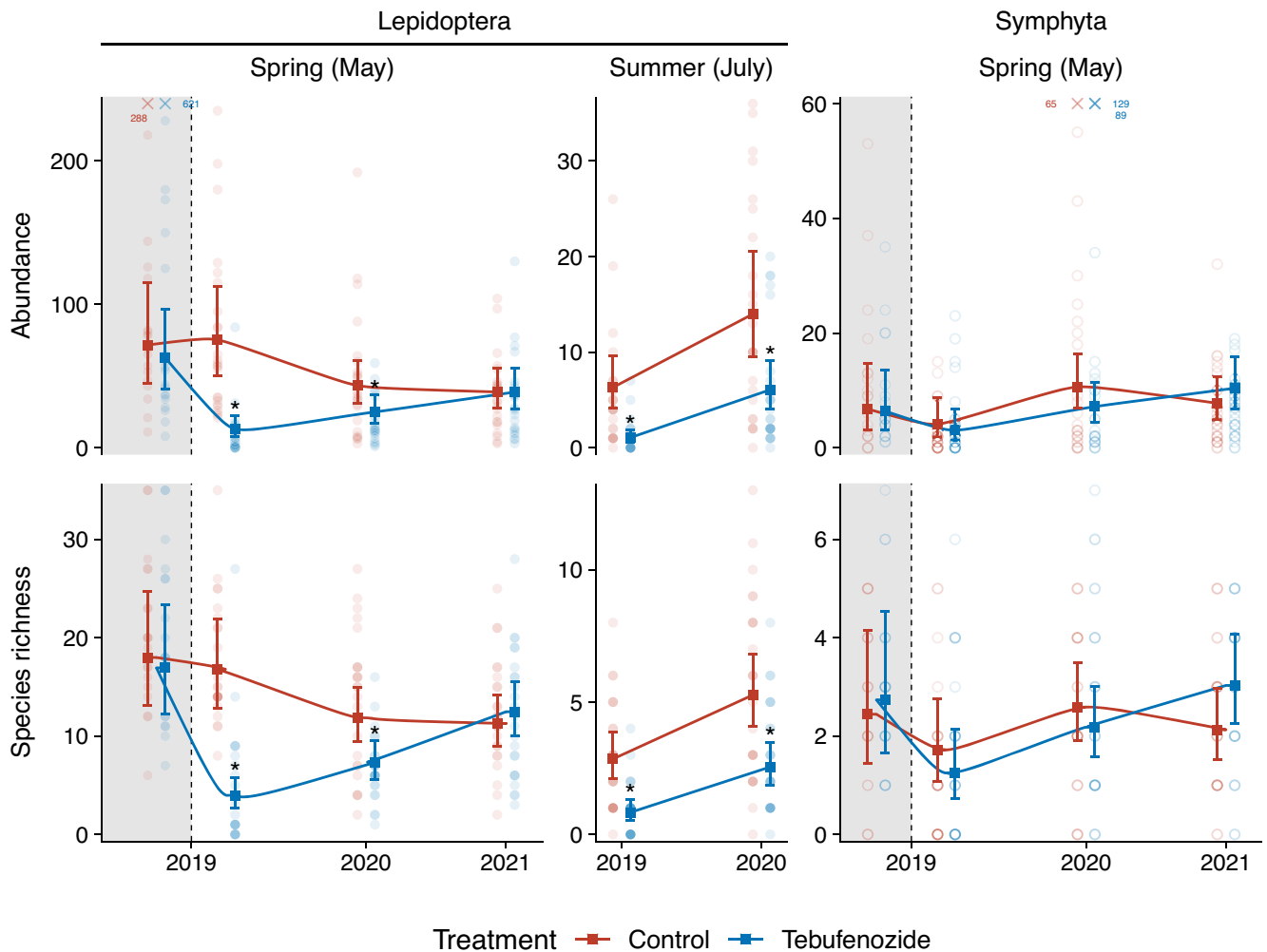
Nested fixed effects are specified using the same syntax as in the linear mixed effect models. The  $s$  function is used to specify smooth terms in the gam model formula. The  $bs$  argument specifies the smoothing basis for the smooth term. The basis "re" stands for "random effects" and the notation  $s(z, \text{bs} = \text{"re"})$  is the gam syntax for modeling random intercepts for a grouping variable  $z$ . The basis "tp" stands for "thin plate regression splines" which is the default and most flexible smoothing function in `mgcv`. The parametric component of the model was fitted to a gamma distribution with a log link function. The model was fitted by restricted maximum likelihood.

## RESULTS

Over 3 years, we collected 22,481 Lepidoptera caterpillars belonging to 152 species and 25 families. Among them, 12,290 were larvae of the spongy moth, 87% of which were caught during the outbreak year in 2019. Sawflies were considerably less abundant, with a total of 1668 caterpillars belonging to 33 species in three families. Full species lists for each sampling session with corresponding abundances are provided in Appendix S5: Tables S1 to S7. In the untreated stands, species abundance and diversity of Lepidoptera linearly declined through the duration of the study in the spring assemblage but increased from 2019 to 2020 in the summer assemblage. By contrast, sawfly larvae showed a more erratic year-to-year fluctuation pattern (Figure 1).

### Effects of tebufenozide treatments on leaf chewer assemblages

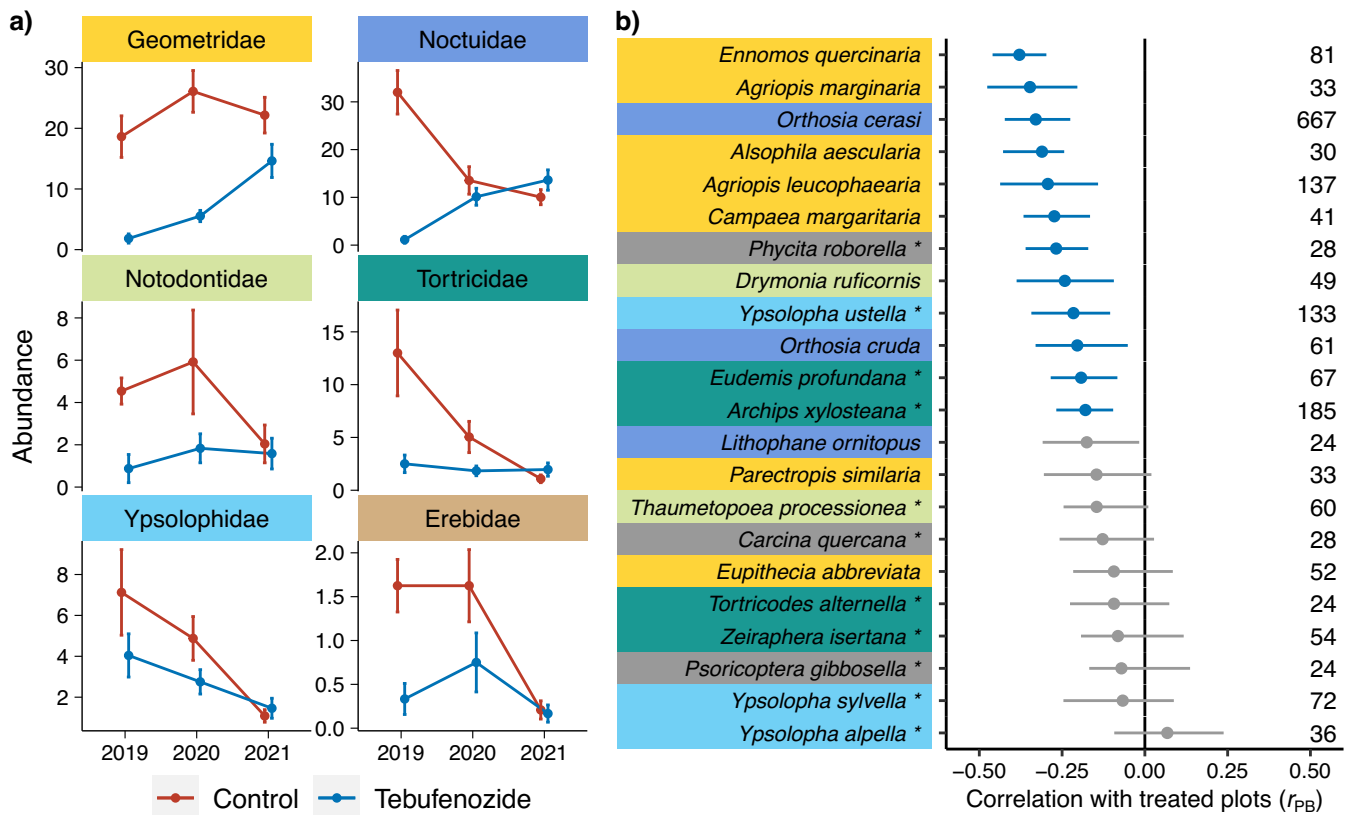
In the acute phase (i.e., 1–3 weeks post-treatment, late May 2019), the abundance of Lepidoptera in treated plots was only 18% of that in control stands ( $z = -5.89$ ,



**FIGURE 1** Changes in abundance and species richness of canopy-dwelling caterpillars over 3 years in response to tebufenozide treatments. Tebufenozide (180 g/ha) was aerially applied in May 2019 during a spongy moth outbreak. The vertical dashed lines separate the pre- (left) and post-treatment periods (right). Lepidoptera assemblages sampled in spring (May 2019–2021) and summer (July 2019–2020) were analyzed separately. Only the spring Symphyta assemblage was analyzed due to very low abundances in the summer. Squares and error bars indicate estimated marginal means and 95% CIs. Asterisks indicate statistically significant differences ( $p < 0.05$ ) between control and treated plots within sampling period. Each point represents a community, excluding the spongy moth, in one sampled plot (raw data). Statistical test results are shown in Appendices S7: Tables S1 and S2, Appendix S8: Tables S1 and S2, and Appendix S9.

$p < 0.001$ ; Figure 1). Summer species sampled in early-July 2019 were similarly affected at 17% the abundance in control plots ( $z = -4.81$ ,  $p < 0.001$ ). The abundances of both spring and summer assemblages remained significantly lower in 2020, 1 year after treatment, at 57% ( $z = -2.01$ ,  $p = 0.045$ ) and 43% ( $z = -2.82$ ,  $p = 0.005$ ) the abundance in control plots, respectively. By May 2021, 2 years after treatment, the spring assemblage had recovered to control levels ( $z = -0.01$ ,  $p = 0.993$ ). Species richness closely followed the abundance pattern in both spring and summer assemblages (Figure 1). No sign of impacts of tebufenozide on Symphyta larvae was observed throughout the study.

All but 1 of the 22 dominant species were negatively associated with tebufenozide treatments, though the magnitude of individual species' responses varied substantially. The six most affected species in the list were all macrolepidopterans belonging to the families Geometridae and Noctuidae, including the dominant non-target species, *Orthosia cerasi* (Noctuidae) (Figure 2). Conversely, most of the species that were less substantially suppressed belonged to the microlepidopteran Tortricidae, Gelechiidae, and Ypsolophidae. There were some exceptions to this general pattern: the microlepidopteran *Phycita roborella* (Pyralidae) and *Ypsolopha ustella* (Ypsolophidae) were significantly more



**FIGURE 2** Response of Lepidoptera taxa to tebufenozide treatments. (a) Change abundance in the six most common families between 2019 and 2021 in sites treatment with tebufenozide (180 g/ha) in May 2019 and unsprayed controls. Points and error bars represent means  $\pm$  1 SE. The spongy moth was excluded from the calculations for the Erebidae. (b) Strength of the association between the most abundant Lepidoptera species and tebufenozide-treated sites in the weeks following spraying. The color background of the species name indicates the family, gray color indicates species not belonging to the six dominant families. Asterisks indicate shelter-building species. Associations between species and treatment were measured using point biserial correlation ( $r_{PB}$ ) and tested for statistical significance using permutation tests (5000 permutations). Error bars represent 95% bootstrap CIs (1000 bootstrap iterations). Colored dots and error bars indicate significant associations after adjustment for multiple testing with the Šidák method.

impacted by tebufenozide than other microlepidopterans, while the geometrids *Eupithecia abbreviata* and *Parectropis similaria* were not significantly affected.

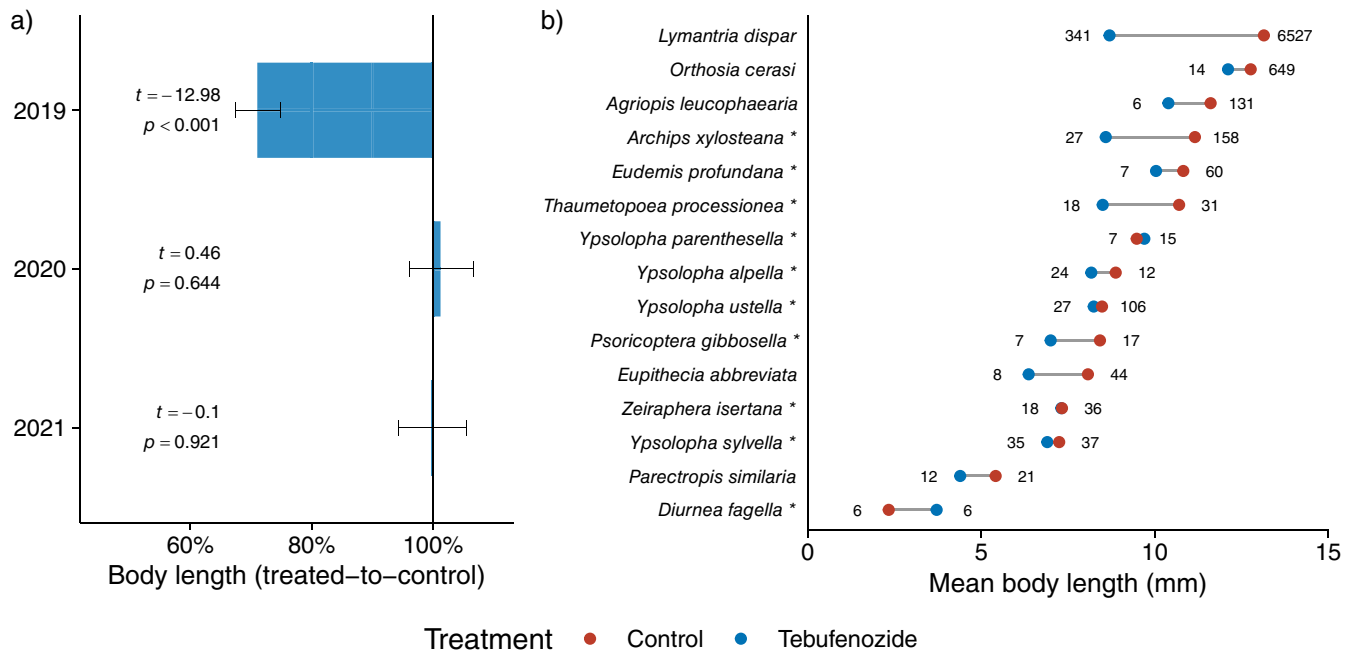
Individual caterpillars sampled in treated plots in the days following insecticide application were 29% shorter in body length than conspecific individuals from the control plots ( $z = -12.98, p < 0.001$ ; Figure 3a). This pattern of reduced body length was consistent in 12 of the 15 most abundant species in treated plots in 2019, with the spongy moth showing the largest differences (Figure 3b).

### Effects of spongy moth outbreaks on caterpillar assemblages

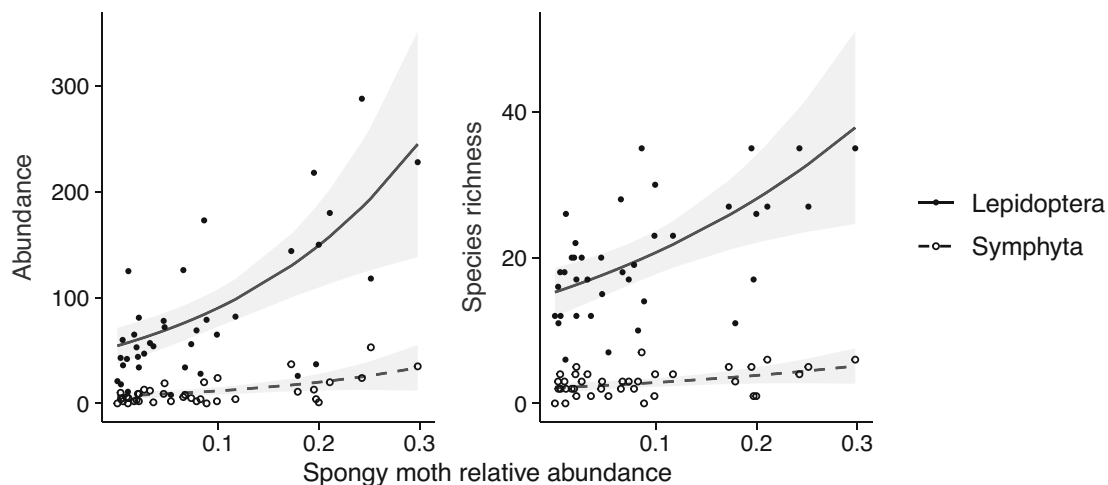
In early-May 2019, before treatment application, the relative abundance of spongy moth caterpillars was

positively correlated with the abundance ( $z = 5.19, p < 0.001$ ) and species richness ( $z = 4.16, p < 0.001$ ) of Lepidoptera and Symphyta (abundance:  $z = 3.90, p < 0.001$ ; species richness:  $z = 2.58, p = 0.010$ ; Figure 4). These patterns were limited to the early spring period and no longer observed in any of the post-treatment samplings in May and July 2019. In contrast, the species richness of Symphyta was negatively correlated with spongy moth abundance in late May 2019 ( $z = -2.68, p = 0.007$ ; Appendix S6: Figure S1). A delayed correlation was observed in 2020, 1 year after the outbreak, when more Lepidoptera species were found in sites that experienced high spongy moth densities the year prior, though the effect was fairly weak ( $z = 2.31, p = 0.021$ ; Appendix S6: Figure S1). However, there was no further influence of the 2019 spongy moth relative abundance on Lepidoptera and Symphyta in 2020 or 2021.

Canopy development (NCDI) during the outbreak had no significant impact on Lepidoptera abundance and



**FIGURE 3** Effects of tebufenozide treatments on individual caterpillar body length. (a) Effect of tebufenozide treatments (180 g/ha) on body length in the treatment year (2019) and the two post-treatment years (2020 and 2021). The statistical significance of the effect was evaluated with  $t$ -tests. Bars and error bars represent parametric coefficients and 95% CIs back-transformed to the response scale. (b) Mean body length in treated and control plots across the 15 most abundant species in the treated plots in late May 2019 (1–3 weeks after treatment). Asterisks indicate shelter-building species. Statistical test results are shown in Appendix S10.

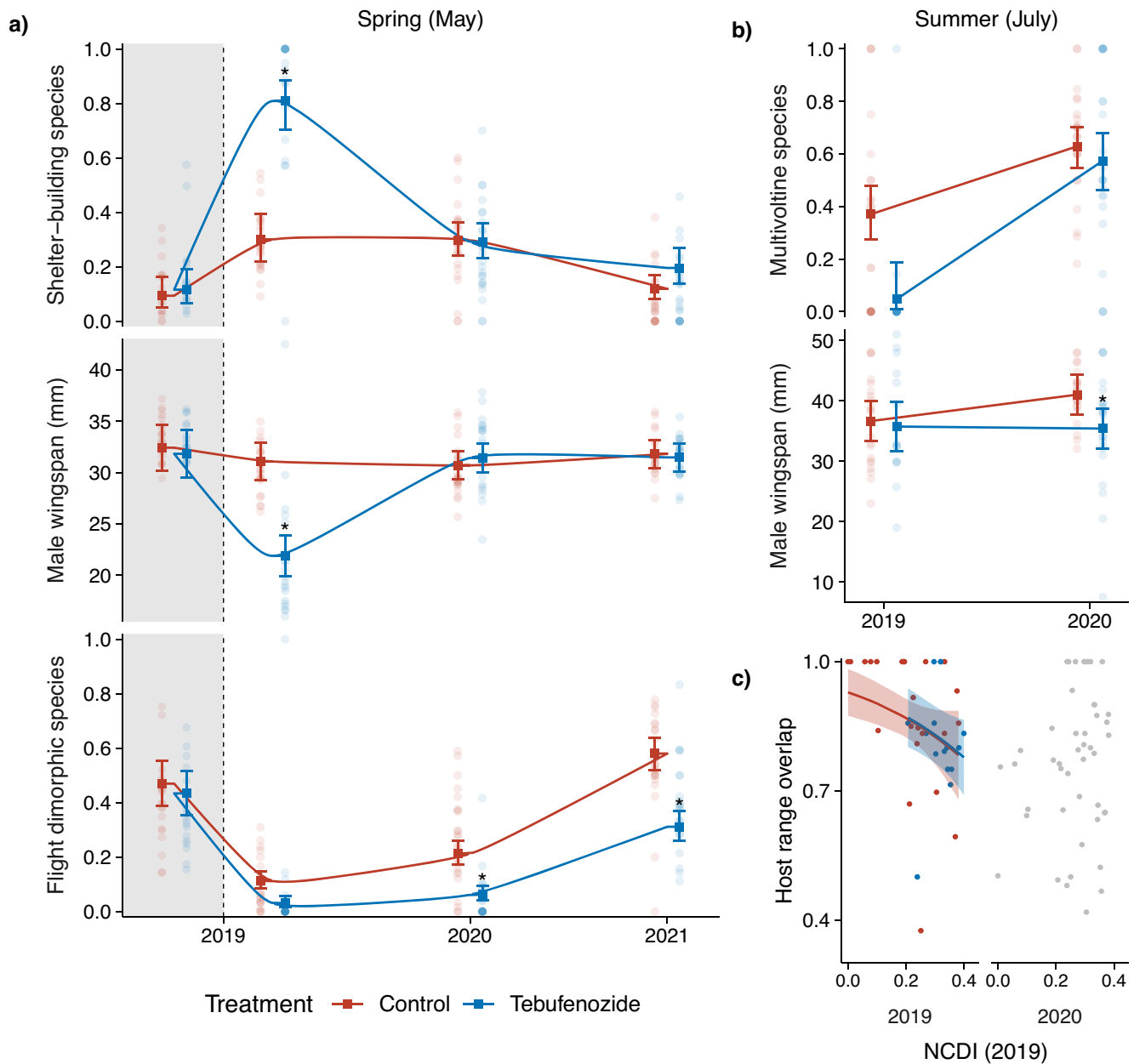


**FIGURE 4** Relationship between the abundance or species richness of arboreal Lepidoptera and relative abundance of the spongy moth in early spring (late April–early May) 2019, before insecticide application. Regression lines show model predictions back-transformed to the response scale (shaded areas indicate 95% CIs). All plots were included, regardless of subsequent treatment allocation. Each point represents one Lepidoptera community excluding the spongy moth (raw data; one community per plot). Statistical test results are shown in Appendix S7: Tables S1 and S2, and Appendix S9.

diversity throughout the study, but Symphyta numbers were significantly depressed in heavily defoliated sites (i.e., low NCDI) in 2020 ( $z = 2.65$ ,  $p = 0.008$ ; Appendix S6: Figure S2), though not in 2019 ( $z = 0.56$ ,  $p = 0.578$ ) and 2021 ( $z = 0.13$ ,  $p = 0.895$ ).

### Role of functional traits in mediating tebufenozide and outbreak impacts

Tebufenozide treatments had both transient and lasting impacts on the functional composition of Lepidoptera



**FIGURE 5** Effects of insecticide treatments and spongy moth defoliation on the functional composition of Lepidoptera communities. (a, b) Changes in community-weighted means (CWM) of four functional traits (flight dimorphism, shelter-building behavior, male wingspan, multivoltinism) in response to insecticide treatments with tebufenozide (180 g/ha) in the treatment year (2019) and post-treatment years (2020, 2021). Different traits were selected for the spring (a) and summer (b) assemblages based on their seasonality. The dashed lines separate the pre- (left) and post-treatment periods (right). Squares and error bars indicate estimated marginal means and 95% CIs. Asterisks indicate statistically significant differences ( $p < 0.05$ ) between control and treated plots. (c) Community-weighted spongy moth host range overlap in summer Lepidoptera assemblages in 2019 and 2020 in relation to canopy development during the 2019 spongy moth outbreak. Normalized canopy development index (NCDI) represents the increase of canopy cover since leaf off and is used as a proxy for defoliation. Lines and ribbons indicate the fitted data and 95% CIs. Circle-shaped points represent a community, excluding the spongy moth, in one sampled plot (observed data). Statistical test results are shown in Appendices S7: Tables S3 to S6, and Appendix S8: Tables S3 to S5.

communities (Figure 5). Soon after spraying in spring 2019, 81% of the Lepidoptera in treated plots were shelter-builders versus 30% in controls ( $z = 8.01$ ,  $p_{\max} < 0.001$ ; Figure 5a). This effect was only transient as

no such differences were found in the post-treatment years. By contrast, tebufenozide had no immediate impact on the proportion of flight-dimorphic species in 2019 ( $z = -4.24$ ,  $p_{\max} = 0.238$ ) but a significant impact in

the post-treatment years 2020 and 2021. Flight-dimorphic species represented only 6% of the species pool in treated plots versus 21% in controls in spring 2020 ( $z = -5.06$ ,  $p_{\max} = 0.050$ ), and 31% versus 58% in 2021 ( $z = -5.66$ ,  $p_{\max} < 0.001$ ). The spring assemblage of treated plots had a greater proportion of short-winged species than the controls during the acute phase ( $z = -9.57$ ,  $p_{\max} = 0.001$ ), yet no differences were found in spring 2020 and 2021. By contrast, shorter-winged species were more prevalent in treated plots than in controls in the summer of 2020, with species having on average 5.6 mm shorter wingspan ( $z = -2.22$ ,  $p_{\max} = 0.048$ ), while no particular pattern could be observed 1 year earlier ( $z = -0.19$ ,  $p_{\max} = 0.909$ ; Figure 5b). Generation time did not appear to influence recovery in the summer species pool, with no difference between treated and control plots in 2020.

Neither spongy moth relative abundance nor defoliation caused major changes in the functional composition of Lepidoptera communities. Severely defoliated sites were almost exclusively composed of species whose host range fully overlapped that of the spongy moth (Figure 5c). However, the effect was weakened by the large variability in dietary overlap with the spongy moth in non-defoliated and treated plots and was not significant after the max test ( $z = -2.11$ ,  $p_{\max} = 0.118$ ). We observed no further sign of outbreak effects on lepidopteran communities neither in the 2019 spring assemblage nor in the post-outbreak years.

## DISCUSSION

In this study, we investigated how spongy moth outbreaks and their treatment with the insecticide tebufenozide affect arboreal chewing herbivores in a large-scale experiment that examined 48 oak stands over 3 years. Our results show that Lepidoptera communities were strongly impacted by tebufenozide as caterpillar abundance declined to 18% and species richness to 24% of that observed in the reference communities in untreated stands in the weeks after spraying. The population recovered over the two post-treatment years such that communities in treated and control sites no longer differed 2 years after treatment in terms of abundance and species richness. Both exposure and recovery patterns appeared to be influenced by species' life history. Shelter-building species better withstood the initial impact of tebufenozide than free-living species, while species with flightless females recovered only slowly and remained less frequent in treated sites 2 years after spraying. The Symphyta communities were not impacted by the tebufenozide treatments at any point. By contrast, the presence of outbreak densities of spongy moth caterpillars and the resulting defoliation

had only moderate and short-lived impacts on herbivore assemblages. Outbreak impacts were stronger in sites that were extensively defoliated, and the overall effect was largely mitigated by broad differences in the magnitude of defoliation among outbreak plots. The Lepidoptera communities sampled in the most severely defoliated stands had lower numbers of individuals and species and were primarily composed of species feeding exclusively on preferred spongy moth hosts. Symphyta were reduced in severely defoliated stands 1 year after defoliation. These results provide valuable information on the relative impacts of defoliator outbreaks and their management with tebufenozide on the most vulnerable guild of non-target fauna and a benchmark to examine indirect effects on other functional groups.

## Effects of tebufenozide treatments

Only a few studies have examined the impact of tebufenozide on forest Lepidoptera thus far. Butler, Kondo, and Blue (1997) monitored tebufenozide effects on larvae over 2 years in northeastern Ohio. They found Lepidoptera abundances and species richness to be at 40% and 51% of control levels up to 7 weeks after the application of 67 g/ha tebufenozide. These effect sizes are half those we report here, reflecting the higher application rate used in our experiment (180 g/ha). Consistent with our predictions (Hypothesis 1), Symphyta, unlike Lepidoptera, showed no sign of susceptibility to tebufenozide throughout the experiment. While this is the first time that the field impacts of tebufenozide on this taxon are documented, the result is unsurprising and consistent with laboratory reports of the high specificity of tebufenozide to Lepidoptera larvae (Smagghe et al., 2012).

Because most oak-associated species are univoltine, Lepidoptera densities generally take several years to converge back to control levels after forest spraying (e.g., Boulton et al., 2007; Butler, Chrislip, et al., 1997; Miller, 1990). It is widely believed that population recovery is primarily driven by immigration from surrounding habitats (Miller, 1990; Sample et al., 1996), but other processes may also play a role. For example, the suppression of caterpillars during the treatment years may cause a drop in parasitism in the following year, reducing mortality in the post-treatment generation (Sample et al., 1996). In our study, the effect of tebufenozide on caterpillar numbers was three times weaker in the post-treatment year and disappeared altogether 2 years after spraying, while Butler, Kondo, and Blue (1997) noted no improvement 1 year after application. Previous research has shown that the size of the treated area is a significant factor in mediating recovery dynamics following BTK treatment. Miller

(1990) reported around 35% lower caterpillar abundance in 2000-ha plots 2 years after treatment. In a study conducted in and around a 12,000-ha spray block on Vancouver Island, Boulton et al. (2007) found Lepidoptera abundance to remain 60% lower in BTK-treated oaks 4 years after spraying. In contrast, Strazanac and Butler (2005) and Wagner et al. (1996) reported complete recovery by the second post-treatment year in experiments conducted on substantially smaller areas (200 and 20 ha, respectively), which is consistent with our findings. Notably, the plots used in the present study were considerably smaller than those used in most North American studies, ranging from 6.7 to 27.7 ha, with an average of 12.9 ha. Thus, our results suggest that the duration of non-target effects of tebufenozide is comparable to that of BTK when the treated areas are relatively small. In addition, while the higher fragmentation of Bavarian oak forests may hinder the dispersal of adult moths among forest islands, many areas of untreated habitat, for example, in buffer edge strips or protected stands, are in close vicinity to the sprayed plots. The combination of small-sized treatment areas and locally available untreated source habitats probably contributed to the swift post-treatment recovery in our study. However, it is important to consider the variable population trajectories observed in different families when discussing recovery dynamics (Figure 2a). Populations of forest Lepidoptera experience considerable year-to-year fluctuation controlled by biotic and abiotic drivers (Berryman et al., 1987), and this natural variation may influence recovery dynamics by either reinforcing or mitigating treatment effects.

Our results show that caterpillars using semi-concealed microhabitats are partially protected from exposure to tebufenozide, enhancing their survival. In the weeks following treatment, shelter-building species comprised 81% of the Lepidoptera assemblage versus only 11% before spraying and 30% in post-treatment controls. The use of shelters appears to be the main factor driving differences in sensitivity among species, with most of the least affected dominant species being shelter-builders (Figure 2b). Moreover, among the 15 species found the most frequently in treated plots during the acute phase, 10 are shelter-builders (Figure 3b). However, the protection granted by microhabitat shelters is partial and transient, as the abundance of shelter-building families remained substantially lower in treated plots (Figure 2a) and their dominance was restricted to the treatment year. Moreover, we observed substantial differences in the magnitude of treatment effects among different shelter-building species, most strikingly between the substantially impacted *Ypsolopha ustella* and its seemingly unaffected congeners *Y. sylvella* and *Y. alpella* (Figure 2b). This finding suggests that, while microhabitat use mitigates exposure to a large extent, the intrinsic sensitivity of species

may still be a driving factor of population-level outcomes. In fact, comparable broad differences in tebufenozide sensitivity among congeners have been documented on *Spodoptera* caterpillars (Noctuidae) in laboratory bioassays (Smaghe & Degheele, 1994). Importantly, the dominance peak of shelter-building species during the acute phase was associated with a collapse of the mean species wingspan (Figure 5). Both traits are strongly correlated (Appendix S2: Figure S1) due to most shelter-builders being Microlepidoptera. As an alternative to the “microhabitat shield hypothesis,” we may speculate that lower per capita consumption rates in smaller species might delay the exposure to a lethal dose, as tebufenozide toxicity does not appear to scale with body size, either within or among species (Smaghe & Degheele, 1994). Therefore, while our findings tend to validate our predictions regarding the buffering role of microhabitat shelters (Hypothesis 2), potential confounding physiological effects could not be excluded.

By analyzing the differences in body size among treated and control caterpillars, we uncovered evidence of sublethal effects in situ, consistent with our predictions (Hypothesis 3). Caterpillars from treated plots were on average 29% smaller than those from controls after correcting for species identity, stand location and sampling date. These findings are consistent with past research reporting on the antifeedant activity of tebufenozide on caterpillars (Sundaram et al., 1996) and indicate that sublethal effects likely play a role in short-term impacts at the community level. The magnitude of these effects and the abundance reductions reported otherwise makes it seem implausible that locally surviving individuals are capable of contributing significantly to population recovery. Tebufenozide is therewith known to have reproductive effects, such as reduced fecundity and fertility (Biddinger & Hull, 1999; van Frankenhuyzen & Régnière, 2017). Altogether, these data support the view that community recovery in the post-treatment years is rather driven by the immigration of unaffected individuals from surrounding areas than by the reproductive output of survivors.

We hypothesized that species with a strong dispersal ability, approximated by a large male wingspan, should recover from insecticide exposure faster than smaller, less mobile species (Hypothesis 4). We were unable to validate this prediction as no difference in wingspan was observed in treated spring assemblages beyond 2019. In the summer assemblage, the mean wingspan was in fact lower in treated plots in 2020, but this was solely driven by the dominance of *Campaea margaritaria* (Lepidoptera: Geometridae; Appendix S5: Table S5). These results may also reflect the limitations of wingspan as a proxy for dispersal ability in moths. Using body mass and wing shape variables as dispersal proxies could have yielded more

accurate results, as they integrate aspects pertaining to flight speed, flying technique, as well as energy requirements and costs (Betts & Wootton, 1988). However, these data are not readily available for most species and wingspan remains the best available proxy for studies involving large numbers of species.

Besides the lack of apparent influence of wingspan, dispersal appeared to contribute to delayed recovery dynamics in the case of flight-dimorphic species. In the absence of female dispersal at the adult stage, these species primarily depend on the airborne dispersal of neonate larvae to reach new habitats (Barbosa et al., 1989). Larval ballooning is generally associated with high mortality rates (Zalucki et al., 2002), which plausibly explains the slow recolonization of treated plots by these species.

## Outbreak effects

In contrast to tebufenozide, spongy moth outbreaks had relatively subtle effects on caterpillar communities. We observed a significant positive relationship between spongy moth dominance and the abundance of other species in the early spring. Interspecific synchrony, that is, linkages of the population dynamics of different species, has been extensively studied in forest Lepidoptera (e.g., Klapwijk et al., 2013; Liebhold et al., 2020; Raimondo et al., 2004). Stochastic influences (e.g., weather) can create such synchrony over large spatial scales by synchronizing environmental conditions, a phenomenon known as the Moran effect (Liebhold et al., 2004). However, in the present study, the fact that these abundance correlations manifest at both low- and high-spongy moth density within relatively small areas (i.e., an experimental block) rather suggests that they are primarily driven by local processes such as biotic interactions. Previous studies have shown that the functional response of shared antagonists to an outbreak can generate population synchrony across multiple species (Klapwijk et al., 2013; Liebhold et al., 2020; Raimondo et al., 2004).

Importantly, we noted that abundance correlations between the spongy moth and non-target species were limited to the early spring, that is the oak leaf extension phase, between late April and early May when neonates of most spring species colonize the tree canopy. Aggregation of early larval instars has been reported in multiple species, including the spongy moth (e.g., Carroll et al., 2008; Holliday, 1977; McCormick et al., 2016), and is assumed to improve the fitness and survival of neonates (Zalucki et al., 2002). Though dispersal cannot synchronize the population of different species, it may explain temporary aggregations driven by induced plant volatiles. In our study system, it is a plausible mechanism as the early spring assemblage is dominated by generalist

species often hatching in poor synchrony with their host plants, unspecific in their choice of oviposition site and capable of larval dispersal through ballooning (Barbosa et al., 1989; Kulfan et al., 2018). Such species are highly reliant on movement to locate suitable hosts and could conceivably aggregate while using plant volatile induced by already feeding individuals as navigation cues (Zalucki et al., 2002). Later in the season, older larvae contrastingly tend to switch to a more avoidant behavior in response to damage-induced changes in plant quality (Edwards & Wratten, 1983; Karban, 2011, 2017; Mauricio & Bowers, 1990), and this behavior may be exacerbated in outbreak situations. Such behavioral changes may explain the transient nature of the aggregation pattern observed here.

Contrary to our expectations, spongy moth defoliation had weak apparent effects on caterpillar communities. Defoliation varied substantially among outbreak plots: 6 out of the 12 outbreak plots experienced severe defoliation (NCDI <0.15), of which only 2 were near completely defoliated (i.e., NCDI near 0; Appendix S3: Figure S1b). Although the relationships between canopy development and the abundance and diversity of caterpillars at peak defoliation were non-significant, caterpillars were nearly suppressed in these two plots (Appendix S6: Figure S2), suggesting that the ecological impacts of a defoliator outbreak are indeed proportional to its intensity (Hypothesis 5). We can therefore attribute the relative weakness of the reported outbreak effects to the broad defoliation gradient within outbreak plots. From this perspective, our results are in line with both the limited effects reported by Sample et al. (1996) in partially defoliated stands and the suppression of Lepidoptera in a completely defoliated woodland reported by Luciano and Lentini (1999).

Outside of the two completely defoliated sites, any competition between the spongy moth and other species is likely to have been indirect, that is, mediated by herbivory-induced plant defense compounds or changes in natural enemy assemblages (Nykanen & Koricheva, 2004). Contrary to our expectations (Hypothesis 6), we observed that summer assemblages in heavily defoliated plots were almost exclusively composed of species whose host range fully overlapped that of the spongy moth (Appendix S5: Table S3). Of the 12 non-target species present in heavily defoliated plots, only 1—*Campaea margaritaria* (Lepidoptera: Geometridae)—can use host plants generally avoided by the spongy moth, and many have narrow host ranges (Appendix S5: Table S3). With 41 individuals, *C. margaritaria* was the most common non-target species in the summer samples, yet it was only found twice in severely defoliated stands. These results suggest that generalist caterpillars may have either shifted to non-spongy moth hosts to escape defoliation stress, or experienced higher mortality due to induced plant defenses on damaged trees. Caterpillars



with more narrow host ranges may be better adapted to handle high levels of defensive chemicals in foliage (Nykanen & Koricheva, 2004), explaining their dominance in plots where defoliation was extensive. These findings directly contradict those of Work and McCullough (2000), who reported that oak specialists were significantly reduced in defoliated plots but not generalists. However, they align with the results of Timms and Smith (2011), who found that polyphagous late-season species were the most adversely affected by the spongy moth. Here it is important to stress that the spongy moth is non-native to the USA, where both studies were conducted, which brings an additional layer of complexity to the interaction with its competitors. For example, attempts at biological control with the introduction of spongy moth antagonists have intensified the top-down pressure on the native fauna. This is particularly striking with *Compsilura concinnata* (Diptera: Tachinidae), a parasitoid introduced in the early twentieth century and known to parasitize more than 150 native lepidopterans in North America (Arnaud, 1978; Elkinton & Boettner, 2012).

Unlike tebufenozide effects, the impact of the outbreak on Lepidoptera was limited to 2019 and did not persist after the outbreak had subsided. In contrast, Symphyta larvae significantly declined in 2020 in stands that were defoliated in 2019. Delayed-induced resistance of defoliated trees has been shown to impair the development and survival of herbivores in post-defoliation years (Nykanen & Koricheva, 2004). It is however unclear why no such impact could be found in Lepidoptera.

## Ecological trade-offs

Our results paint a rather sharp contrast between the strong short-term impacts of tebufenozide treatments and the altogether more subtle consequences of defoliation for Lepidoptera communities. However, caution should be exercised in formulating management decisions based on these results, as they remain limited by the scope of our experiment and the variable levels of defoliation in our study plots. Besides the heavy impacts of single extreme defoliation events, repeated defoliation is a major driver of oak decline (Fajvan & Wood, 1996; Thomas et al., 2002), posing a long-term threat to the rich diversity of organisms associated with oak woodlands (Mitchell et al., 2019). Such a threat cannot be appraised over the relatively short timescale of the present work. Ultimately, it is essential to recognize that the species assemblages most affected by the application of insecticides and defoliation are temporally distinct. In Central European oak forests, the decision to spray insecticides or not should lead to a short-term conservation trade-off between the spring assemblage, rarely exposed to

significant defoliation but heavily impacted by insecticide use, and summer herbivores, subjected to more intense defoliation and other outbreak-induced effects. Against this backdrop and based on our results, we can reasonably infer that tebufenozide poses a greater short-term risk to non-target Lepidoptera compared to BTK. Although the toxicity of tebufenozide appears to be similarly variable across species than that of BTK, its superior environmental stability results in the lethal exposure of summer species, which is typically not observed with BTK (Miller, 1992; Rastall et al., 2003; Wagner et al., 1996). However, it is noteworthy that free-living caterpillars constitute only a minor proportion of the summer Lepidoptera assemblage of Central European oaks, which is instead dominated by leaf miners (Southwood et al., 2004). These species are less vulnerable to insecticides, as they feed exclusively on internal plant tissues (Leroy, Gossner, et al., 2021). However, they are very sensitive to competition by leaf chewers due to their sessile nature. Past research showed no conclusive evidence of notable exposure of leaf miners to tebufenozide but uncovered positive indirect effects of the treatments through the reduction of herbivore damage, even in the absence of significant defoliation (Leroy, Gossner, et al., 2021). In an outbreak context, it makes little doubt that these species should benefit from the suppression of spongy moth outbreaks regardless of whether tebufenozide or BTK is applied.

Altogether, the wide variation in defoliation, and hence its impacts, among outbreak stands put forward our current difficulties in accurately predicting situations that warrant insecticide treatments. A major objective for future research lies in improving our mechanistic understanding of egg-mass density—defoliation relationships, striving toward more accurate risk assessment and hence more targeted insecticide treatments.

## Management implications

In the USA, tebufenozide has been used extensively against the spongy moth in the past decades on privately owned forests (Tobin et al., 2012), and sometimes as an alternative to BTK on public lands (Eggen et al., 2022). The recommended application rate of 67 g AI/ha determined in early efficacy trials (Reardon et al., 2000) has remained unchanged, although the legally defined upper limit allows concentrations up to 134 g AI/ha (Valent Biosciences Corporation, 2017). In contrast, tebufenozide is a recent addition to the list of insecticides licensed for forest use in Germany, and the recommended application rate determined during the pesticide approval process is substantially higher than in the USA, at 180 g AI/ha. This concentration was applied during the 2018–2020

northwestern Bavarian outbreak but could be subject to future revision based on evidence from efficacy and persistence testing. Considering the history of successful tebufenozide use at lower rates in the USA as well as the strong short-term effects reported here, we anticipate the current dosage rates to bring only little in terms of overall efficacy while worsening non-target effects. We, therefore, suggest a reduction of application rates down to the levels applied in the USA. Such change could be particularly critical in reducing the residual toxicity of tebufenozide to summer species, as the bulk of tebufenozide residues degrades within a few weeks of application (Sundaram et al., 1996). A substantial reduction of the damage to summer species would make tebufenozide a highly reliable alternative to BTK with comparable environmental side effects.

An important feature of the present work is the remarkably fast recovery of the Lepidoptera communities compared to most North American studies. We primarily attribute this difference to the comparatively small size of the study plots in Bavaria, essentially as a consequence of forest fragmentation and spraying restrictions by nature protection laws (Leroy, Lemme, et al., 2021). Specifically, individual sprayed areas in Bavaria had a median size of 16, 7 and 6 ha in 2019, 2020, and 2021 (Hahn et al., 2021). In situations where affected areas are much wider, as is generally the case in the USA (STS Program, 2022), fragmenting spray blocks by scattering purposefully untreated buffer zones could minimize the duration of insecticide effects on non-target communities. Nevertheless, we still observed effects depending on mobility in our small plots. Management policies should consider the conservation status of species with apterous females, as they are, based on our assessments, by far the most vulnerable species to insecticide treatments in the long term.

Increasing tree species diversity can increase the resilience of forests to defoliation, and hence mitigate its impact on associated biodiversity (Mitchell et al., 2019). It is generally assumed that forests composed of a mix of host and non-host species are less susceptible to catastrophic defoliation and may harbor a greater diversity of predators and parasitoids that mitigate outbreaks (Muzika & Liebhold, 2000). In our study, we observed a significant positive relationship between canopy development and the diversity of host trees in the canopy, supporting this concept (Appendix S3: Figure S2). Because many summer species can exploit alternative host species, admixing tree species that are generally ignored by spongy moth caterpillars may foster the tolerance of herbivore communities to defoliation. Though likely ineffective to preserve oak specialists, the integration and maintenance of resistant tree species should provide refugia for polyphagous species and contribute to maintaining a degree of canopy cover to

mitigate the alteration of microclimatic conditions in the forest interior (Lovett et al., 2006). In Bavarian oak stands, the species with the most potential in this regard is the field maple *Acer campestre* L., as it is well adapted to susceptible forest types, generally avoided by spongy moth caterpillars, and used as a secondary host by many oak-feeding Lepidoptera.

Although our results are only a snapshot of the ecological impacts of defoliator outbreaks and their treatment with insecticides, they are of great value in both supporting further research and informing management decisions, as they document impacts on the most vulnerable component of the ecosystem in an operational setting. The present study could therefore provide a benchmark for future research investigating the ecological implication of defoliator management in temperate forests. As a follow-up to this work, we intend to use our high-quality sequencing data to characterize host-parasitoid networks to investigate the role of parasitism in mediating caterpillar population dynamics in outbreak situations. Responses of other taxa, including leaf-miners and tebufenozide tolerant arthropods, will also be addressed for a more comprehensive assessment of spongy moth management trade-offs.

## AUTHOR CONTRIBUTIONS

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#### CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

#### DATA AVAILABILITY STATEMENT

All raw and derived data (Leroy et al., 2023) used in the statistical analyses and to produce the figures are available in figshare at <https://doi.org/10.6084/m9.figshare.20992177.v2>. A complete list of trait data sources used for this manuscript can be found in Appendix S1: Table S1.

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## SUPPORTING INFORMATION

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

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