



TUM School of Life Sciences

Lehrstuhl für Terrestrische Ökologie

Effects of aerial insecticide treatments on forest arthropod communities – limitations and opportunities of ecological impact assessment

Benjamin Michel Laurent Leroy

Vollständiger Abdruck der von der TUM School of Life Sciences der Technischen Universität München zur Erlangung des akademischen Grades eines Doktors der Naturwissenschaften (Dr. rer. nat.) genehmigten Dissertation.

Vorsitzender: Prof. Dr. Rupert Seidl

Prüfende/-r der Dissertation:

1. Prof. Dr. Wolfgang W. Weisser
2. Priv.-Doz. Dr. Carsten Brühl

Die Dissertation wurde am 19.05.2021 bei der Technischen Universität München eingereicht und durch die TUM School of Life Sciences am 20.10.2021 angenommen.

Acknowledgements

I would first like to thank my supervisor, Prof. Wolfgang Weisser, for trusting me with this project and giving me just the right amount of freedom and guidance to conduct my thesis research in optimal conditions. I am very grateful to Martin Gossner for teaching me so much during the first year and always lifting my spirits through the harsh times, and for his continued care about my progress even long after leaving the research group. Special thanks also to Sebastian Seibold for his ability to bring my motivation back up with his great ideas and pieces of advice. I would also like to thank Ralf Petercord for seeing opportunities rather than problems and Peter Eichel for his friendliness and critical logistical support. This project would not have been possible without the hard work of Monika Plaga, who showed outstanding skills and professionalism in the field and the lab. I could not have dreamed of better technical support through these five years. I want to thank Florian Lauer for sharing good and hard times, especially through the endless and incredibly tough sampling in tree crowns infested with poisonous caterpillars. I am very grateful to Jessica Jaworek for her invaluable assistance with project organization and for helping me not drown in my chaos. Importantly, I want to acknowledge each of the countless student helpers who brought their essential contribution to the project.

I cannot stress enough how much I enjoyed the last five years working at the Terrestrial Ecology Research Group in Freising. I would like to thank everyone in the group for making it such a great place. I am incredibly thankful to Jan Leidinger for his unwavering support, kindness, and wise insights. Thank you also to Sebastian Meyer and Sharon Zytynska for their brutal honesty and critical inputs that unquestionably helped me improve as a scientist. Last but not least, I am grateful to Petra Freynhagen for being always ready to help with small and big practical issues, as well as Brigitte Grimm, Sonja Seidenberger and Claudia Seilwinder for their always patient and helping hand in my journey down the meanders of German bureaucracy.

Thanks to Ieva for being such a kind, loving and supportive presence and for showing unconditional patience and support in the face of my mood swings and, at times, unreasonable commitment to my work. Everything feels so much easier with you by my side.

Un immense merci Gaby et Klene pour leurs encouragements permanents et leur écoute patiente.

Table of contents

Zusammenfassung	i
Summary	v
Foreword	1
1 Introduction	3
1.1 Insect outbreaks in crops and forests	3
1.2 Major forest defoliators of the Holarctic region.....	4
1.3 Environmental drivers of defoliator outbreaks	6
1.4 Impacts of defoliator outbreaks on forest resources and ecosystems.....	7
1.4.1 Tree growth.....	7
1.4.2 Tree mortality	8
1.4.3 Stand development.....	8
1.4.4 Nutrient cycling	8
1.4.5 Animal communities	9
1.5 Economic costs of defoliator outbreaks	9
1.6 Insecticidal management of defoliator outbreaks in forests	10
1.6.1 Extent and benefits of insecticide use.....	10
1.6.2 A history of aerial insecticide applications in forest	11
1.7 Non-target effects of registered forestry insecticides	13
1.7.1 Diflubenzuron.....	13
1.7.2 Bacillus thuringiensis var. kurstaki (BTK)	14
1.7.3 Tebufenozide	14
1.8 Methodological limitations of insecticide impact studies in forests.....	15
1.8.1 Lack of adequate replication	15
1.8.2 Lack of integration of species life-history	17
1.8.3 Sampling bias and taxonomic impediment.....	18
1.8.4 Relative impacts of outbreaks and insecticides.....	19
1.9 Overall aims and structure of this thesis.....	20
2 Methods.....	23
2.1 Research area.....	23
2.2 Drone experiment	24
2.2.1 Study site	24
2.2.2 Experimental design.....	26
2.2.3 Data collection and processing	26

2.3	Helicopter experiment	29
2.3.1	Study sites.....	29
2.3.2	Experimental design.....	29
2.3.3	Data collection and processing	30
2.4	Stand-level experiment.....	33
2.4.1	Study sites.....	33
2.4.2	Experimental design.....	33
2.4.3	Data collection and processing	34
2.5	Statistical analyses.....	35
2.5.1	Effect of insecticides applied by drone on crown-dwelling Lepidoptera	36
2.5.2	Direct and indirect effects of insecticides and defoliators on sessile herbivores....	36
2.5.3	Effects of insecticides on canopy arthropod communities	38
2.5.4	Efficacy of tebufenozide and accuracy of defoliation risk assessment in a large-scale experimental setting	39
3	Chapter overview	41
4	Discussion	51
4.1	Higher replication improves the detection of non-target effects.....	51
4.2	Life history mediates exposure to insecticides	54
4.3	Species interactions mediate insecticide effects	57
4.3.1	Alteration of competition between herbivore guilds	57
4.3.2	Losses of species in non-sensitive groups	59
4.4	Importance of large-scale and long-term studies	61
5	Conclusion.....	65
6	Outlook: What does the future hold?	67
6.1	Insect outbreaks in future forests.....	67
6.2	Current and future trends in defoliator control.....	68
6.3	Towards the birth of forest ecotoxicology?	69
7	References.....	71
	Appendix A: A methodological analysis of insecticide impact assessment studies in forests	93
	Appendix B: Chapter 1	96
	Appendix C: Chapter 2	97
	Appendix D: Chapter 3.....	98
	Appendix E: Chapter 4	99

Zusammenfassung

Massenvermehrungen pflanzenfressender Insekten gehören zu den kritischsten Störungen in Wäldern der gemäßigten und borealen Zonen. Die Populationen mehrerer Arten folivorer Insekten, die meisten davon Lepidoptera, weisen unter dem Einfluss verschiedener abiotischer und biotischer Faktoren Schwankungen auf, die zu periodisch auftretenden Massenvermehrungen in Nadel- und Laubwäldern führen. Diese Massenvermehrungen treten regional oft synchron auf und können innerhalb weniger Wochen zu großflächiger Entlaubung führen. Kahlfraß kann Waldökosysteme durch die Einschränkung des Baumwachstums und die Erhöhung der Baumsterblichkeit, aber auch über Nahrungsnetze und Nährstoffdynamik, auf vielfältige Weise verändern. Die resultierenden Rohstoffverluste können beträchtlich sein und zwingen die Stakeholder dazu, Strategien zur Verhinderung von Kahlfraß zu verfolgen. Die Ausbringung von Insektiziden aus der Luft ist die effektivste Maßnahme zur Bekämpfung pflanzenfressender Insekten und ist in vielen Ländern seit den 1950er Jahren die Methode der Wahl. Aufgrund zunehmender öffentlicher Kritik am Einsatz von Pestiziden über die letzten 70 Jahre hat sich der Einsatz von Insektiziden in Wäldern von der großflächigen Ausbringung von Nervengiften zu gezielteren Spritzungen mit höherer Spezifität entwickelt. Nach wie vor stehen Pestizideinsätze jedoch bei Umweltschützern in der Kritik, und ihre Nebenwirkungen auf Waldökosysteme sind immer noch nur unzureichend untersucht.

Die derzeit für den Einsatz in Wäldern zugelassenen Insektizide wirken toxisch auf Nicht-Zielinsekten, insbesondere auf Lepidoptera, und können die Struktur der Arthropodengemeinschaften verändern. Mehrere Fachveröffentlichungen haben bereits Auswirkungen des Pestizideinsatzes aus der Luft auf Nicht-Zielarten untersucht, aber die meisten dieser Studien leiden unter schweren methodischen Mängeln. Erstens sind Studien zur Abschätzung ökologischer Folgen von Pestizideinsätzen in Wäldern selten mit den Mitteln ausgestattet, die der planungsintensive Einsatz von Pestiziden aus der Luft erfordert. Dies führt in den meisten Fällen zu mangelhaften und unzureichend replizierten Versuchsanordnungen. Zweitens werden Eigenheiten von Lebenszyklen, die die Insektizidexposition von Organismen stark beeinflussen können, selten berücksichtigt, was den Nachweis von Effekten in biologisch diversen Gruppen erschweren kann. Zuletzt haben Forscher auch selten die Möglichkeit, große Mengen an Insekten bis auf Artniveau zu bestimmen. Deshalb konzentrieren sie sich meistens auf wenige, bekannte Taxa, was die Bewertung von Effekten auf die Artengemeinschaft als Ganzes erschwert. Insgesamt tragen

diese Einschränkungen dazu bei, dass die Nebenwirkungen von Insektizideinsätzen in Wäldern systematisch unterschätzt werden. Es ist daher wichtig, innovative Methoden zu entwickeln, mit denen diese Limitationen überwunden werden können.

In der vorliegenden Arbeit habe ich mich mit den oben genannten Herausforderungen auseinandergesetzt, indem ich neue methodische Ansätze in zwei Geländeversuchen in Eichenwäldern in Nordbayern getestet habe. Im ersten Experiment habe ich untersucht, wie Insektizide mit Sprüh-Drohnen ausgebracht werden können, wodurch die Behandlung von Einzelbäumen und in der Folge eine größere Anzahl Versuchseinheiten möglich werden. In dem Experiment mit 60 Bäumen wurden außerdem die Auswirkungen der Insektizide Diflubenzuron und Tebufenozid auf unterschiedlich sensitive Gilden von Lepidoptera getestet. Durch die hohe Anzahl an Replikaten konnten auch weniger deutliche negative Effekte der Insektizide auf Blattminierer und auf solche Arten nachgewiesen werden, die sich in Blattrollen oder -wickeln schützen. Diese Ergebnisse zeigen, dass bestimmte Life history-Eigenschaften die Exposition zwar abmildern, aber nicht verhindern können. Unterschiede in den Reaktionen der verschiedenen Gilden deuten darauf hin, dass die Effekte der Insektizidbehandlung durch komplexe Interaktionen von biologischen Eigenschaften und Umweltprozessen bestimmt werden. Im zweiten Experiment wurden die Insektizide Diflubenzuron, Tebufenozid und *Bacillus thuringiensis* var. *kurstaki* per Hubschrauber über kleinen Waldbeständen ausgebracht. Zuerst habe ich die Effekte der Insektizidbehandlung auf die Konkurrenz zweier Gilden pflanzenfressender Insekten untersucht: Blattfresser (i.e. folivore Insekten) und sessile Herbivoren (Blattminierer und gallenbildende Insekten). Danach habe ich Pyrethrum-Knockdown und DNA-Metabarcoding eingesetzt, um ganze Gemeinschaften baumbewohnender Arthropoden identifizieren und so deren Reaktionen auf Insektizideinsätze analysieren zu können. Behandlungen mit Diflubenzuron und Tebufenozid hatten indirekt positive Auswirkungen für zwei Gilden sessiler Pflanzenfresser, Blattminierer und Gallenverursacher, indem sie Fraßschäden durch folivore Insekten in den besprühten Bäumen reduzierten. Auf Ebene der Lebensgemeinschaften war ein signifikanter Rückgang in der Diversität mehrerer Arthropodengilden feststellbar, einschließlich toleranter Gilden wie xylobionten Käfern. Dies deutet darauf hin, dass sich die asymmetrischen Effekte von spezifisch für blattfressende Insekten entwickelten Insektiziden über das Nahrungsnetz ausbreiten und so indirekte Auswirkungen auch auf weniger sensitive Arten haben.

Die Ergebnisse dieser Arbeit unterstreichen wie wichtig robuste Methoden zur Bewertung von Nebenwirkungen forstlich genutzter Insektizide sind. Die Erhöhung der Anzahl an

Replikaten und der taxonomischen Auflösung und Abdeckung ermöglichte die Erkennung von unbeabsichtigten Auswirkungen in moderat und wenig sensitiven Taxa. Es konnte erfolgreich gezeigt werden, dass gängige methodische Einschränkungen ein hohes Risiko der systematischen Unterschätzung von Insektizideffekten bergen. Die vorgeschlagenen Methoden sind geeignet, unser Verständnis der Auswirkungen von Insektizideinsätzen in Wäldern zu verbessern, müssten aber noch hochskaliert werden um für die Praxis relevante Ergebnisse zu produzieren. Als Ausblick präsentiere ich im letzten Kapitel ein Experiment auf Bestandesebene, das dieses Ziel verfolgt. Diese Studie soll sowohl die kurz- als auch die langfristigen relativen Auswirkungen von massenhafter Vermehrung blattfressender Insekten und deren Behandlung mit Insektiziden auf Waldökosysteme und die Holzproduktion untersuchen. Die Implementierung der hier vorgestellten Methoden würde aussagekräftige Studienergebnisse produzieren, die von Forstbetrieben und politischen Entscheidungsträgern zur Verbesserung der Nachhaltigkeit bei der Bekämpfung von Massenvermehrungen von Schädlingen genutzt werden können.

Summary

Insect outbreaks are among the most critical disturbances of temperate and boreal forests worldwide. Several species of folivorous insects, most of them Lepidoptera, display population oscillations under the combined action of biotic and abiotic drivers, causing periodic outbreaks in deciduous and coniferous woodlands. These outbreaks are often spatially synchronous over entire regions and can be sufficiently intense to defoliate large swathes of forest within a few weeks. Defoliation can affect forest ecosystems in various ways, primarily by limiting tree growth and increasing tree mortality and altering food webs and nutrient dynamics. The resulting timber losses can be substantial, pushing forest stakeholders to deploy a broad range of strategies to prevent defoliation. The aerial application of insecticides over tree canopies is the most effective measure to combat defoliator outbreaks and has been the principal management strategy in many countries since the 1950s. Amid growing public agitation about pesticides over the last 70 years, the use of insecticides in forests gradually moved away from the large-scale application of neurotoxicants to more targeted spraying with defoliator-specific compounds. However, these treatments are still a major concern for environmentalists, and their side effects on forest ecosystems remain poorly understood.

Insecticides currently licensed for forest use have adverse toxic effects on non-target insects, which may disrupt the structure of arthropod communities. Several publications reported impacts of aerial spraying on non-target species, but most of these studies suffer from severe methodological shortcomings. Firstly, impact assessment studies in forests are rarely sufficiently funded to properly handle the heavy logistics associated with aerial spray trials, which led to the routine use of inadequately or insufficiently replicated experimental designs. Secondly, life-history traits that can strongly influence exposure to insecticides are rarely considered in the delimitation of study systems, which may obscure the detection of effects in the analysis of biologically diverse groups. Lastly, the challenge of determining large numbers of insects to species often prevents the assessment of community-wide impacts. Altogether, these limitations likely contribute to a systematic underestimation of the side effects of forestry insecticides. It is therefore essential to develop innovative strategies to overcome these hurdles.

In the present thesis, I addressed each of the aforementioned challenges by implementing novel methodological approaches in two field experiments carried out in oak woodlands in Northern Bavaria, Germany. In the first experiment, I exploited the ability of spray drones to

apply insecticides on single trees to increase replication in a cost-effective way. The experiment, including 60 trees, was used to test the impacts of the insecticides diflubenzuron and tebufenozide on different guilds of Lepidoptera with differential field susceptibility. The high replication allowed the detection of inconspicuous adverse effects of the insecticides on shelter-building and leaf-mining species. These findings showed that life-history traits could mitigate exposure but do not necessarily prevent it. Discrepancies in the response of the two guilds to the different treatments suggest that insecticide effects are driven by a complex interaction of biological traits and environmental processes that determine exposure dynamics *in situ*. In the second experiment, the insecticides diflubenzuron, tebufenozide and *Bacillus thuringiensis* var. *kurstaki* were applied by a manned helicopter over small forest plots. I first explored the effects of insecticides on the competition between two guilds of herbivores: leaf-chewers (i.e., defoliators) and sessile herbivores (i.e., leaf-miners and gall-inducers). I then combined pyrethrum knockdown and DNA-metabarcoding to identify a diverse assemblage of arboreal arthropods with the aim to analyse the impact of insecticide on the structure of arthropod communities. Treatments with diflubenzuron and tebufenozide indirectly benefited two tolerant guilds of sessile herbivores, namely the lower-surface leaf-miners and the gall-inducers, by reducing the occurrence of chewing damage in the sprayed trees. At the community level, I noticed a significant reduction in the diversity of several arthropod guilds, including tolerant guilds such as xylophagous beetles. This outcome suggests that the asymmetric effects of selective insecticides propagated through the food web, indirectly impacting tolerant species.

The findings in this thesis emphasise the importance of robust methodologies to assess the side effects of forestry insecticides. The increase of replication, taxonomic resolution, and taxonomic coverage allowed the detection of non-target impacts in moderately sensitive and non-sensitive taxa. It was successfully demonstrated that the routine use of methodological compromises poses high risks of systematic underestimation of insecticide effects. The proposed methods could be widely implemented to improve our understanding of the acute impacts of insecticides in forest ecosystems. However, they should be ultimately upscaled to produce results more relevant to practice. As an outlook for this thesis, I presented and evaluated a stand-level experiment recently set up to pursue this objective. This experiment will be used to investigate the relative impacts of defoliator outbreaks and their treatments with insecticides on forest ecosystems and timber production over both short- and long-time scales. Implementing the different methods explored in this thesis into a realistic setting should produce reliable results readily usable by forest managers and policymakers to improve the sustainability of defoliator management in forests.

Foreword

When I started my PhD project in 2016, I had never heard about insecticide use in forests before. Due to my formation as an agronomist, I saw aerial spraying as little more than a relic of the Green Revolution and forests as sanctuaries where the slow pace of human management allowed nature to flourish. I was hence little surprised at the reactions I received when answering questions about my work during the years that followed, from the rather comical “Is it a German thing?” to the more telling “Why would anyone do that?”. In hindsight, such reactions make much sense indeed. Recent surveys revealed that Europeans rate the environmental and recreational value of forests highly while having comparatively little knowledge of the economic aspects of forestry (Ranacher et al., 2020). As for aerial spraying, the practice was already very negatively perceived two decades ago (Wagner et al., 1998), and assuming that its reputation did not improve since then seems not too big of a stretch. In recent years, announcements of aerial treatment programmes in local media have been met with shock and anger by the public. In 2019, a forest spray operation conducted in north-eastern Germany sparked considerable outrage that quickly escalated while spreading on social media, culminating with misinformation and harassment campaigns towards forest administration and political authorities (Möller, 2020). Such emotionally driven reactions are a telling symptom of the current state of unprecedented public concern on pesticides and nature protection.

One has to admit that the evidence produced in recent years on the adverse effects of pesticides gives little cause for optimism. Extensive research on the widely used neonicotinoid insecticides uncovered consistent harmful effects on beneficial insects and vertebrates (Goulson, 2013). These findings have received worldwide media coverage in the early 2010s, sparking a wave of public outcry reminiscent of the movement that emerged following the publication of *Silent Spring* (Carson, 1962) during the so-called “DDT era” (Kurwadkar & Evans, 2016). Over the last five years, pesticides were brought into the spotlight once again as potential drivers of insect declines reported in multiple scientific articles (Hallmann et al., 2017; Seibold et al., 2019; Wepprich et al., 2019).

So far, aerial spraying in forests has not made major headlines, most likely due to the relatively exceptional nature of the practice. Yet, in the current climate of fear and mistrust, providing context on the extent of insecticide use in forests is an essential prerequisite to the critical appraisal of their ecological impacts. Forestry is but a dwarf on the pesticide market,

amounting to, for example, approximately 2 % of the total pesticide sales in Canada, a major player in worldwide timber production (Thompson, 2011). It is noteworthy that agrochemical companies generally show little interest in investing in the development and registration of forestry insecticides, likely due to the small size and unpredictability of the forest protection market (Holmes & MacQuarrie, 2016). Contrasting with the systematic preventative pesticide treatments that predominate in agriculture, forest spraying is exclusively performed curatively to protect trees from essentially sporadic eruptions of defoliating insects. In short, these treatments are rare and concern only a tiny proportion of the forested area each year (Möller, 2020; Thompson, 2011). Nevertheless, aerial spraying inflicts an additional disturbance onto already fragile ecosystems, and their impacts should hence be thoroughly scrutinized.

While screening background literature on the side effects of forestry insecticides on arthropods, I noticed that most published studies reported serious methodological shortcomings. Side effects experiments are often inadequately or insufficiently replicated and suffer from undersampling and limited availability of taxonomic and biological knowledge of the focal communities. These issues have been long acknowledged by scientists, who deplored logistical difficulties associated with insufficient funding (Cadogan & de Groot, 1995; Sample, Butler, et al., 1993; Wagner et al., 1996). The resulting routine use of methodological compromises in aerial field trials may have led to a systematic underestimation of the ecological impacts of forestry insecticides. Cadogan and Scharbach (2003) proposed an experimental approach to overcome the hurdles associated with the design of insecticide efficacy trials. They emphasized the importance of producing transparent and credible results that can withstand scientific scrutiny to support a wider public acceptance of selective insecticides in forest protection. Adopting such approaches is all the more essential in non-target impact trials considering the serious risk of overlooking critical effects when using subpar methods.

In this thesis, I propose different strategies to improve the methodological robustness of insecticide impact assessment in forests. In the following section, I provide comprehensive background information on the causes, consequences, and management of outbreaks of forest insects. I then review the existing literature on the effects of insecticides on non-target arthropods and the methodological limitations of these studies. Finally, I propose and apply novel approaches to remedy these shortcomings and report my findings in a series of chapters.

1 Introduction

1.1 Insect outbreaks in crops and forests

Insect outbreaks can be fundamentally described as explosive increases in the density of a particular species. More commonly, they are defined as a rapid increase in the population of a species (referred to as a pest) that is, to some extent, detrimental to human activities and well-being (Berryman, 1987). Whether a given insect species is granted the pest status is hence, in most cases, determined by its impact on the marketable production of the ecosystem (Letourneau, 2012). This anthropocentric definition of insect outbreaks underlies one fundamental difference between agricultural and forest outbreaks. In crop production, economic value is generated chiefly over relatively short time scales so that even brief episodes of herbivory can strongly impact crop yields. Short rotation times and artificial selection make annual crops particularly vulnerable to herbivory due to their lack of long-term co-evolution with native insect populations (Letourneau, 2012). Besides, most cropping systems are characterised by large and structurally homogeneous monocultures that only support a low diversity of natural resources, non-crop habitats, and hence natural enemies (Bianchi et al., 2006). All these characteristics make conventional crop fields frequently affected by economically harmful levels of herbivory.

By contrast, forests are characterised by long rotation periods and long-term management objectives. Except for high-productivity monocultures, forests are characterised by high structural and compositional complexity, providing resources and habitats to a wide variety of organisms (Sobek et al., 2009). As a result, forests typically harbour diverse natural enemy assemblages that co-evolved with native herbivores over long timescales, providing sufficient biological control to prevent the frequent occurrence of insect outbreaks (Pschorn-Walcher, 1977). Likewise, regular exposure to moderate levels of herbivory allows trees to develop adaptive defence strategies, further increasing the system's tolerance to herbivory. The

economic thresholds (i.e. critical insect densities) used to characterise an outbreak are therefore much higher in forestry than in agriculture (Letourneau, 2012). Unless they cause massive increases in tree mortality, localised population eruptions are not considered sufficient to give a forest species the pest status, which is instead motivated by the spatial scale of its outbreaks (Liebhold et al., 2012).

The majority of economically injurious insect outbreaks in forests are caused by two types of insects: bark beetles and defoliators. Bark beetles are a diverse subfamily of weevils (Coleoptera: Curculionidae: Scolytinae) that feed primarily on the inner bark of trees and bark-inhabiting fungi. Bark beetle outbreaks cause widespread tree mortality and have been deemed the most critical insect disturbance in temperate and boreal forests (Raffa et al., 2015). Most of the economically significant forest defoliators are larval stages of moths (henceforth caterpillars; Lepidoptera) and sawflies (Hymenoptera: Symphyta). These insects reduce the photosynthetic capacity of trees by feeding on foliage, altering tree growth and survival (MacLean, 2016). Because of broad differences in their life history and impact pathways, bark beetles and defoliators mobilise different management strategies. In particular, recourse to insecticides in bark beetle management is restricted to preventative treatments on high-value individual trees via bole sprays or stem injections with systemic insecticides (Fettig et al., 2013). By contrast, forest defoliator control has long relied on curative applications of contact or ingestion insecticides applied by aircraft over large areas. Aiming to investigate the side effects of aerial insecticide treatments on forest ecosystems, the present work thus focuses only on defoliator outbreak management.

1.2 Major forest defoliators of the Holarctic region

A very diverse assemblage of insects feed on the foliage of trees, yet only a remarkably small number of species can become abundant enough to have a significant economic impact (Mason, 1987). In the US, the gypsy moth *Lymantria dispar* L. (Lepidoptera: Erebididae) has been the most impactful defoliator since its accidental introduction in 1869. Early efforts to eradicate the first outbreak populations have been unsuccessful, and the species keeps causing severe damage to north-eastern deciduous forests each year while extending its range south- and westwards (Liebhold & McManus, 1999). The gypsy moth defoliated more than 34 million ha since 1924 in the United States (McManus, 2007), including 15 million ha in the last 30 years alone (Liebhold et al., 2021). In Canada, gypsy moth outbreaks have been mostly confined to warmer regions bordering the north-eastern US. However, global change is

expected to extend the climate zone suitable for the gypsy moth, posing a severe threat to future forests (Régnière et al., 2009). Outbreaks of native defoliators can also have massive impacts on North American forests, as strikingly illustrated by the spruce budworm *Choristoneura fumiferana* Clemens (Lepidoptera: Tortricidae). This species caused economically injurious levels of defoliation on a staggering 450 million ha between 1975 and 2000 in Canada, representing 64 % of the total area defoliated during this period (MacLean, 2016). Other species regularly cause more localised but economically significant damage across the continent. These include the forest tent caterpillar *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae), the western spruce budworm *Choristoneura freemani* Razowski (Lepidoptera: Tortricidae), the Douglas-fir tussock moth *Orgyia pseudotsugata* McDunnough (Lepidoptera: Erebidae), the hemlock looper *Lambdina fiscellaria* Guenée (Lepidoptera: Geometridae), the balsam fir sawfly *Neodiprion abietis* Harris (Hymenoptera: Diprionidae) and the jack-pine budworm *Choristoneura pinus* Freeman (Lepidoptera: Tortricidae), to name a few (Berryman, 1988; Canadian Council of Forest Ministers, 2021; Man, 2016).

In Europe, native species make up the bulk of economically significant defoliators. The larch budmoth *Zeiraphera diniana* Guenée (Lepidoptera: Tortricidae) and the autumnal moth *Epirrita autumnata* Borkhausen (Lepidoptera: Geometridae) are the most extensive defoliators of the alpine and boreal regions (Berryman, 1988). In the temperate zone, oak- and pine-dominated woodlands are the most affected (Brunk et al., 2019). Notorious pine pests include the diprionid sawflies (Hymenoptera) *Neodiprion sertifer* Geoffroy and *Diprion pini* L, and several species of moths such as the pine-tree lappet *Dendrolimus pini* L. (Lasiocampidae), the nun moth *Lymantria monachal* L. (Erebidae), the pine beauty moth *Panolis flammea* Denis & Schiffermüller (Noctuidae) and the pine looper *Bupalus piniaria* L. (Geometridae) (Berryman, 1988). Historically, oak woodlands have been affected by sporadic outbreaks of a spring-feeding assemblage comprising several species of loopers (Geometridae; most notably the winter moth *Operophtera brumata* L. and the mottled umber *Erannis defoliaria* Clerck), leaf-rollers (Tortricidae; mainly the European oak leaf-roller *Tortrix viridana* L.) and owlet caterpillars (Noctuidae; mainly *Orthosia* sp.) (Csóka, 1998; Raimondo et al., 2004). Europe lies within the native range of the aforementioned gypsy moth, and the insect has long been considered only a minor forest pest. The small extent and fragmentation of European oak forests and a less diverse natural enemy assemblage in North America have been suggested to explain the disparity in the impact of gypsy moth outbreaks between both continents (McManus & Csóka, 2007). Nevertheless, outbreaks of increased magnitude have been recorded in the last decades throughout Europe (Villemant, 2010; Wulf

& Graser, 1996; Zúbrik et al., 2021). During the early 1990s, an unprecedentedly large gradation across 15 European countries lead to the defoliation of hundreds of thousands of hectares (Alalouni et al., 2013; Wulf & Graser, 1996). Besides, the last decades have witnessed a constant increase in the frequency, severity and range of outbreaks of warmth- and light-loving processionary caterpillars (*Thaumetopoea processionea* L. and *Thaumetopoea pityocampa* Denis & Schiffermüller; Roques, 2015).

1.3 Environmental drivers of defoliator outbreaks

Populations of forest defoliators are characterised by oscillations whose magnitude and periodicity vary among species (Berryman, 1996). These population cycles are heterogeneous at small spatial scales, driven by variation in local environmental factors, such as forest type (Johnson et al., 2006), host tree density (Haynes, Liebhold, & Johnson, 2009) and elevation (Haynes et al., 2012). Over large geographical areas, however, changes in the abundance of disjunct populations are somewhat congruent, a phenomenon referred to as spatial synchrony (Liebhold et al., 2012). Spatial synchrony is a major component of the threat posed by outbreaks to land resources, as the sheer scale of population eruptions vastly overwhelms the regulation ability of both humans and ecosystems (Bjørnstad et al., 2008).

Researchers have long attempted to characterise a life-history basis for the tendency of certain defoliator species to outbreaks (Hunter, 1991, 1995; Nothnagle & Schutlz, 1987). Although a combination of traits including egg stage overwintering, spring feeding or poor female flying ability appears to predispose species to outbreaks, the evidence accumulated during the last decades suggests that outbreak dynamics cannot be explained by life history alone (Koricheva et al., 2012). On the one hand, the oscillating nature of defoliator populations seems to primarily result from delayed density-dependent feedbacks between the herbivore, the host plant or one or several antagonists, namely predators, parasitoids or pathogens (Berryman, 1996). The existence of such feedbacks has been described across various species and study systems (e.g. Cooke & Lorenzetti, 2006; Jones et al., 1998; Klemola et al., 2014; Régnière & Nealis, 2007; Tanhuanpää et al., 1999). On the other hand, spatial synchrony was shown to be primarily explained by density-independent stochastic factors such as temperature or precipitations. This process of synchronisation of two separate populations by spatially correlated environmental variables was first described by Moran (1953) and has since then been referred to as the “Moran effect”. While initially seen as the manifestation of direct impacts of weather on mortality and reproduction, it now seems

increasingly clear that Moran effects are primarily indirect, synchronising the dynamics of defoliator populations through synchronisation of trophic pressures (Liebhold et al., 2012). Extensive research on North American gypsy moth populations provided an excellent example of such mechanisms. Results of empirical and modelling studies showed that synchrony of mast seeding could propagate across higher trophic levels. Weather-driven fluctuations in mast production drive oscillations of the gypsy moth by impacting the population dynamics of its chief predator, the white-footed mouse, which uses acorns as its winter food source (Haynes et al., 2013; Haynes, Liebhold, Fearer, et al., 2009; Jones et al., 1998; Liebhold et al., 2000). Besides, short- and long-distance dispersal of defoliators and their antagonists can reinforce synchrony by phase-locking separated populations (Bjørnstad et al., 2002; Haynes et al., 2019; Jansen, 1999).

1.4 Impacts of defoliator outbreaks on forest resources and ecosystems

Defoliator species differ widely regarding patterns, intensity and duration of feeding, and these factors mediate the magnitude of defoliation impacts (MacLean, 2016). Moderate to severe defoliation has profound impacts on tree growth, tree mortality and stand development, which propagate within the ecosystem.

1.4.1 Tree growth

Defoliation causes trees to redistribute the energy normally allocated to stem-wood, root and mast production to maintain minimal photosynthetic capacity for survival (Gottschalk, 1990; MacLean, 2016). The primary consequence of this process is the decline of tree growth. These losses are directly proportional to the extent of the defoliation, a pattern which is remarkably consistent across pest and host species (Iqbal et al., 2011; Jacquet et al., 2012; Lyttikäinen-Saarenmaa et al., 2002; Man et al., 2008; Mason et al., 1997; Naidoo & Lechowicz, 2001; Simmons et al., 2014; Twery, 1991). Substantial radial and volume losses can occur even at moderate levels of defoliation (Straw, 1996) and annual growth can be nearly completely stopped during heavy defoliation (Lyytikäinen-Saarenmaa et al., 2002). Growth reduction generally lasts for several years after the disturbance before the stand recovers to pre-outbreak levels (Gross, 1992; Iqbal et al., 2011; R. Man et al., 2008; Mason et al., 1997; Twery, 1991). Such losses directly impact timber volumes, but timber quality is also affected, as defoliation more strongly affects latewood than earlywood production (Simmons et al., 2014; Twery, 1991).

1.4.2 Tree mortality

Increased tree mortality during and after outbreaks is another common consequence of defoliation, although it does not occur as consistently as growth reduction. Although not nearly as lethal as bark beetles, defoliators occasionally cause catastrophic levels of mortality. Instances of total mortality of susceptible hosts have been reported in some stands defoliated by gypsy moths or spruce budworms (Campbell & Sloan, 1977; Iqbal et al., 2011; MacLean, 1980). The probability of tree death increases with the intensity, duration, and frequency of defoliation. It is further amplified by poor tree vitality and the presence of abiotic stresses or secondary insect pests and pathogens, such as bark beetles, wood-borers and fungi (Davidson et al., 1999; MacLean, 2016). However, intermediate and suppressed trees, which often have a lower market value, are generally more strongly impacted than dominant and co-dominant individuals (Davidson et al., 1999; Gross, 1992).

1.4.3 Stand development

In the long run, defoliation can alter the course of stand development, with long-term effects including changes in competitive interactions between host and non-host species, age-class distribution and species composition, as well as altered regeneration and succession dynamics (MacLean, 2016). Host trees reallocating their energy for refoliation may lose their direct competitive advantages for growing space with non-hosts (Twery, 1991), and differential mortality among host and non-host species can influence successional dynamics (Amos-Binks et al., 2010). Regeneration can be directly impacted by the defoliation of seedlings and the cessation of seed production by defoliated trees (Twery, 1991). Moreover, the reduction of canopy foliage cover increases light, rainwater and nutrient inputs to the forest floor, promoting the rapid development of the herb layer that can induce dominance-shifts towards resource-efficient species (Fajvan & Wood, 1996; Jepsen et al., 2013; Twery, 1991).

1.4.4 Nutrient cycling

Intense canopy-to-soil nutrient fluxes in the form of throughfall, green litter (i.e. prematurely abscised foliage and leaf debris), and insect frass (i.e. faeces) can modify nutrient dynamics and microbial activity in the soil (I-M-Arnold et al., 2016; Lovett et al., 2002; McMillin & Wagner, 1997; Mellec & Michalzik, 2008). Inputs of carbon (C) and especially nitrogen (N) are considerably higher in outbreak than in non-outbreak stands, leading to decreases in soil

C/N ratio over time (I-M-Arnold et al., 2016) and positive feedback loops for future plant growth (McMillin & Wagner, 1997). As substantial tree mortality reduces the retention capacity of soil nutrients, elevated N losses can occur in severely impacted stands (Lovett et al., 2002).

1.4.5 Animal communities

Communities of forest animals can be directly and indirectly affected by defoliator outbreaks. First and foremost, the sheer abundance of insect herbivores is not without consequences for other species. The activity of caterpillar predators, such as some species of cuckoos or ground beetles, is strongly influenced by caterpillar gradations (Barber et al., 2008; Weseloh, 1985). Increased predation and parasitism can, in turn, pose a threat to non-outbreak herbivore insects (Faeth, 1986; Redman & Scriber, 2000). Defoliation is another driver of changes in animal communities, both directly and through induced alteration of the composition and structure of the vegetation. Substantial reduction of green leaf biomass, damage-induced changes in leaf-chemistry or secondary infestation by leaf pathogens may intensify bottom-up pressure on competing herbivores (Csóka et al., 2015; Nykanen & Koricheva, 2004; Redman & Scriber, 2000; Tack et al., 2012; Work & McCullough, 2000). Defoliation-induced mortality increases the proportion of snags and lying dead trees, supporting a diverse animal community that rely on dead wood and tree cavities for food and habitats (Koenig et al., 2011; Twery, 1991). Reduced mast production can differentially impact species relying on mast as a food source depending on their diet plasticity (Clotfelter et al., 2007; Kasbohm et al., 1996; Twery, 1991). Furthermore, high vegetation density in the herb and shrub layers increased the availability of habitat for understory-nesting birds (Cooper et al., 1993; Gale et al., 2001), and shifts in dominance patterns in the low vegetation layers can trigger bottom-up trophic cascades (Jepsen et al., 2013).

1.5 Economic costs of defoliator outbreaks

Due to their large spatial extent and their adverse effects on forest resources, defoliator outbreaks have non-trivial economic impacts, especially in countries where forestry is an essential contributor to the national economy (Niquidet et al., 2016). Economic loss on the timber market is the principal cost generally associated with defoliator outbreaks. Losses in timber harvest volumes caused by growth reduction and tree mortality can correspond to the production levels of multiple non-outbreak years (e.g. Austarå et al., 1987; Lyytikäinen-

Saarenmaa et al., 2002; Straw, 1996). In Canada, annual market losses attributed to forest pests have been estimated to match approximately half of the timber harvest volume (Maclean, 2004). Montgomery and Wallner (1988) reported estimated timber losses linked to gypsy moth outbreaks amounting to \$72 million in Pennsylvania alone in 1981. In recent years, an increasing emphasis has been put on including non-market costs, such as loss of recreational and property value, that often account for a significant fraction of the total costs (Aukema et al., 2011; Bradshaw et al., 2016; Holmes et al., 2009). Finally, the ecological costs and benefits of defoliator outbreaks are hardly monetisable and often not assessed (Bradshaw et al., 2016; Schowalter, 2012).

1.6 Insecticidal management of defoliator outbreaks in forests

1.6.1 Extent and benefits of insecticide use

Substantial resources have been invested in developing effective strategies to mitigate the economic costs of defoliating insects. Management efforts include a variety of techniques, such as targeted silvicultural practices (Muzika & Liebhold, 2000), biological control (MacQuarrie et al., 2016), mating disruption (Régnière et al., 2019; Tcheslavskaja et al., 2005), and insecticide treatments. While all these methods have their merits, insecticide treatments are by far the most efficacious and cost-effective control measures to date. Insecticides are sprayed over the canopy by aircraft (i.e. fixed-winged aeroplane or helicopter) during the early stages of the pest development to kill the larvae before they cause significant damage. Aerial applications have been performed throughout Europe and North America since the early 1950s. Between 1970 and 2020, in the US, about 8.5 million ha of forests have been sprayed with insecticides as part of eradication, containment, and suppression treatments against the gypsy moth (USDA Forest Service, 2020). In Canada, no less than 75 million ha have been treated with chemical and biological insecticides to combat spruce budworm outbreaks (Holmes & MacQuarrie, 2016 and references therein). While treatment expenditures make up a non-negligible fraction of total outbreak costs (e.g. \$282 million were spent in gypsy moth aerial treatments in the US during the last 40 years; USDA Forest Service, 2020), their economic benefits vastly outweigh their costs. Gray and McKinnon (2007) estimated that insecticide treatments carried out in spruce budworm-infested forests in New Brunswick between 1965 and 1992 reduced the extent of defoliation by 42 %. An economic simulation by Chang et al. (2012) predicted that aerial treatments on 40 % of the area affected

by spruce budworm in New Brunswick could reduce economic losses by up to 66 % over a 30-year period. However, insecticidal treatments have been long associated with controversy due to their potential nefarious effects on human health and the environment.

1.6.2 A history of aerial insecticide applications in forest

“Yet, before everything, special care should be taken that intended remedies are not productive of ill results; as these may arise from either remedial measures being applied in excess or at unseasonable times.”

The wise insight from Pliny the Elder’s *Natural History* remains valid to the present day. Unfortunately, the history of the pesticide industry is a telling example of the failure to live up to this principle. Certainly, the chemical industry has been striving to develop decreasingly harmful substances, but these efforts were essentially reactive to growing public opposition. The harm caused by massive and careless use of dangerous pesticides in the mid-20th century is still perceptible to this day in the form of persistent and harmful residues accumulated in soils and food webs (Bussian et al., 2015; Mrema et al., 2013).

Birth of aerial pesticide application. The use of aerial applications to control forest pests was first suggested in 1910 and taken up a year later by the Prussian chief forester Alfred Zimmerman, who patented a process for dusting forest defoliators with pesticides from a nacelle suspended to an aircraft (Reisch, 1974). However, the practice was initially vehemently opposed by forest management authorities, and early trials proved unsuccessful. It is only in the 1920s that further trials with lead arsenate and calcium arsenate were conducted in several countries (Holmes & MacQuarrie, 2016; Majunke, 2016; Prien, 2016). At the time, arsenicals were the most widely used pesticides both in timber and food production (Davis, 2014). As the toxicity of arsenic was common knowledge, protests against arsenicals quickly arose once the public became aware of their widespread use. Public concerns culminated in the US with the publication of *100,000,000 Guinea Pigs* (Kallet & Schlink, 1933), which propounded that American people were being used as experimental subjects in a huge experiment conducted by the food and pharmaceutical industries.

The neurotoxicant era. The development of the first organic (i.e. carbon-based) insecticides was an important milestone in the history of chemical pest management. The organochlorine dichlorodiphenyltrichloroethane (DDT) was immensely successful in controlling disease vectors during World War II and rapidly replaced arsenicals in crop protection from 1945 onwards (Metcalf & Horowitz, 2014). The advent of DDT and major progress in spray

technology marked the actual birth of aerial application as a silvicultural pest control practice in North America and Europe (Reisch, 1974). However, public concerns about the persistence of DDT residues and their toxicity to pollinators, fish and wildlife continuously increased through the 1950s. In the US, the rising agitation about DDT led to the decision to gradually phase out its use against forest pests in 1958 (Liebhold & McManus, 1999). Four years later, the resounding publication of *Silent Spring* (Carson, 1962) spurred the emergence of the American environmental movement and marked a significant turning point in the national pesticide policy (Liebhold & McManus, 1999), eventually leading to a complete ban of DDT in 1972 (Whitney, 2012). In Canada and Central Europe, DDT and other organochlorines remained in use for forest protection despite public outcry and were only discontinued between the late 1960s and early 1970s (Holmes & MacQuarrie, 2016; Prien, 2016; Schwenke, 1973).

Nevertheless, the rise of public concerns about insecticides inspired worldwide changes in pesticide science and policies, marked by a gradual decline in production and use, as well as an intensification of research to develop new chemicals (Holmes & MacQuarrie, 2016; Liebhold & McManus, 1999; Prien, 2016). Through the 1960s and 1970s, various products belonging to three classes of neurotoxicants, the organophosphates, carbamates and pyrethroids, were successively added to the defoliator management toolbox (Holmes & MacQuarrie, 2016; Liebhold & McManus, 1999; Majunke, 2016). These novel insecticides marked a significant departure from organochlorines due to their low bioaccumulation and persistence properties. However, they were not less toxic (Davis, 2014) and were all eventually found to harm birds, pollinators, soil invertebrates or aquatic fauna to some extent (Courtemanch & Gibbs, 1980; Kevan, 1975; Miliczky & Osgood, 1979; Peakall et al., 1983; Sibley et al., 1991).

The advent of selective insecticides. In the 1980s, the introduction of insect growth regulators (IGRs), characterised by negligible vertebrate toxicity, marked the second major turning point in the history of insecticides (Graf, 1993). The moulting inhibitor diflubenzuron soon became the substance of choice in the US and Europe (Knížek et al., 2001; Liebhold & McManus, 1999). By contrast, the rise of IGRs was at first relatively inconsequential in Canada due to the poor field efficacy of diflubenzuron against the spruce budworm (Retnakaran et al., 1980). As a result, the organophosphate fenitrothion continued making up the bulk of Canadian defoliator control strategies until the 1990s (Holmes & MacQuarrie, 2016; van Frankenhuyzen et al., 2016). In the US, the advent of IGRs did not put an end to the strict scrutiny of environmentalists towards the aerial spraying of chemicals. Diflubenzuron was

notably criticised for its adverse effects on aquatic invertebrates and its persistence in the environment for several months (Liebhold & McManus, 1999).

Extensive research and development on the Lepidoptera-specific microbial insecticide *Bacillus thuringiensis* var. *kurstaki* (BTK) led to its widespread adoption in North America in the early 1990s. Over the following years, BTK progressively overtook diflubenzuron as the most used product for defoliator treatments (Liebhold & McManus, 1999; van Frankenhuyzen et al., 2016). Europe followed the same trend (van Frankenhuyzen, 2000) though diflubenzuron remained the preferred choice in some countries until well into the 2000s due to its superior efficacy (Matyjaszczyk et al., 2019; Petercord, 2013). From the late 1990s onwards, tebufenozide, a Lepidoptera-specific IGR, was gradually adopted as a possible alternative to BTK in both North America and Europe (Holmes & MacQuarrie, 2016; Lemme et al., 2019; Liebhold & McManus, 1999), for what is to date the latest significant development in the history of forestry insecticides.

1.7 Non-target effects of registered forestry insecticides

As of today, insecticide-based forest protection has moved away from the widespread use of neurotoxicants. Treatments with broad-spectrum insecticides are now rare and, when not banned altogether, restricted to emergencies, such as suppressing outbreaks in already defoliated coniferous stands where non-contact substances are ineffective (Holmes & MacQuarrie, 2016; Matyjaszczyk et al., 2019; Möller, 2014). The insecticidal management of forest defoliators now nearly exclusively relies on BTK and tebufenozide for lepidopteran pests and diflubenzuron for sawflies (Forest Stewardship Council, 2019; Holmes & MacQuarrie, 2016; USDA Forest Service, 2020). Due to the established vertebrate safety of these insecticides (Durkin, 2004b, 2004a; Durkin & Klotzbach, 2004), impact assessment studies mainly aimed at assessing side effects on non-target arthropods, although indirect impacts on birds and mammals were occasionally addressed (Awkerman et al., 2011; Bellocq et al., 1992; Cooper et al., 1990; Holmes, 1998). In the following section, I review the state of knowledge on the side effects of all three substances on non-target forest arthropods.

1.7.1 Diflubenzuron

Diflubenzuron is a benzoylurea insecticide that inhibits chitin production in juvenile arthropods, causing a lethal moult following ingestion (Maas et al., 1981). There is substantial

evidence that it has adverse effects on non-target arthropods. Declines in abundance were observed in Lepidoptera (Horstmann, 1982; Martinat et al., 1988; Sample, Butler, et al., 1993; Butler, Chrislip, et al., 1997; Hacker, 1997) and other chewing herbivores (Martinat et al., 1988), as well as Thysanoptera (Rieske & Buss, 2001) and Orthoptera (Martinat et al., 1993). Declines in species diversity were also reported, albeit less consistently than abundance reductions (Martinat et al., 1988; Butler, Chrislip, et al., 1997; Sample, Butler, et al., 1993; but no significant effect in Hacker, 1997). Although Webb et al. (1989) found no significant impact of diflubenzuron on the abundance of the gypsy moth parasitoid *Cotesia melanoscela* Ratzeburg (Hymenoptera: Braconidae), increased mortality of various parasitoid species was observed on intoxicated hosts (Madrid & Stewart, 1981; Page et al., 1982). Inconsistent responses, ranging from significant decline to the absence of effects and even significant population growth were observed for flies (Jäkel & Roth, 1999; Sample, Butler, et al., 1993), soil microarthropods (Perry et al., 1997; Jäkel & Roth, 1999; Rieske & Buss, 2001; Beck et al., 2004), ground-dwelling spiders (Martinat et al., 1993; Perry et al., 1997; Rieske & Buss, 2001) and ground beetles (Klenner, 1996; Rieske & Buss, 2001).

1.7.2 *Bacillus thuringiensis* var. *kurstaki* (BTK)

BTK is a variant of the soil bacterium *Bacillus thuringiensis* Berliner, which produces toxins acting as stomach poisons in caterpillars (Gill et al., 1992). Negative effects of varying magnitudes on abundance and diversity of non-target Lepidoptera have been reported (Miller, 1990, 1992; Lih et al., 1994; Wagner et al., 1996; Rastall et al., 2003; Boulton et al., 2007). As laboratory evidence confirms the specificity of BTK towards Lepidoptera (Glare & O'Callaghan, 2000), only a few studies investigated its impacts on other arthropod taxa. No treatment effects could be evidenced on field populations of predaceous spiders (Winter & Glatz, 2000) and ants (Wang et al., 2000). Impacts on parasitism of Lepidoptera were found to be either positive, negative or null, and appeared to be primarily mediated by the targeted larval stage of the host (Hamel, 1977; Wallner et al., 1983; Weseloh, 1984; Niwa et al., 1987; Nealis & van Frankenhuyzen, 1990; Schoenmaker et al., 2001).

1.7.3 Tebufenozide

Tebufenozide is an agonist of the juvenile hormone of Lepidoptera that kills caterpillars by triggering a premature lethal moult. Like diflubenzuron and BTK, it needs to be ingested to be effective at standard operational rates (Smagghe et al., 1999). The Lepidoptera specificity of tebufenozide has been thoroughly tested and confirmed in laboratory and semi-field

bioassays (Addison, 1996; Dhadialla et al., 1998; Smagghe & Degheele, 1994). By contrast, there are relatively few published studies addressing the side effects of tebufenozide in forests, plausibly due to its relatively recent addition to the list of approved forestry insecticides. Butler et al. (1997) reported reductions in abundance and richness in Lepidoptera that persisted in the post-treatment year but did not find any measurable effect on other arthropod taxa. Westwood et al. (2019) detected depressed abundances on a few species of adult Macrolepidoptera, but all had fully recovered 15 months after treatment. McCravy et al. (2001) found no impact of tebufenozide on parasitism of the Nantucket pine tip moth *Rhyacionia frustrana* Comstock (Lepidoptera: Tortricidae).

1.8 Methodological limitations of insecticide impact studies in forests

The main conclusion of this review is that the effects of forestry insecticides on non-target arthropods can be easily predicted on the mere basis of laboratory studies. On the one hand, diflubenzuron has the least specific mode of action and is indeed the only substance for which effects were documented beyond Lepidoptera and their parasitoids. Likewise, reported effects of BTK and tebufenozide are restricted to Lepidoptera and may affect their parasitoids. One could take these results at face value and conclude an absence of effects beyond the insecticides' spectra of action. However, another interpretation is that because these results merely reflect the mode of action of the insecticide, it is plausible that only the strongest, direct toxic effects were detected. The failure to detect an existing signal, known in statistics as type II error, often stems from methodological problems. Therefore, I conducted a critical evaluation of the methodologies used in forest impact assessment studies, unveiling widespread limitations. In the following section, I review the causes and implications of these shortcomings before proposing novel approaches to improve the precision of insecticide risk assessment studies in forests.

1.8.1 Lack of adequate replication

Aerial trials in forests present inherent obstacles that challenge the application of good design practices (i.e. principles of replication randomness and blocking; Hurlbert, 1984) in impact assessment studies. Firstly, the selection of suitable sites faces multiple hurdles. Forests can widely differ with regards to basal area, species composition, tree age, structural diversity, and overall silvicultural management system (Cadogan & de Groot, 1995). For realistic insecticide trials and to obtain spraying clearance, site selection must be based on the

documented occurrence of an outbreak. Extensive winter populations surveys that require considerable organisation, time, and workforce must be performed to predict outbreaks. Due to a lack of resources, the total area surveyed may be too small to allow the selection of comparable forest plots for impact assessment trials. Additionally, because public perception of forest spraying is generally negative, the risk of untimely legal actions delaying or even preventing spraying on certain stands must be considered.

Secondly, most steps of aerial field trials are associated with complex logistics and hence high costs. Mobilising aircraft for treatment application can be prohibitively expensive in research projects that are often poorly funded. Besides, insect sampling also requires considerable human, material, and financial resources and a careful organisation of sampling designs that is further challenged by problems of scale and accessibility in large study areas.

Lastly, timing is critical to the success of aerial field trials. Mistimed treatment or sampling can obscure the detection of insecticide effects or lead to patterns that are irrelevant to practice. On deciduous trees, the time window for an efficacious treatment is restricted to a few weeks, as insecticides must be applied on early larval instars and sufficiently large leaf areas to ensure adequate control. Depending on the relative timing of the host plant budburst and hatching of the target species, the spraying window can be narrowed down to only a few days. Yet, the need for calm and dry weather conditions instrumental to the accuracy of aerial spraying can generate further delays. Therefore, conducting a well-timed insecticide application can be incredibly challenging and requires great flexibility and the ability to adapt to changing conditions rapidly.

To tackle these hurdles, researchers often opt to simplify the methodological procedures by designing opportunistic, underpowered, or pseudo-replicated studies (Fig. 1A). In opportunistic assessments, investigations are performed on sites operationally sprayed to combat outbreaks (e.g. Manderino et al., 2014; Sample, Butler, et al., 1993) to free scientists from the financial, logistical, and administrative burden of spray flights. However, sprayed sites are hence *de facto* imposed by the operational treatment setting, leading to inadequate interspersions of experimental units (Hurlbert, 1984) and poor control of environmental heterogeneity. Aerial trials conducted on purposefully selected sites allow to randomise treatment allocation and better control heterogeneity, yet they are often under- or inadequately replicated (Fig. 1A). The resulting lack of statistical power can lead to a systematic underestimation of non-target effects and questions the reliability of these experiments.

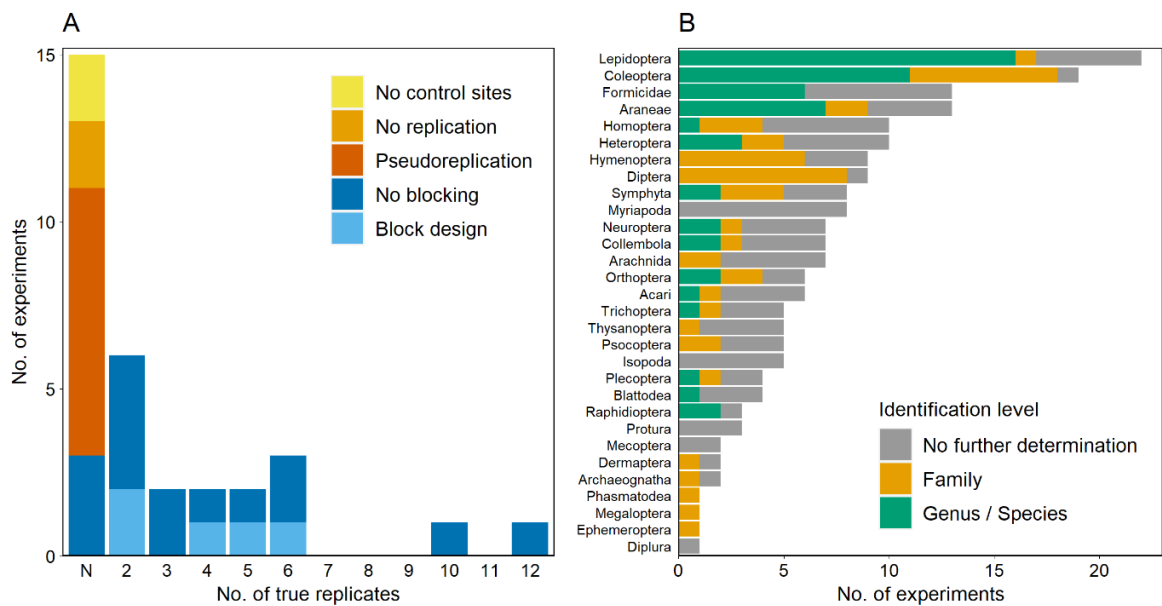


Figure 1. Statistical power and taxonomic coverage of published studies investigating the impacts of aerially applied insecticides on non-target forest arthropods. (A) Distribution of impact assessment experiments based on their number of true replicates. Experiments lacking a control treatment (yellow colour), true replicates (i.e. only raw data reported; light orange), and pseudo-replicated (dark orange) are grouped into one category designated as “N” (i.e. no true replicate). The use of blocking (i.e. arranging treated and control plots within homogeneous and closely located groups) in replicated studies is indicated by the blue colour (light blue = block design; dark blue = no blocking). **(B) Number of experiments reporting results per arthropod taxon and taxonomic resolution level.** Colours indicate the taxonomic resolution achieved for each taxon: no further identification (grey colour), identification to family (orange) and identification to species (or genus when not possible; green). Data was mined from a comprehensive list of 44 scientific articles and technical reports corresponding to 32 experiments (sister studies are pooled) retrieved on scientific article search engines with a standardized search string. Publications produced as part of this thesis are not included. Details of each included study (e.g. bibliographic record, forest type, insecticide used...) are given in Appendix A.

1.8.2 Lack of integration of species life-history

Diﬂubenzuron, BTK and tebufenozide are all oral poisons with poor contact activity. This property considerably narrows their field toxicity by allowing theoretically vulnerable species to escape exposure. For example, species feeding on internal plant tissues (e.g. phloem or mesophyll) or using partially or fully concealed micro-habitats are expected to be considerably less exposed. Likewise, species with high dispersal ability and short generation

times have a greater ability to recover following exposure (Rubach et al., 2011). Life-history traits that mediate the exposure of species are thereby referred to as avoidance and resilience traits. Exposure avoidance and resilience can be more broadly defined as the ecological sensitivity of species (Kefford et al., 2012). In this framework, the vulnerability of a species to an insecticide is the product of its physiological sensitivity, measured as the nature and magnitude of toxic effects experienced after exposure, and its ecological sensitivity.

In experiments with forestry insecticides, ecological sensitivity is implicitly acknowledged but often reduced to a binary notion, such that species considered safe are often overlooked in field experiments. In theory, knowledge of the mode of action and the physicochemical properties of insecticides allow one to anticipate to a large extent the exposure of a species with a known life history. However, the environmental dynamics of insecticides can have a certain degree of plasticity. For example, the non-systemic ingestion compound diflubenzuron was shown to have a weak contact activity (Grosscurt, 1978) and a limited ability to translocate inside plant tissues (Bull & Ivie, 1978). Therefore, hypotheses on ecological sensitivity need to be formally tested by including presumably safe taxa into impact assessment studies, which is rarely done in practice.

As a matter of fact, life-history information has seldom been considered to delineate study systems in previous studies (see Martinat et al., 1988). Due to cost limitations, many impact assessment studies test the response of taxa identified to a coarse taxonomic level, such as order or family (Baird & Hajibabaei, 2012). On the one hand, the taxonomic relatedness of species should correlate well with their physiological sensitivity, as BTK and IGRs act on physiological processes shared among closely related species. On the other hand, avoidance traits like feeding guild are not strongly conserved across high-rank taxa (van den Berg et al., 2021). Failing to account for life history when selecting study organisms bears the risk of obscuring response patterns by throwing together species with different sensitivities (Baird & Hajibabaei, 2012; Sample, Butler, et al., 1993).

1.8.3 Sampling bias and taxonomic impediment

So far, no study approached the impact of forestry insecticides from the framework of community ecology, rather focusing on analysing the response of selected taxa. There is an important knowledge gap to be addressed here, as insecticide effects in the field cannot be restricted to short-term acute toxicity. By asymmetrically affecting species with different relative sensitivity, insecticides can change the dynamics of species interactions and the

structure of communities. Therefore, it is essential to enlarge the scope of field studies by examining the response of more diverse species assemblages.

It is not surprising that community approaches lack thus far, as conducting such comprehensive surveys implies overcoming two daunting challenges. Firstly, all arthropod sampling techniques are biased towards specific taxa due to the diversity in life history and habitat use among species. For canopy arthropods, pyrethrum knockdown is by far the most comprehensive method. However, it presents several disadvantages, such as the high sensitivity to atmospheric conditions, that are often considered prohibitive in diversity studies (Ozanne, 2005). In fact, the common approach in previous non-target impact studies has been to focus on specific groups (often those with the highest expected sensitivity to insecticides) and pick the most suited sampling technique to evaluate non-target effects (Sample, Butler, et al., 1993).

Second, analysing the community structure of very diverse assemblages requires a considerable investment in determining specimens to the species level. Such undertaking, if at all possible, is very time- and resource-consuming with traditional identification methods. For many arthropod taxa, identification relies on examining morphological traits specific to a certain life stage or sex (e.g. male genitalia), such that specimens falling outside of this category can be at best identified to genus level. Moreover, using complex species keys requires high levels of expertise often only possessed by a few taxonomists, thus restricting the access to species-level data for so-called “dark taxa”. This problem intensifies when the number of focal taxa is high, necessitating logistically challenging collaborations with dozens of experts (Morinière et al., 2019). Limitations of the availability of taxonomic expertise put further constraints on the selection of study systems which, as a result, mainly focus on a subset of well-known taxa for which expert knowledge is relatively accessible (Fig. 1B).

1.8.4 Relative impacts of outbreaks and insecticides

Based on a comprehensive review of the respective effects of defoliation and BTK on forest Lepidoptera, Scriber (2004) suggested that the decision of non-intervention could be as damaging as insecticides for these insects. This statement could be outright rejected on the premise that natural disturbances are an integral part of ecosystem dynamics, and thus no management practice could be reasonably justified on ecological grounds. However, it takes on a different dimension when considering the anthropogenic contributions to insect disturbance regarding invasive species or in light of increasing evidence of the reinforcing effect of climate change on outbreaks (Pureswaran et al., 2018). The possibility of addressing

the relative impacts of insecticide treatments and defoliation would hence be a desirable asset of risk assessment studies to support management policies. However, this is an undeniably ambitious goal that has rarely been pursued in field studies (but see Manderino et al., 2014; Sample et al., 1996). This is somewhat unsurprising considering the already existing struggles that scientists face to assess non-target effects alone (see section 1.8.1 *Lack of adequate replication*). Integrating both insecticide and outbreak disturbances into a single experimental design demands an even higher number of replicates, especially considering the low predictability of defoliation.

1.9 Overall aims and structure of this thesis

In this thesis, I aim to address the methodological weaknesses that hinder the study of the effects of aerial insecticide applications on non-target forest arthropods. In the following chapters, I propose alternative approaches to conducting such experiments by integrating state-of-the-art techniques in spraying technology and arthropod determination and extending assessment to arthropod groups with presumed low susceptibility to current forestry insecticides. Ultimately, I implement these methods in field experiments to determine whether they can improve our understanding of forestry insecticides' impacts.

In **Chapter 1**, I addressed the replication problem by exploiting the ability of Unmanned Aerial Vehicles (UAVs; henceforth drones) to spray insecticides on single trees, to simplify logistics and allow increasing replication. To evaluate the adequacy of the method, I investigated the short-term response of target and non-target crown-dwelling Lepidoptera to diflubenzuron and tebufenozide and compared the results with findings from large-scale studies. I addressed the following questions:

- Are drones well-suited to apply insecticides on trees?
- Does increasing replication by downscaling study design allow to detect weak effects of insecticides?

In **Chapter 2**, I tested the response of sessile herbivores (leaf-miners and gall-inducers) to diflubenzuron and tebufenozide in the experiment described in Chapter 1 and a similar design using small scale spraying with a manned helicopter. Leaf-miners and gall-inducers are assumed to be shielded from exposure through their internal feeding habits and have been shown to be adversely affected by foliar damage caused by defoliators. Thus, they are ideal model organisms to test the concept of ecological avoidance and the influence of spraying on species interactions (in this case, competition). I addressed the following questions:

- Does internal feeding allow sessile herbivores to avoid exposure to surface-binding insecticides? Is ecological sensitivity further mediated by differences in life history among sessile herbivores?
- Do insecticides alter competition between defoliators and sessile herbivores?

In **Chapter 3**, I combined the use of pyrethrum knockdown to comprehensively sample crown-dwelling arthropod communities and DNA-metabarcoding to delimit species across the whole community. I used taxonomic information and feeding guild data to classify species according to their expected physiological and ecological sensitivity. I used these species data to explore the impacts of diflubenzuron and BTK on the whole community and the different sensitivity categories. I addressed the following questions:

- Do insecticides alter the structure of diverse arthropod communities?
- Do insecticides alter the diversity of presumably non-sensitive taxa?

In **Chapter 4**, I present a full factorial stand-level experimental design that aims to bring the approaches described in the other chapters into a more realistic setting. The experiment was designed as part of a new project funded in 2019 to study an ongoing gypsy moth outbreak. The chapter will serve as an outlook for the present thesis. Lessons learned from the previous chapters will be used to assess the relative impacts of tebufenozide and gypsy moth outbreaks on various taxa and evaluate economic and ecological trade-offs between insecticide management and non-intervention strategies.

2 Methods

The first chapter of this thesis is based on a single-stand experimental design where we sprayed individual trees with a drone (“drone experiment”) in 2016 and 2017. The second chapter combined investigations carried out in the drone experiment and a larger-scale experiment where small plots were sprayed with a crewed helicopter (“helicopter experiment”). The third chapter is based on investigations conducted in the helicopter experiment. The fourth and last chapter describes a large-scale stand-level experiment including 48 plots (“stand-level experiment”). I contributed to the conceptualisation and design of the experiments, conducted large parts of the data collection, and performed all statistical analyses in all three experiments. In the following, I provide a detailed description of the study region and introduce each of the experiments and the sampling and analytical procedures performed in each chapter.

2.1 Research area

We conducted all investigations in the region of Franconia, north-western Bavaria, Germany, within an approximately 15,000 km² area delimited by the towns of Schweinfurt, Bamberg, Ansbach and Würzburg (Fig. 2). The study region covers the North and the East of the Main triangle (*Maindreieck*), the East of the *Steigerwald* hill range and the *Gollachgau* area in the South. The area is characterised by an agricultural landscape sprinkled with small to medium-sized lowland forest patches and hills mainly covered with forests and vineyards. Elevations range from 181 m, along the Main river, to 498 m at the *Scheinberg*, the highest point of the *Steigerwald* nature park. The study region is located in the temperate zone, with a mean annual temperature of 7–10 °C and annual precipitations ranging from 550 mm in the dry *Maindreieck* to 800 mm in the *Steigerwald* heights. Due to continental influences, the region is characterised by hot and dry summers, with temperatures up to 35 °C and frequent thunderstorms, and cold winters with temperatures frequently as low as -10 °C. Large

woodlands are dominated by European beech *Fagus sylvatica* L., especially in the northern and eastern parts of the study region. In contrast, smaller patches in the lowlands and the southwestern part of the *Steigerwald* are mainly oak-hornbeam communities. Oak forests in this region are frequently subjected to outbreaks of lepidopteran defoliators. During the 1970s and 1980s, significant outbreak species were mainly spring defoliators such as the winter moth complex (Lepidoptera: Geometridae) and the oak leaf-roller *Tortrix viridana* L. (Lepidoptera: Tortricidae). However, the gypsy moth *Lymantria dispar* L. (Lepidoptera: Erebidae) recently became the most damaging defoliator in the region, with larger and longer-lasting eruptions re-occurring at intervals of 8 to 15 years. Since 2001, the oak processionary has also displayed regular but more localised outbreaks. Since the late 1970s, outbreaks are thoroughly monitored and centrally recorded by the Bavarian State Institute of Forestry (Bayerische Landesanstalt für Wald und Forstwirtschaft, LWF) to implement aerial treatments with insecticides. The populations of economically important species are surveyed during the winter using various monitoring methods, and management decisions are taken based on density thresholds derived from observation (Bayerische Landesanstalt für Wald und Forstwirtschaft, 2014). A map of the study regions showing the location of all stands included in our experiment is provided in Fig. 2.

2.2 Drone experiment

2.2.1 Study site

The drone experiment was set up in early spring 2016 in the 80-ha forest stand "Greutholz" located between the town of Iphofen in the North and the village of Willanzheim in the South (49.6919°N, 10.2409°E; Fig. 2). The dominant overstory species are deciduous oak *Quercus robur* L. and *Quercus petraea* Mattuschka. The understory layer is mainly composed of common hornbeam (*Carpinus betulus* L.), field maple (*Acer campestre* L.) and common hazel (*Corylus avellana* L.). The stand is managed as coppice-with-standards (in German *Mittelwald*), a traditional silvicultural system involving selected cuttings of mature trees (standards), understory clearing and harvest of regrown stems (coppice) within delimited coupes (also known as cants), with a rotation period of 10 to 30 years (Short & Campion, 2014). This type of management grants the forest an unusual structure, with sparsely distributed large oak trees embedded in a matrix of herbaceous vegetation and shrubs. The height and the density of the understory increase with the time since the last harvest, resulting in a

structural gradient along the cants. The open stand structure in young cants made this stand particularly suitable for spraying with drones. The high number of canopy gaps facilitates drone manoeuvring in visual line of sight. However, the stand was primarily selected based on the results of defoliator population surveys carried out by the LWF in the previous winter, which forecasted high densities of the oak processionary moth for 2016.

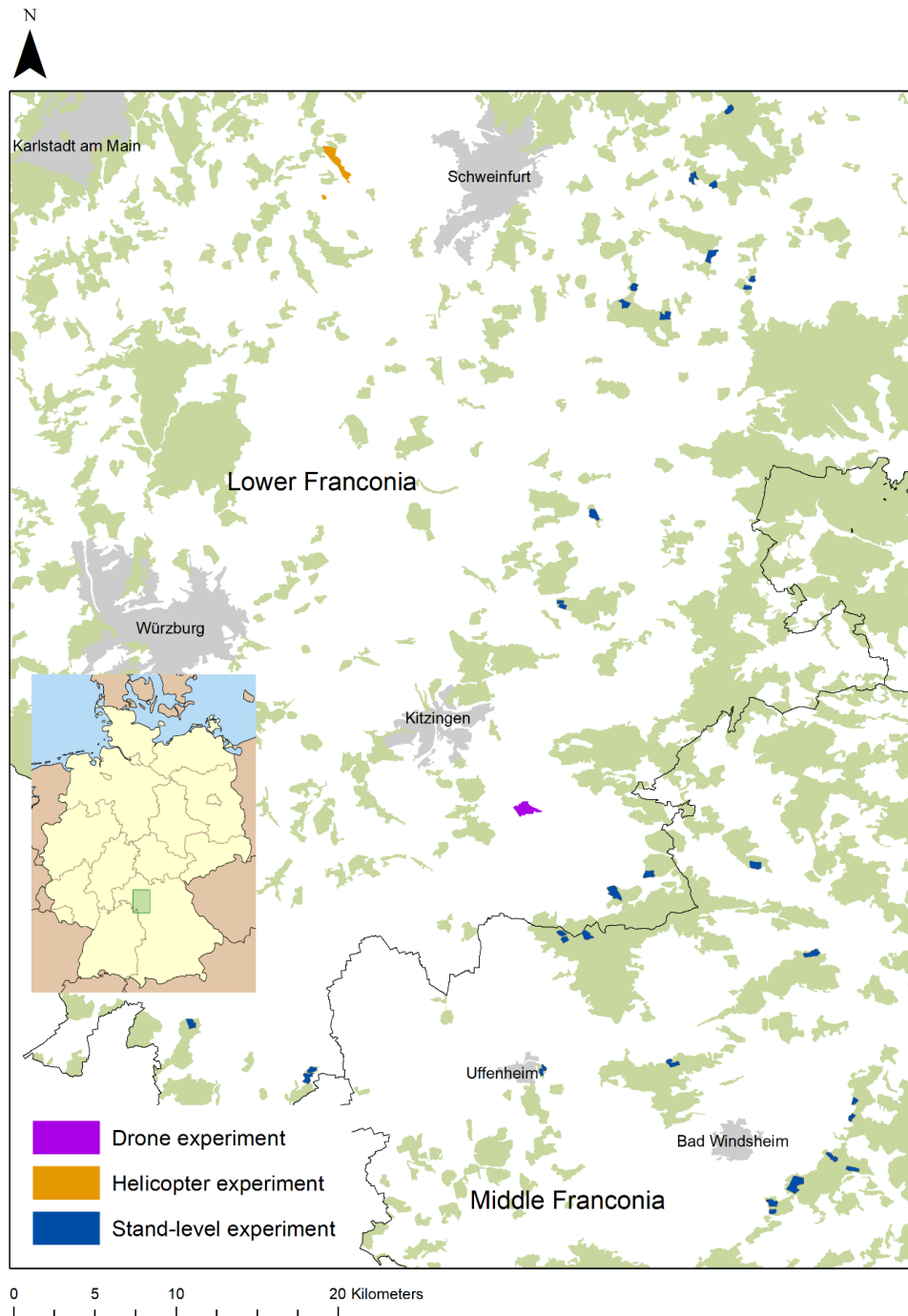


Figure 2. Map of the study plots included in all the experiments. Purple colour = drone experiment; orange = helicopter experiment; blue = stand-level experiment. NB: three sites of the helicopter experiments are not shown as their owners wish to remain anonymous.

2.2.2 Experimental design

The principal aim of the drone experiment was to implement a small-scale approach to achieve high statistical power cost-effectively. The use of single trees as experimental units within a single stand allows comparing closely related insect communities. It also greatly simplifies logistics, enabling the inclusion of a high number of randomly interspersed units. We searched for suitable trees within several homogeneous areas across the stand to account for variation in forest structure. In each area, we monitored the early spring density of leaf-chewing insects with so-called "faeces traps", consisting of rectangular wooden plates covered with a sheet of baking paper sprayed with insect glue and placed below the tree crowns (Fischbacher et al., 1998). Density was monitored in several comparable mature oak trees (i.e. diameter at breast height > 35 cm; one trap per tree) by counting frass droppings (i.e. caterpillar faeces) in a randomly selected 20 cm² area of each trap after 4-6 days of exposure. Each tree was given a density score based on relative frass counts: "low" (< 20 frass pellets per sample and day), "medium" (20-35) and "high" (> 35). Whenever three high- and three low-density trees were located within the same areas, those were grouped to form an experimental block. One insecticide treatment among diflubenzuron, tebufenozide and control (i.e. unsprayed) was randomly allocated to each tree within each density class. We formed ten blocks for a total of 60 trees (ten high- and ten low-density per treatment). Treatments were applied block-wise at the standard operational rates for forest use with a remotely controlled helicopter drone between 12 and 21 May 2016. Diflubenzuron was sprayed as Dimilin 80WP® (12 g active ingredient [a.i.] ha⁻¹) and tebufenozide as Mimic® (69.6 g a.i. ha⁻¹). The amount of solution sprayed per tree was standardised to an average crown projection area of 100 m².

2.2.3 Data collection and processing

In the drone experiment, I monitored the effects of insecticides on the focal guild (free-living macrolepidopteran caterpillars) and biologically distinct herbivore guilds (microlepidopteran leaf-rollers and leaf-miners, and gall-inducers). I followed the methodologies suggested by Ralf Petercord to monitor caterpillar mortality and feeding activity and by Martin Gossner to sample foliage (Gossner et al., 2014). I was responsible for the tree canopy measurements, for which I followed methods described by Röhle (1986), Pretzsch et al. (2015) and KaDonna (2010). I performed all sampling together with Florian Lauer and Jessica Jaworek, with the support of technical staff and student helpers. Florian Lauer directed the vegetation assessment that we performed together with our head technician Monika Plaga. Caterpillars

were determined to family by Florian Lauer, Jessica Jaworek, and trained student helpers, according to Patočka (1980). I designed the laboratory procedures for herbivory assessment and directed the training of technical staff and student helpers. The leaf-miner key was mainly based on the work of Ellis (2020) with a few minor adjustments. I designed a stepwise key for gall-inducers based on morphological descriptions and pictures gathered from multiple specialised sources, mainly Williams (2010) and Buhr (2012). A detailed description of the various field and laboratory protocols is given below.

Free-living and leaf-rolling caterpillars. The number of free-living caterpillars fallen from tree crowns was used as a proxy for mortality, with control trees providing a measure of background mortality. We sampled larvae by exposing one 3-m² polyester tarpaulin sheet below the crown of each tree. A weight was placed at the centre of the sheet, where multiple small holes were pierced to ensure good rainwater drainage. Caterpillars fallen from the crown were hand-picked daily during the application period (12-21 May) and then twice per week for an additional three weeks (21 May-9 June). The target species, the oak processionary moth, was identified to species and other caterpillars to family.

Caterpillar feeding activity. To better appraise insecticide effects, we further monitored faeces traps to measure continuing feeding activity in the crown. Frass droppings were sampled and counted weekly from spraying until 14 June (i.e. 3 to 4 weeks depending on the spraying date) following the protocol used for tree selection.

Caterpillar chewing damage. We collected foliage in each oak in August to measure chewing damage (i.e. damage caused by caterpillars). We used single rope climbing to collect two 50-cm twigs in each tree, one from the upper canopy and one from the lower canopy, and haphazardly sampled 50 leaves from the tip to the base of each twig. Leaves were then stored at 6 °C in low moisture conditions to prevent moulding and desiccation. In the laboratory, the percentage area removed was scored on each leaf in 13 classes: 0 % | 0-1 % | 2-5 % | 6-10 % | 11-20 % | 21-30 % | 31-40 % | 41-50 % | 51-60 % | 61-70 % | 71-80 % | 81-90 % | > 90 %. Before starting scoring, each operator was trained for several weeks on a set of oak leaves on which leaf area removal was accurately measured with a leaf area metre. Operators were allowed to start scoring the field samples once they could score most leaves from the training set accurately and calibrated their estimates on actual samples. The median of each class was used to measure the magnitude of chewing damage at the leaf level. Additionally, leaves were further classified into "intact" (< 2 % leaf area removed) and "damaged" (2 % removal and higher) categories. We used this lower threshold as most leaves in summer

present residual leaf area loss that can more often be attributed to fungal spots gone brittle than actual chewing damage.

Sessile herbivores. Simultaneously with the scoring of chewing damage, leaves were thoroughly checked for the presence of mines (i.e. characteristic scars left by leaf-miners upon feeding on the mesophyll) and galls (i.e. abnormal outgrowth of plant tissue triggered by the oviposition of some insect species, and use by those as habitat and food). Leaf-miners and gall-inducers were identified to species or genus by examining the shape and position of mines and galls. Additionally, we examined each mine for the presence of a larva, a pupa, a characteristic exit hole, or predation marks (i.e. the surface of the mine is torn apart). The presence of an exit hole or a pupa was used as a proxy for survivorship, as it implies that the larva completed its development inside the leaf. As for the mortality of free-living caterpillars and leaf-rollers, controls were used to estimate the baseline survivorship.

Crown structure. To account for differences in crown structure among trees, I calculated the crown projection area and volume based on crown radii and crown length measurements for each tree taken during winter 2017-2018. I measured crown radii (r), which correspond to the length from the centre of the trunk to the edge of the crown in each intercardinal direction (N, NW, W, SW, S, SE, E, NE). I used a clinometer to measure the length of the crown (cl), which corresponds to the difference between the height of the tree and the height of the lowest live primary branch. Crown projection area (cpa) and volume (cv) were calculated as:

$$(1) \quad cr = \sqrt{\frac{\sum_{i=1}^n r^2}{n}} \quad (2) \quad cpa = \pi \times cr^2 \quad (3) \quad cv = cpa \times cl$$

Where cr is the crown radius, r the length from the trunk to crown edge in the i^{th} intercardinal direction and n the number of intercardinal directions (i.e. $n = 8$).

Lastly, I estimated crown density (cd) as the percentage of the target tree branches, foliage and reproductive structures blocking light visibility through the crown using a crown density card (KaDonna, 2010). Two estimates made from two positions at least 20 m and 90° apart were averaged to obtain the crown density for one tree.

Vegetation assessment. To further control the heterogeneity in the vegetation structure of the different blocks, we performed vegetation surveys within a 400-m² area centred on each tree. We estimated percentage cover of the different forest strata: herb layer, lower understory (i.e. woody plants > 0.15 m and < 5 m), upper understory (i.e. woody plants > 5 m below the overstory) and the overstory (i.e. uppermost canopy layer). The relative percentage

cover for each species of woody plant in each layer was estimated and used to calculate species richness and Shannon diversity (i.e. each species is weighted by its percentage cover).

2.3 Helicopter experiment

2.3.1 Study sites

The helicopter experiment was set-up in spring 2017 in the three neighbouring stands “Bauernschlag” (52 ha; N 50.05706°, E 10.08311°), “Vorberg” (58 ha; N 50.0534°, E 10.08899°) and “Brunnholz” (6 ha; N 50.03170° E 10.07715°) located West of the town of Schweinfurt, near the villages of Sömmersdorf and Egenhausen (Fig .2). In all three sites, the overstory is dominated by deciduous oaks *Q. robur* and *Q. petraea*, but the degree of dominance varies between stands (from around 85 % in Bauernschlag to > 95 % in Brunnholz). Other overstory species include European beech and European ash (Vorberg only). The understory is mainly composed of European hornbeam and lime *Tilia* sp. in Bauernschlag and Vorberg, and almost exclusively young oaks in Brunnholz. The stands are managed as even-age high forests (in German *Hochwald*) with selection logging, which is the most common silvicultural system for this forest type in the region. The sites were selected based on gypsy moth population surveys carried out in the previous winter. Gypsy moth egg masses were counted on the trunk of oak trees within 10-trees transects throughout the stands. The results predicted low (< 5 egg masses per transect; 11 transects; Bauernschlag), high (5 to 10; 28 transects; Vorberg) and outbreak densities (> 10; 23 transects; Brunnholz) for the spring 2017 (Chapter 3, Fig. S1-1).

2.3.2 Experimental design

The helicopter experiment aimed to transpose the single tree approach into a more realistic setting using a manned helicopter instead of a drone for insecticide application. I mapped the target stands to identify homogeneous areas in which to set up the study plots by scoring tree species composition, age class, tree density and the presence of water bodies across each site. Using GIS software (ArcMap 10.7; ESRI, 2020), I defined 40-m-wide buffer areas along the forest edge and water bodies to delimit the sprayable area following European regulations on aerial pesticide applications (Official Journal of the European Union, 2009). I then excluded areas that were not dominated by mature oak trees (DBH < 35 cm) outside the buffer zones. In the remaining area, I delimited 11 structurally homogeneous blocks (i.e. three in Bauernschlag, seven in Vorberg and one in Brunnholz), within which I set up four 3,000-m²

(100 × 30 m) rectangular plots. One of the four treatments (diflubenzuron, tebufenozide, BTK, and unsprayed control) was randomly assigned to each plot to obtain a full factorial block design. One mature oak tree was selected near the plot centroid to be used for data collection. Insecticide treatments were applied by helicopter at the maximal legal rate for forest use on 15 May 2017. Diflubenzuron was sprayed as Dimilin 80WP© (60 g a.i. ha⁻¹), tebufenozide as Mimic© (180 g a.i. ha⁻¹), and BTK as Dipel ES (1.75 BIU ha⁻¹). Although rarely applied operationally, maximum concentrations are commonly used for pesticide risk assessment to quantify the strongest possible treatment effects.

2.3.3 Data collection and processing

I planned and performed the sampling of gypsy moth populations in the experimental trees. I helped organise the pyrethrum knockdown sampling, which was coordinated on-site by Jessica Jaworek and Sebastian Seibold, with the help of student helpers. I conducted the foliage sampling with the assistance of Monika Plaga and contracted tree climbers and the measurements of crown structure with two student helpers. I directed and supervised the herbivory assessment identically as in the drone experiment. I drafted the protocols for arthropod sorting with Wolfgang Weisser and Sharon Zytynska and supervised it with the help of Monika Plaga and Jessica Jaworek. Metabarcoding of canopy arthropod communities was performed by Jérôme Morinière, Vedran Bozicevic and their technical staff (Advanced Identification Methods GmbH). As in the drone experiment, I organised and supervised the herbivory assessment (i.e. chewing damage assessment and identification of sessile herbivores). A detailed description of the various field and laboratory protocols is given below.

Gypsy moth population. Late instar gypsy moths feed exclusively at night and spend the daytime sheltering in bark crevices or leaf litter (Doane & McManus, 1981). This behaviour can be taken advantage of to produce rapid abundance assessments by wrapping cloth or plastic bands around tree trunks, under which the caterpillars will take shelter. I used 10 cm-wide barricade tape to count and collect gypsy moth caterpillars on each tree on 12 and 13 June 2017.

Free-living arthropods. Arboreal arthropods were sampled by pyrethrum knockdown (fogging) with a 1 % pyrethrum-petroleum white soil solution. Fogging was performed during

nighttime when weather conditions are generally calmer to minimise variation. The fogging machine was operated until at least 50 % of the focal tree crown was enveloped in the fog cloud (i.e. between 5 and 10 minutes). Due to resource limitations, this sampling campaign was only performed on the diflubenzuron-, BTK-treated and control trees. In control plots, we selected two trees to account for the patchiness of gypsy moth population across blocks without losing statistical power (i.e. by including a roughly equal number of high- and low-density trees; Chapter 3, Supplementary information file S1). Arthropods fallen from the crown were collected after a 30-minute exposure period on four 15-m² tarpaulin sheets laid on the forest floor. The catch was then stored in 99 % ethanol, and the specimens were sorted into coarse taxonomic groups (mostly order or sub-order). Five taxa (Arachnida excluding Acari, adult Coleoptera, Orthoptera, Myriapoda and Isopoda) were morphologically determined to species by expert taxonomists, while the remainder was identified by DNA-metabarcoding. Because species relative abundances cannot be reliably inferred from the number of sequence reads (Lamb et al., 2019), we divided each sample (i.e. sheet) into three subsamples containing an approximately equal number of specimens from each sorted taxon. The subsamples were sequenced separately, and read numbers converted into incidence data aggregated at the tree level to produce an estimate of species abundance ranging from 0 (i.e. species absent) to 12 (i.e. species detected in each subsample).

The taxonomic and metabarcoding datasets were processed and analysed separately. I used a classic approach with taxonomic species as a reference type and true species abundance for morphologically determined taxa. For taxa identified via DNA-metabarcoding, I used Barcode Index Numbers (BIN, i.e. putative species constructed based on genetic distances; Ratnasingham & Hebert, 2013) and aggregated incidence (i.e. pooled incidence across 12 subsamples per tree) as a proxy for species and abundance, respectively. For clarity, we will further refer to abundance and species regardless of the reference metric and type. Using taxonomy and life-history data mined from specialised literature, I then assigned each species to coarse "sensitivity groups", describing in binary terms their expected physiological and ecological sensitivity to diflubenzuron and BTK (i.e. sensitive/non-sensitive; Table 1). Physiological sensitivity was defined based on the mode of action of both insecticides: diflubenzuron is virtually toxic to all arthropod juvenile stages (Grosscurt, 1978), and BTK is toxic only to caterpillars (i.e. Lepidoptera larvae; Gill et al., 1992). Ecological sensitivity was defined by the type of tissue of prey consumed, based on the fact that both insecticides are non-systemic and remain on the surface of leaves upon application (Maas et al., 1981; Sundaram et al., 1997). Species feeding externally on plants were tagged as sensitive, while those feeding on internal tissues were tagged as non-sensitive. Carnivores, scavengers and

parasitoids were kept in separated groups as they can be exposed by consuming intoxicated prey but differ in how tightly they are associated with their prey (Table 1). Traits were attributed at the family level when homogeneity of life history could be established so that BINs unassigned to a taxonomic species could still be included in the analysis (e.g. for hymenopteran parasitoids). In other cases, and for all herbivorous species, traits were assigned at the species level.

Table 1. Sensitivity groups used in our analyses and their expected physiological and ecological sensitivity to diflubenzuron (DFB) and *Bacillus thuringiensis* var. *kurstaki* (BTK). 0 = no sensitivity; 1 = sensitivity present; a = primary exposure (direct ingestion); b = secondary exposure (trophic transfer)

Sensitivity group	Physiological sensitivity		Ecological sensitivity	
	DFB	BTK	DFB	BTK
Lepidopteran external feeders	1	1	1a	1a
Non-lepidopteran external feeders	1	0	1a	1a
Internal herbivores ^{1,*}	1	0 / 1 ²	0	0
Scavengers	1	0	0 / 1b ³	0 / 1b ³
Predators*	1	0	1b	1b
Parasitoids	1	0	1b	1b

¹ Includes fully concealed herbivores (e.g. leaf-miners) and free-living herbivores that feed on internal tissues (e.g. sapsuckers).

² Only leaf-mining Lepidoptera are physiologically sensitive.

³ Necrophagy is a potential route of exposure.

* Zoophytophagous species (e.g. *Phytocoris tiliae*) were included in both groups.

Chewing damage and sessile herbivores. As in the drone experiment, I collected foliage in each sampling tree to score chewing damage and sample sessile herbivores. However, the sampling was performed earlier in the season (19-21 June 2017). The reason behind this choice is that I anticipated a potential influence of pyrethrum on the survivorship of leaf-miner and did not want to risk potential bias by sampling later in summer. Therefore, I directed the foliage collection with a day team, while a night team took over in the evening to perform fogging on the same trees. Scoring of chewing damage and determination of leaf-miners and gall-inducers were performed following the protocol applied in the drone experiment (see section 2.2.3 *Data collection*). However, I did not measure leaf-miner survivorship because

the early sampling timing overlaps with the larval development period of most species. As on-site assessment was not feasible, estimates of survivorship based solely on mine occupancy would have been inappropriate to address insecticide impacts due to the naturally high occupancy rate of mines in early summer.

Crown structure. During winter 2017-2018, I measured the structure of the crown following the protocol applied in the drone experiment (see section 2.2.3 *Data collection*). However, no vegetation assessment was conducted due to the much higher homogeneity in vegetation structure than in the drone experiment study site.

2.4 Stand-level experiment

2.4.1 Study sites

Site selection for the stand-level experiment was based on a large-scale population survey effort supervised by Hannes Lemme (LWF) in the administrative regions of Upper Franconia, Middle Franconia, Lower Franconia, and Swabia in fall 2018. Local district rangers conducted egg-mass surveys transects as previously described (2,802 transects in total; see section 2.3.1 *Study sites*) and scored additional variables such as stand vitality, age, and recent outbreak history. These data were used to calculate an index estimating the risk of defoliation (defoliation risk index [DRI]; Appendix E, Supplementary information file S1). All sites are dominated by a deciduous oak overstory but differ regarding their relative proportion of oaks (from about 60 % to > 90 %). Other overstory species include mostly European beech and a few other species (European ash, linden) in one mixed oak block. The main understory species is the common hornbeam, followed by field maples and lindens in variable proportions. Ten blocks are managed as high forests with selection cutting, the other two as coppices-with-standards. It is noteworthy that several study plots in the southern part of the study region (Middle Franconia) are former coppices-with-standards that underwent a transition towards high forest during the last century. Detailed information on each plot is available in the supplementary information of Appendix E, file S4.

2.4.2 Experimental design

The main objective of the stand-level experiment is to transpose the design principles applied in the drone and helicopter experiments to a scale more relevant to the practice of aerial

applications. To this end, we identified areas comprising at least two stands at high risk ($\text{DRI} > 1$) and two stands at low risk of defoliation ($\text{DRI} < 0.5$) and selected 12 of them as experimental blocks in compliance with nature protection guidelines and terms agreed upon with local forest owners. In each block, one stand within each defoliation risk class was randomly assigned treatment with tebufenozide and the other was kept as a control, so to obtain a full factorial design (high risk – control, high risk – tebufenozide, low risk – control and low risk – tebufenozide) with 12 replicates. As in the helicopter experiment, tebufenozide was applied by a manned helicopter as Mimic© at the maximal legal rate ($180 \text{ g a.i. ha}^{-1}$) between 3 and 23 May 2019. While the application was mostly performed block-wise, the length of the spraying window was substantially extended by late legal procedures and unfavourable weather conditions, such that plots belonging to the same block were sprayed on different days in some instances.

2.4.3 Data collection and processing

Although the set-up of the study design was partially covered by the funding agency supporting my PhD, the large-scale gypsy moth experiment is part of a new ongoing research project. Therefore, the data analysed in Chapter 4 is exclusively focused on testing the performance of the experimental design. I directed the sampling of canopy arthropods (including gypsy moth caterpillars) by pyrethrum knockdown and subsequent sorting of caterpillars, with the help of Jessica Jaworek, Sebastian Seibold, Sebastian Kienlein, and several student helpers. Egg-masses, older larvae, pupae and adults were sampled by Philipp Braumiller, Hannes Lemme, and Sophia Hochrein with their respective field teams. Torben Hilmers and Martin Jacobs performed terrestrial laser scanning.

We intensively sampled the different life stages of gypsy moth populations: egg, early instar larvae, late instar larvae, pupae, and adults, from April to July 2019. In April, egg masses were counted on the lowest 2 m of 48 oak trees around the plot centre. We collected young larvae (second to third instar) with pyrethrum knockdown of the tree canopy within a $100\text{-}150\text{-m}^2$ area centred on one mature oak tree. We used a 2.5 % pyrethrum-white oil solution to fog the trees until the crowns were coated with the fog cloud (approximately 3-12 minutes, depending on the conditions). Arthropods fallen on four 15-m^2 -tarpaulin sheets laid beneath tree crowns were collected after a 30-minute exposure period stored at $-18 \text{ }^\circ\text{C}$. Gypsy moths were later identified and counted in the laboratory. Older larvae (fourth to sixth instar) and pupae were sampled using the tree-banding method previously described (see section 2.3.3 *Data collection*). Fifty-cm-wide burlap bands, on which two 300-cm^2 -windows were delimited

for sampling, were placed on eight trees near the plot centre. Gypsy moths sheltered under the band were counted in each window on two occasions (11-20 June and 02-18 July) and identified as live larvae, dead larvae, or pupae. Adult gypsy moths were sampled with light traps in July. One trap was operated for one entire night at the centre of each plot. Insects attracted by the lighted fluorescent tubes were trapped into a bucket containing a chloroform-soaked wick. The catch was collected the following morning, stored at -20 °C, and gypsy moths were counted and identified as male or female. Additional to monitoring gypsy moth populations, defoliation was quantified using terrestrial laser scanning. Scanned point clouds higher than 10 m were kept and divided into 125 cm³ voxels.

To measure the intensity of defoliation, I calculated the ratio of the number of voxels at peak feeding (t_2) to the baseline (t_1), further referred to as the foliation ratio:

$$(4) \text{ Foliation ratio} = \frac{\text{No. of voxels}_{t_2}}{\text{No. of voxels}_{t_1}} - 1$$

2.5 Statistical analyses

I performed all the statistical analyses described in each chapter in R versions 3.4.3 to 4.0.3 (R Core Team, 2020). In this section, I present the main approach and methods. Further details on each analysis, including information on the R packages and function used, are provided in the corresponding chapter (Appendices B-E). In each experiment, I analysed the effects of insecticides on various guilds of target and non-target arthropods and the damage caused by defoliators to oak foliage.

Because all three experiments were designed as a randomised block design, I applied the same approach for the analysis of quantitative responses, namely (generalised) linear mixed effect models (henceforth (G)LMMs) with block as the random term. I used nested random effects when analysing patterns at hierarchical levels lower than the basic experimental unit, for example, when analysing the occurrence of leaf-miners on individual leaves. In each model, I tested the significance of the fixed effects using Kenward Roger's F, likelihood ratio or Wald tests depending on the error family distribution. I performed pairwise comparisons of estimated marginal means as a *post hoc* test when applicable, namely when independent predictors were categorical variables with more than two levels. To reduce the likelihood of Type I errors, I corrected p-values for multiple comparisons using the Tukey and multivariate-*t* method. I calculated the marginal (i.e. variance explained by the fixed terms

only) and conditional R^2 (i.e. variance explained by both fixed and random terms) as a measure of the goodness-of-fit of each model.

Additionally, I conducted two complementary analyses to address specific research questions. Firstly, I performed a structural equation model (SEM) to assess the indirect effects of insecticides on leaf-miners and gall-inducers. Secondly, I carried out an analysis of diversity partitions to measure the impacts of insecticides on communities of arboreal arthropods. The following section describes the different mixed effect models and complementary analyses used to address the research questions listed in the introduction section.

2.5.1 Effect of insecticides applied by drone on crown-dwelling Lepidoptera

In **Chapter 1**, I evaluated the adequacy of spray drones for small-scale impact studies by testing the effects of diflubenzuron and tebufenozide applied by a drone on individual trees.

I analysed the effects of diflubenzuron and tebufenozide on the feeding activity and the mortality of free-living and leaf-rolling caterpillars by fitting log-normal LMMs to the number of frass droppings (i.e. feeding activity) and the number of fallen caterpillars (i.e. mortality; overall and separately for the target pest, the oak processionary moth, and each abundant non-target family). Data were aggregated over the entire sampling period to account for potential time lag effects between the death of caterpillars or excretion of frass pellets and their fall into the traps. Independent variables included treatment (control, diflubenzuron or tebufenozide), pre-spray defoliator density (high or low) and their interactions as fixed effects, and a random intercept for block as a random effect. The inclusion of vegetation and crown structure covariates did not improve the goodness-of-fit, so the models were kept parsimonious (Appendix B, Supplementary information file C).

2.5.2 Direct and indirect effects of insecticides and defoliators on sessile herbivores

In **Chapter 2**, I tested the direct and indirect effects of diflubenzuron and tebufenozide, as well as chewing damage, on different guilds of sessile herbivores (upper-surface leaf-miners, lower-surface leaf-miners and gall-inducers) using data from the drone and helicopter experiments.

Treatment efficacy. With the drone experiment data, I used the results from the mortality assessment described in the previous section as a measure of control efficacy. Additionally, I tested the influence of insecticides on chewing damage by fitting LMMs to the mean proportion of leaf area removed per sampled branch (i.e. magnitude of chewing damage) and

the occurrence of chewing damage per leaf (i.e. frequency of chewing damage). Independent variables included insecticide treatment (diflubenzuron or tebufenozide as separate dummy-coded variables), canopy stratum (upper or lower), and their interaction as fixed effects, and a random intercept for block as a random effect. Crown volume was identified as an important covariate and added to the models (Appendix C, Supplementary information file S1). With the helicopter experiment data, I tested the efficacy of insecticides on the abundance of gypsy moth caterpillars under burlap bands (i.e. per tree), the mean proportion of leaf area removed per branch, and the occurrence of chewing damage per leaf. Gypsy moth abundance was fitted as the response variable in a GLMM with negative binomial error distribution. Treatment was included as a fixed effect (diflubenzuron or tebufenozide; dummy-coded) and a random intercept for block as a random effect.

Direct effects. I investigated the direct effects of insecticides on the abundance (tree-level), occurrence (leaf-level) and survivorship (leaf-level) of sessile herbivores with the drone experiment data. For each of the three focal guilds (upper-surface leaf-miners, lower surface leaf-miners, and gall-inducers), I fitted a GLMM with negative binomial (abundance data) and binomial (occurrence data) error distribution. I tested insecticide effects on survivorship of the two most abundant leaf-miner genera (upper surface *Stigmella* [Nepticulidae] and lower surface *Phyllonorycter* [Gracillariidae]) by fitting binomial GLMMs. Independent variables included insecticide treatment (diflubenzuron and tebufenozide, each as a dummy-coded variable), chewing damage (i.e. the percentage of damaged leaves in branch-level models and damage occurrence in leaf-level models), and canopy stratum (upper or lower), as well as the interactions between treatment and canopy stratum, and treatment and chewing damage. Random intercepts for tree nested into block and branch nested into tree nested into block were added as random terms for the tree- and leaf-level models, respectively. When necessary, the random effect structure was simplified to correct convergence problems by removing random terms with near-zero estimated variance (singular fits). Tree diameter at breast height (DBH) was identified as an important covariate and added to the models as a covariate (Appendix C, Supplementary information file S1).

Indirect effects. I tested for indirect treatment effects (i.e. insecticides effects through reduction of chewing damage) on the occurrence of sessile herbivores with the helicopter experiment data. I performed one separate structural equation model (SEM) for each treatment (diflubenzuron or tebufenozide). Measured variables included the incidence of upper-surface mines, lower-surface mines, and galls, as well as the incidence of chewing damage (all binary) at leaf level. Insecticide treatment and canopy stratum (both dummy-

coded) were included as fixed terms. I added random intercepts for branch nested into tree nested into block as a random term. When necessary, the random effect structure was simplified to correct convergence problems by removing random terms with near-zero estimated variance (singular fits). Crown volume and crown density were identified as important covariates and added to the model. The strength of an indirect treatment effect on leaf-miners and gall-inducers was calculated as the product of the coefficients (at the logit scale) of the paths connecting insecticide and chewing damage on the one hand, and chewing damage and leaf-miner or gall-inducer incidence on the other hand, provided both paths were statistically significant. The total effect of treatment was calculated as the sum of the coefficients of significant intermediate paths. The overall fit of the SEMs was assessed with Shipley d-separation tests, summarised using Fisher's C statistic.

2.5.3 Effects of insecticides on canopy arthropod communities

In **Chapter 3**, I assessed the impacts of diflubenzuron and BTK on the structure of a diverse community of canopy arthropods using data from the helicopter experiment.

Treatment efficacy. I used the approach described in the previous section to test the effect of the treatments on gypsy moth abundance, replacing the tebufenozide-treated trees with the BTK-treated trees (i.e. to allow comparisons with the community data, as tebufenozide-trees were not sampled by fogging).

Effects on abundance. For various non-target taxa, I fitted abundance as the response variable in a GLMM. Error distribution family was selected by fitting multiple models and picking the best fit for each taxon based on AIC. Treatment was included as a fixed effect (diflubenzuron or BTK; dummy-coded) and a random intercept for block as a random effect. I fitted abundance models for various taxa at different taxonomic levels: the whole community, the separate sensitivity groups (separately for morphologically determined species and species identified via DNA metabarcoding), as well as the most common taxonomic families and species.

Effects on species diversity. I analysed the effects of insecticides on arthropod community structure on the whole community and separately for each sensitivity group, excluding tourists. I compared the average abundance per tree, the abundance of the most common taxa, the total species diversity (γ -diversity), the mean species diversity per tree (α -diversity) and the compositional heterogeneity among tree communities (β -diversity) between treatments. Importantly, I excluded four of the ten blocks from the analysis of diversity due

to a pyrethrum dosing mistake causing under-sampling too large to be statistically corrected. To account for uneven sampling effort among the remaining plots, I extrapolated species richness up to twice the observed sample size for each tree within sensitivity group using abundance-based rarefaction and extrapolation curves. For each sensitivity group, I then selected the associated lowest sampling coverage value as "base coverage" (Chao & Jost, 2012). Species richness was interpolated or extrapolated to the abundance value corresponding to the base coverage for each tree (i.e. "base sample size"). I eventually estimated the diversity per treatment (γ -diversity) using the sum of base sample sizes for each treatment. For the control treatment, this number was halved to correct for the higher number of trees (i.e. $n = 12$ versus $n = 6$ in diflubenzuron and BTK). I then produced a diversity profile for each treatment and group by multiplicatively partitioning γ -diversity according to Jost (2007):

$$(5) \gamma_i = \alpha_i \times \beta_i$$

where γ is the total species diversity in the treatment i , α is the average diversity per tree within the treatment i , and β is the effective number of compositionally distinct tree assemblages within the treatment i . Additionally, I used the Hill numbers of order 0 and 1 (Hill, 1973) to analyse the effect of insecticides on species richness and evenness within a single framework. Hill numbers qD are standardised indices that quantify diversity in units of equivalent numbers of equally abundant species. In this framework, 0D corresponds to the species richness, in which species are given equal weights independent of their relative frequencies in the community, and 1D corresponds to the exponential of Shannon entropy, in which species are weighted proportional to their relative frequency in the community. I tested for significant differences in arthropod abundance between treated and control trees and within sensitivity groups using Wald tests. To estimate the uncertainty of γ -, α - and β -diversity, I constructed 95 % confidence intervals using a bootstrap method (500 replicates). Differences were considered significant at a level of 5 % in the absence of overlap of the confidence intervals of the different treatments (Chao & Jost, 2012).

2.5.4 Efficacy of tebufenozide and accuracy of defoliation risk assessment in a large-scale experimental setting

In **Chapter 4**, I present a large-scale experimental design aiming at addressing the relative impacts of gypsy moth outbreaks and tebufenozide on various aspects of forest management and ecology. I evaluated the validity of the design by testing the efficacy of the treatment and

the accuracy of the risk estimation index used to select study sites at high and low risk of defoliation.

To assess the treatment efficacy and the accuracy of defoliation risk estimates, I used the same approach as in the drone and helicopter experiments applied separately to the different life stages of the gypsy moth (i.e. egg, early instar larvae before spray, early instar larvae after spray, live late instar larvae, dead late instar larvae, pupae and adults) and to defoliation estimates. For each life stage, I fitted abundance data aggregated at the plot level to GLMMs with negative binomial error distribution, adding a zero-inflation component for variables for which strong insecticide effects were expected (i.e. caterpillars and pupae sampled after the treatment). Independent variables included insecticide treatment (control or tebufenozide), pre-spray defoliation risk (high or low) and their interactions (when relevant) as fixed effects, and a random intercept for block as a random effect. I fitted the foliation ratio to a beta regression model with treatment, pre-spray defoliation risk and their interaction as independent variables. I decided not to add block as a random effect in this model due to its near-zero estimated variance when included (i.e. singular fit).

3 Chapter overview

This thesis contains four chapters consisting of three published research articles and a manuscript ready for submission. In the following, a summary of and a statement of all the authors' contributions in each chapter will be presented. The complete chapters are attached in Appendices B - E.

Chapter 1. Assessing insecticide effects in forests: a tree-level approach using Unmanned Aerial Vehicles

Benjamin M. L. Leroy, Martin M. Gossner, Florian P. M. Lauer, Ralf Petercord, Sebastian Seibold, Jessica Jaworek, and Wolfgang W. Weisser

Published in *Journal of Economic Entomology* **112**(6), 2019, 2686-2694.

DOI: 10.1093/jee/toz235

Summary

Impact assessment of aerially applied insecticides in forests is inherently challenging. Aerial forestry trials are complex undertakings that require careful planning and substantial financial resources. More often than not, researchers must adapt to insufficient funding, logistic challenges, and legal obstacles by resorting to subpar experiments designs lacking sufficient replication or a proper interspersion of experimental units. The use of such designs has been virtually institutionalised in forestry trials, to the point where one can legitimately question the reliability of the current knowledge on insecticide side effects in forests. We tested a tree-level approach using a spray drone in a randomised block design with ten replicates to test the effects of two moulting disruptors on oak-dwelling caterpillars. We selected three trees with high and three trees with low defoliator density within each block. Each was randomly assigned one of the three treatments (diflubenzuron, tebufenozide or unsprayed control). We monitored the mortality and feeding activity of caterpillars for one month after spraying. Both insecticides caused higher overall mortality and reduced feeding activity compared to control levels. Tebufenozide had the strongest effect, with significantly higher mortality in all macrolepidopteran families and a marginally significant increase in the mortality of leaf-rolling caterpillars (Tortricidae). Diflubenzuron strongly affected the target pest, the oak processionary moth, but did not cause significantly greater mortality in non-target families. We suggest that differences between insecticides are likely associated with their relative speed of action and the phenology of spring Lepidoptera in oak rather than differences in potency. The impact of tebufenozide on leaf-rollers indicates that this group, often presumed non-sensitive due to its shelter-building habits, experiences lethal insecticide effects, albeit weaker than those detected on free-living species. These findings further emphasise the need to increase the statistical power of aerial forest trials to avoid a systematic underestimation of insecticide side effects. Our small-scale approach using spray drones is a cost-efficient alternative to under-replicated large-scale designs that allows more accurate assessments of the short-term effects of insecticides.

Authors' contributions

RP, MG, and WW drafted the original concept. BL, MG, and FL designed the experiment. RP organised and supervised the insecticide application. BL and FL sampled the caterpillar and frass data. BL collected the crown structure data. FL directed the vegetation assessment and conducted it with the help of BL. JJ and FL sorted and identified the specimen. BL conducted the statistical analyses and prepared all the figures. BL wrote the manuscript. All authors reviewed and edited the manuscript.

Chapter 2. Side-effects of insecticides on leaf-miners and gall-inducers depend on species ecological traits and competition with leaf-chewers

Benjamin M. L. Leroy, Martin M. Gossner, Gabriele Ferrini, Sebastian Seibold, Florian P. M. Lauer, Ralf Petercord, Peter Eichel, Jessica Jaworek, and Wolfgang W. Weisser

Published in *Environmental Toxicology and Chemistry* 40(4), 2021, 1171-1187.

DOI: 10.1002/etc.4969

Summary

Insecticide impact assessment in forests generally focuses on investigating the response of organisms which exposure to insecticides is unambiguous. Because most forest use insecticides are non-systemic larvicides that need to be ingested to be effective, insects feeding internally, such as sessile herbivores, are usually considered protected from exposure, though this has not been tested. Besides, chewing damage caused by defoliating insects, the usual target of insecticide treatments, is known to affect the survivorship and oviposition behaviour of sessile herbivores. Feeding traits and competition may hence mediate the non-target effects of insecticides on these species. We tested the sensitivity of three guilds of sessile herbivores – upper surface leaf-miners, lower-surface leaf-miners and gall-inducers – to the insecticides diflubenzuron and tebufenozide in two small-scale aerial spray trials. We compared the incidence of mines and galls on sprayed and unsprayed leaves to address the impact of insecticides on oviposition behaviour. Additionally, we scored the presence of exit holes and pupae as a measure of larval survivorship. We recorded a lower incidence of upper-surface leaf-miners and lower survivorship of lower-surface leaf-miners on diflubenzuron-treated trees, while gall-inducers were unaffected. Despite a similar tendency, tebufenozide had no significant impact on any of the three guilds. Both insecticides offset the negative effect of competition on leaf-miners and gall-inducers by reducing the proportion of damaged leaves in sprayed trees. Therefore, insecticides selectively affected different guilds of sessile herbivores depending on their ability to avoid exposure. Our findings show that forest use insecticides can impact organisms traditionally considered safe through subtle exposure dynamics and alterations of species interactions. Our study advocates for the extension of impact assessment studies beyond unambiguous lethal effects and give more consideration to discrete pathways such as residual toxicity and indirect effects.

Authors' contributions

BL participated in the conceptualisation of the study and methodologies together with MG, RP, PE, and WW. BL, MG, and FL designed the drone experiment; BL designed the helicopter experiment. RP and PE organised and supervised the insecticide application. BL, MG, and FL sampled the foliage in the drone experiment; BL sampled the foliage in the helicopter experiment. BL collected the crown structure data. BL conceived the protocol for herbivory assessment, supervised the training and directed the herbivory assessment. GF scored leaf-miner survivorship after receiving the training from BL. BL formatted and analysed the data and prepared all the artwork and figures. BL wrote the manuscript. All authors reviewed and edited the manuscript.

Chapter 3. Metabarcoding of canopy arthropods reveals negative impacts of forestry insecticides on community structure across multiple taxa

Benjamin M. L. Leroy, Sebastian Seibold, Jérôme Morinière, Vedran Bozicevic, Jessica Jaworek, Nicolas Roth, Sebastian Vogel, Sharon Zytynska, Ralf Petercord, Peter Eichel, Wolfgang W. Weisser

In preparation.

Summary

Insecticides aerially sprayed against outbreaks of defoliating insects can adversely impact non-target arthropod species. Most of the damage occurs during the acute phase of toxicity, in the days following treatment application. Toxicity rapidly fades out as the active substance is broken down in the environment, but residual amounts stabilising on the surface of foliage can have measurable impacts over longer timescales. Moreover, population drops during the acute phase may continue to reverberate in the community via species interactions. While acute non-target effects are well documented, longer-term legacy and residual effects are still poorly understood, owing to several methodological shortcomings challenging non-target experiments. The lack of taxonomic and biological knowledge of many species restricts diversity assessment to a handful of well-known taxa. We propose a metabarcoding approach using subsampling of arthropod communities to derive estimates of species abundances to address these issues. We applied this protocol to diverse arthropod communities sampled by pyrethrum knockdown in trees either treated with diflubenzuron or *Bacillus thuringiensis* var. *kurstaki* (BTK) or left unsprayed within a small-scale randomised block design in German oak woodlands. The use of DNA-based identification allowed us to retain most of the diversity of the sampled communities in our analyses. We organised arthropod species into assemblages delimited by their expected sensitivity rather than their taxonomic relatedness to facilitate the interpretation of observed treatment effects. We showed that treatments with diflubenzuron and BTK both led to lower species diversity across multiple taxa. These effects were not restricted to groups with high expected sensitivity, suggesting that acute and residual toxicity played only a minor role in the observed patterns. These results instead suggest indirect impacts induced by initial alterations of the community structure. By asymmetrically impacting arthropods during the acute phase of toxicity, forestry insecticides can trigger cascading effects across trophic levels that outlive direct toxic effects. Our results advocate for integrating state-of-the-art methods to assess the indirect effects of insecticides on non-target communities comprehensively.

Authors' contributions

BL participated in the conceptualisation of the study and methodologies together with RP, SS, SZ, and WW. BL designed the experiment. RP and PE organised and supervised the insecticide application. BL sampled gypsy moth caterpillars under burlap bands. JJ and SS sampled the arthropod communities by pyrethrum knockdown. SZ, WW and BL drafted the methodology for estimating species abundances. JJ supervised arthropod sorting and subsampling. JM and VB performed the metabarcoding pipeline. BL analysed the data and prepared all the artwork and figures. BL wrote the manuscript. All authors reviewed and edited the manuscript.

Chapter 4. Relative impacts of gypsy moth outbreaks and insecticide treatments on forest resources and ecosystems: An experimental approach

Benjamin M. L. Leroy, Hannes Lemme, Philipp Braumiller, Torben Hilmers, Martin Jacobs, Sophia Hochrein, Sebastian Kienlein, Jörg Müller, Hans Pretzsch, Kilian Stimm, Sebastian Seibold, Jessica Jaworek, W. Andreas Hahn, Stefan Müller-Kroehling, and Wolfgang W. Weisser

Published in *Ecological Solutions and Evidence* 2(1), 2021, e12045

DOI: 10.1002/2688-8319.12045

Summary

Gypsy moth outbreaks can cause large scale defoliation that can substantially damage timber production by reducing growth rates and increasing tree mortality. Forest managers frequently resort to insecticide applications to mitigate economic losses. These treatments can harm non-target species via direct toxicity or disruption of species interaction networks. However, gypsy moth outbreaks can also substantially affect other animal communities via habitat degradation and disruption of community structure. Robust field experiments are needed to address the economic and ecological trade-offs of outbreaks and their management with insecticides. However, such investigations are rare, especially in the native range of the gypsy moth. In this paper, we review the different processes through gypsy moth outbreaks and their management with insecticides affect forest resources and ecosystems. We then present an experimental design set-up in South Central Germany in early 2019 to assess the relative impacts of gypsy moth eruptions and aerial insecticide treatments on different components of oak forest ecosystems. The study design comprises forest stands at high or low risk of defoliation either sprayed with tebufenozide or left unmanaged within 12 homogeneous blocks. We evaluated the performance of our design by intensively monitoring gypsy moth populations and defoliation. Our results confirmed the efficacy of tebufenozide in suppressing outbreaks and preventing defoliation. Although our estimates of defoliation risk forecasted gypsy moth population densities relatively accurately, their predictive power regarding defoliation was much more contrasted. Some stands experienced near-complete defoliation. Others were only superficially damaged despite high densities of caterpillars, emphasising the importance of using many replicates and blocking to account for heterogeneity among outbreaking populations. Our large-scale approach proved successful in addressing the different methodological challenges traditionally faced by aerial field trials and will allow a comprehensive study of the various processes at play over short and medium timescales. Measurements of forest growth and structure, tree mortality, gypsy moth density, and composition of lepidopteran, bird, bat, ground beetle, and canopy arthropod

communities will be conducted for several years to support data-driven outbreak management.

Authors' contributions

WW, JM, HP, and HL drafted the project proposal and obtained the funding. HL coordinated the gypsy moth population surveys, gathered, and formatted the data. BL directed the site selection and the design of the experiment together with WW and with the active contribution of HL, SK, TH, KS, SH, WW, JM, HP, and SS. BL, JJ and SS collected the arthropod data by pyrethrum knockdown. PB and HL sampled egg masses and older caterpillars under burlap bands. SH sampled adult moths by light-trapping. TM and MJ performed terrestrial laser scanning to quantify defoliation. BL formatted and analysed the data. BL and SH prepared all the artwork and figures. BL wrote the manuscript. All authors reviewed and edited the manuscript.

4 Discussion

Insecticides may affect arthropods through multiple mechanisms. During the acute phase, namely the days after treatment application when environmental concentrations are maximal, direct lethal and sublethal effects drive changes in community composition. Insecticides degrade at a fast rate such that only a fraction of the original concentration persists in the environment beyond the acute phase (Sundaram et al., 1997; Sundaram, 1995; Wimmer et al., 1993). However, this residual fraction can stabilise on foliage until leaf fall and induce toxic effects over longer periods (i.e. residual toxicity). Marked differences in sensitivity mediated by the selective mode of action of the active ingredients and exposure avoidance traits increase the likelihood of indirect effects (Fleeger, 2020). The importance of these different pathways fluctuates over space and time along with changes in community structure and environmental conditions, such that even initially weak effects can become significant. Therefore, it is essential to design experiments that allow the detection of both strong and weak effect signals. In this thesis, I showed the modern technologies such as spray drones and DNA-metabarcoding could substantially improve the reliability of forest impact assessment by allowing increased replication and better taxonomic resolution and coverage. In the following, I comment on the processes underlying the effects observed in the different experiments and discuss the implications of these findings for future impact assessment in forests.

4.1 Higher replication improves the detection of non-target effects

When designing insecticide efficacy trials in forests (i.e. assessing pest control performance), observing the basic principles of replication, randomness and blocking (Cadogan & Scharbach, 2003) should be given more importance than achieving a high number of replicates. The underlying rationale is that such trials aim at measuring the strength of the effect of products and treatment modalities that have been purposefully designed to suppress

pest populations. The effect sizes expected in such trials are by design considerably larger than those typically reported in observational ecology, which mitigate the need for high replication.

In contrast, non-target trials aim to demonstrate the absence of adverse effects, which demands a much higher statistical power. While treatment efficacy depends on the rapid onset of toxic effects on the target species, side effects can arise from various processes and across longer timescales. In fact, given the selectivity of the currently registered forestry insecticides, direct suppressive effects are only expected in species presenting a close physiological and biological resemblance to the target pest. However, these effects are merely the tip of the iceberg, and significant impacts associated with more intricate processes may easily be overlooked in poorly replicated studies.

With the drone experiment, we evaluated the suitability of a small-scale approach for field impact assessments, using drones to apply diflubenzuron or tebufenozide on individual trees. In Chapter 1, we presented the experimental design that includes 20 replicates by insecticide treatment (after accounting for the relative density of defoliators) expected to allow the detection of weak treatment effects on caterpillar mortality. We showed that both diflubenzuron and tebufenozide substantially increased the mortality of the target species, the oak processionary moth, and reduced the feeding activity of defoliators in oak crowns (Appendix B, Fig. 2 & 3). The high treatment efficacy suggests that spray drones are well-suited to apply insecticides in forests and may hence be used as a tool to increase the statistical power of impact assessment studies. Nevertheless, one should keep in mind that drones differ from manned helicopters in terms of flight characteristics (e.g. height, speed), potentially leading to differences in droplet deposition patterns which may influence treatment impacts. Although we did not directly compare both methods, we found similar patterns on leaf-miners sampled in the drone and helicopter experiments (Chapter 2), suggesting no substantial difference between both application methods.

In Chapters 1 and 2, we investigated whether the high statistical power achieved with this approach allowed us to detect inconspicuous non-target effects in leaf-miners (Lepidoptera: Gracillariidae, Nepticulidae, Bucculatricidae) and leaf-rollers (Lepidoptera: Tortricidae). In Chapter 1, we reported a 67 % higher mortality of leaf-rollers (Tortricidae) in the tebufenozide treatment relative to the control (Appendix B, Fig. 3). In contrast, diflubenzuron did not appear to affect this group. In Chapter 2, we showed that sessile herbivores were differently affected depending on their feeding traits. We found 47 % fewer upper-surface species in diflubenzuron-treated trees than in controls, while the number of lower surface species and

gall-inducers did not differ between treatments (Appendix C, Fig. 4). We also noted a decreased survivorship of lower-surface leaf-miners in diflubenzuron-sprayed trees, although this was restricted to intact leaves (Appendix C, Fig. 5). As opposed to leaf-rollers, leaf-miners appeared most sensitive to diflubenzuron. We found no significant effect of tebufenozide on any measured parameters, despite a similar trend for occurrence and survivorship. Previous works reported contrasting short-term responses of Microlepidoptera, the majority finding no significant population effect (but see Butler, Kondo, et al., 1997; Martinat et al., 1988; Sample, Butler, et al., 1993; Sample et al., 1996). By contrast, all of these studies systematically reported strong quantitative effects on Macrolepidoptera. In the drone experiment, tebufenozide had a strong effect on this group, with 2- to more than 3-fold higher mortality across the dominant families compared to controls. Diflubenzuron was seemingly weaker, with a significantly higher overall mortality but no significant difference when the response of the non-target families was examined separately (Appendix B, Fig. 2 & 3).

One can draw several conclusions from these findings. First, the large differences in the treatment effect sizes between Macrolepidoptera and Microlepidoptera indicate that the latter is indeed less sensitive to diflubenzuron and tebufenozide than the former. However, both leaf-rollers and leaf-miners were found to experience adverse effects from one of the treatments regardless. Because the vast majority of previous studies failed to report such effects, our results confirm that insufficient replication poses substantial risks of type II error in moderately sensitive groups.

Second, the surprisingly marked contrasts between diflubenzuron and tebufenozide suggest that differences in the mode of action and environmental fate of both substances mediate divergent responses among insect guilds. The weak influence of diflubenzuron on non-target Macrolepidoptera contradicts existing evidence on the high field toxicity of this insecticide towards this group (Butler, Chrislip, et al., 1997; Martinat et al., 1988; Sample, Butler, et al., 1993). However, this is more likely due to the relatively slow action of diflubenzuron and the skewed phenological structure of the non-target assemblage than to poor treatment efficacy. Spring species with short larval periods heavily dominate the lepidopteran community in Central European deciduous oaks (Patočka, 1980; Southwood et al., 2004). This phenological pattern is clearly visible when looking at the gradual drop in the number of samples caterpillars in our data (Appendix B, Supplementary information file E). Unlike tebufenozide which triggers a premature lethal moult shortly after ingestion, diflubenzuron is a slow-acting insecticide that kills only at the next moult (Maas et al., 1981; Smaghe & Degheele, 1994). With mid-May application targeting the oak processionary moth, a species that feeds until

early summer, the exposure time in most non-target species was likely too short to elicit substantial population effects. This implies that the impacts of diflubenzuron on Macrolepidoptera were likely underestimated in the drone experiment. Earlier spraying (which is common in practice) would probably have led to much stronger effects, taking us back to the importance of application timing in non-target studies (see section 1.8.1 *Lack of adequate replication*). Furthermore, the failure to report substantial effects on caterpillars does not imply that they are not sensitive, considering that diflubenzuron can also be lethal to pupae (Biddinger & Hull, 1999), which emphasises the importance of assessing insecticide impacts across multiple life-stages (Baird et al., 2008).

Last, the opposite pattern observed on leaf-miners may suggest that diflubenzuron is more potent or more stable inside foliage than tebufenozide. Environmental fate studies suggest that both substances can persist on foliage in comparable concentrations until the winter (Sundaram, 1995; Wimmer et al., 1993), and thus should be present in the summer when leaf-miners are feeding. Absorption dynamics are comparatively poorly known, yet one study showed that a small fraction of diflubenzuron is absorbed and persist inside the mesophyll of cotton leaves (Bull & Ivie, 1978). In the absence of such data for tebufenozide, the underlying mechanisms remain unclear.

4.2 Life history mediates exposure to insecticides

The apparent low sensitivity of Microlepidoptera has led scientists to suggest that the shelter-building and internal feeding behaviours prevalent in this group mitigate its exposure to insecticides (Martinat et al., 1988; Scriber, 2004). Our results support this hypothesis on the basis of effect sizes considerably weaker than those reported on free-living Macrolepidoptera. However, they also provide evidence of the susceptibility of leaf-rollers and leaf-miners to tebufenozide and diflubenzuron, respectively. Therefore, it is crucial not to restrict impact assessment to highly sensitive groups and test hypotheses on ecological avoidance by comparing groups with different life histories.

Our investigations on sessile herbivores in Chapter 2 revealed several interesting patterns that suggest that exposure is determined by the relationship between insecticide dynamics and species life history. Because leaf-miners feed on a single leaf throughout their larval stage, the reduced abundance observed in diflubenzuron-treated trees implies either higher hatching failure or avoidance of treated leaves by gravid females. Laboratory trials on multiple arthropod species have confirmed the ovicidal activity of diflubenzuron (Grosscurt, 1978).

Oviposition deterrent effects are less known, but one study reported an increased rejection of leaves treated with diflubenzuron by the leaf-miner *Liriomyza trifolii* Burgess (Diptera: Agromyzidae) (Smith, 1986). While both mechanisms are plausible, these results clearly indicate that ovipositing on the upper surface of leaves increase the likelihood of residual exposure to diflubenzuron. By contrast, upper-surface feeding appeared not critical to determining exposure, as evidenced by the lack of significant effect of diflubenzuron on the survivorship of larvae. Interestingly, we found the opposite pattern for lower-surface leaf-miners, namely that the number of mines was unaffected, yet survivorship was reduced. Since all species in this group oviposit on the underside of the leaves, it is plausible that the leaf blade acted as a physical barrier to exposure. However, reduced survivorship seems counterintuitive at first glance due to the lack of such effect on upper-surface leaf-miners, which are physically closer to the site of deposition of insecticides. I speculated that differences in the cellular structure of the mesophyll might explain these differences. The absorbed fraction of residues accumulates in the intercellular space, which is much broader in the sponge parenchyma, the tissue on which lower-surface leaf-miners feed (Rohrbaugh, 1934). These species may thus be exposed to higher insecticide concentrations. Such asymmetric responses between different life stages (eggs and larvae) and feeding guilds (upper- and lower-surface species) supports the plea of ecotoxicologists for adopting a trait-based definition of non-target organisms in impact assessment studies (Rubach et al., 2011).

The data on the field response of individual species to diflubenzuron and BTK presented in Chapter 3 (Appendix D, Fig. 5) can be used to discuss further mechanisms of exposure avoidance. For example, we reported divergent impacts of diflubenzuron on different species of epiphyte grazers. The abundance of the barklice *Valenzuela flavidus* Stephens (Psocodea: Caeciliusidae) was reduced two-fold in diflubenzuron-treated trees compared to controls. In contrast, the two other most abundant species *Elipsocus moebiusi* Tetens (Psocodea: Elipsocidae) and *Graphopsocus cruciatus* L. (Psocodea: Stenopsocidae), were not affected. Differences in phenology and feeding ecology are likely underlying these contrasting responses. *V. flavidus* is an obligate folicolous (i.e. leaf-frequenting) species that colonises trees in spring and only mature in June (Schneider, 2007). This delayed colonisation is driven by the progressive colonisation of leaves by the microbes on which it feeds (New, 1987). By contrast, the corticolous (i.e. bark-frequenting) *E. moebiusi* and *G. cruciatus* are not restricted by seasonal limitations in their food supply (New, 1987) and have already reached the adult stage at the time of spraying (Schneider, 2007). Likewise, we did not find any effect of diflubenzuron on *Entomobrya nivalis* L., a common species of springtail in oak trees. In this case, the specificity of diflubenzuron to juvenile stages and the different patterns of habitat

use between adults and may mediate exposure. Adult *E. nivalis* are usually found on lichens growing on tree branches while drought-sensitive juvenile prefers moist habitats in the leaf litter and bark crevices (Meier & Zettel, 1997; Prinzing et al., 1997). Therefore, the species is likely only exposed to significant concentrations of diflubenzuron during its adult phase, thereby effectively escaping toxicity. These interpretations are very speculative and difficult to test, yet response patterns are consistent with the exposure dynamics that one can be expected based on the life history of these species

One pattern that leaves comparatively little room for doubt was the spectacular reduction in the population of the oak bush cricket *Meconema thalassinum* De Geer (Orthoptera: Tettigoniidae) in the diflubenzuron treatment compared to BTK and control (Appendix D, Fig. 5). In Central Europe, juveniles can be found in large numbers in oak canopies throughout the spring. Although occasional phytophagy has been reported (Johnstone, 1970), *M. thalassinum* is primarily carnivorous, feeding on a variety of arthropods, including Lepidoptera larvae (Ingrisch & Köhler, 1998). Because the effect was so pronounced and no comparable response was observed in trees treated with the Lepidoptera-specific BTK, the collapse in abundance most likely result from the secondary poisoning of juveniles in the weeks after spraying. Trophic transfers of diflubenzuron (i.e. lethal effect through the ingestion of contaminated prey) have been reported in laboratory bioassays for various predators (Castro et al., 2012; Medina et al., 2002; Smith & Lockwood, 2003). These findings suggest that trophic transfer can be an additional mediator of ecological sensitivity with strong relevance to field populations. While many of the previously discussed examples of trait-mediated exposure dealt with exposure avoidance, trophic transfers are a prime illustration of exposure facilitation through life history.

It is worth noting that other presumably sensitive species displayed patterns that cannot easily be explained by merely examining their life history. The free-living Lepidoptera *Eilema sororcula* Hufnagel (Erebidae), *Parectropis similaria* Hufnagel (Geometridae) and *Pseudoips prasinana* L. (Nolidae) are all summer feeders that were sampled as first instar caterpillars and hence potentially exposed to persistent residues. However, abundance patterns of all three species among treatments were surprisingly contrasted: *E. sororcula* was markedly rarer in both treatments, *P. similaria* was only marginally affected by diflubenzuron, and *P. prasinana* appeared unaffected by either insecticide (Appendix D, Fig. 5). These findings suggest differences in physiological sensitivity among these species. However, sensitive species can display a wide array of dose-response relationships mediated by differences in physiological traits, such as age, consumption rate and metabolic rate. Granett et al. (1980)

measured that the Douglas-fir tussock moth retained much greater amounts of diflubenzuron in its body than the non-susceptible spruce budworm as a result of metabolic differences. Such processes may drive very marked contrasts in the sensitivity of closely related species. For example, differences in diflubenzuron toxicity up to 200-fold were measured between tortricid con-generics (Grosscurt, 1978). In an impressive series of laboratory bioassays with 42 species of North American Lepidoptera, Peacock et al. (1998) unveiled a broad spectrum of sensitivity to BTK, ranging from complete mortality to the total absence of an effect. However, apart from this remarkable effort, laboratory assessments of physiological sensitivity are rare for forest species. Therefore, coarsely sorting species into susceptible and resistant groups based on the mode of action of the insecticide and exposure trait data remain the best option in field studies for now.

4.3 Species interactions mediate insecticide effects

Insecticide side effects are not restricted to direct toxicity, as non-target organisms can also be affected independently of their physiological and ecological sensitivity. One could broadly refer to such processes as indirect effects. Yet, it is foremost essential to distinguish “true” indirect effects from toxic effects resulting from indirect exposure (i.e. trophic transfers discussed in the previous section). Specifically, a species may be indirectly affected when insecticides directly impact a taxon with which it is involved in a critical interaction, such as competition, predation, or parasitism. Indirect effects can be explicitly tested in systems allowing the precise quantification of ecological interactions. However, as most interactions are difficult to sample, the presence of indirect effects can be more simply inferred by examining the response of taxa for which direct sensitivity can be reasonably dismissed. In the following, I first examine the influence of diflubenzuron and tebufenozide on the competitive interaction between leaf-chewers (i.e. free-living defoliators) and leaf-miners based on the results described in Chapter 2. I then discuss the potential mechanisms underlying diversity losses on non-sensitive taxa detected in Chapter 3.

4.3.1 Alteration of competition between herbivore guilds

In Chapter 2, we investigated how insecticides may mediate competition between two temporally separated guilds of oak-feeding herbivores, namely the spring-dominating leaf-chewers and the summer-dominating sessile herbivores. In line with the findings of previous studies (Cornelissen & Stiling, 2008; Digweed, 2006; Faeth, 1986; Roslin & Roland, 2005), we

observed that sessile herbivores are less abundant in the presence of chewing damage. Using a path model, we revealed that insecticides interact with this pattern by reducing the incidence of damaged leaves (Appendix C, Fig. 6). Guilds of sessile herbivores that were not directly affected by the treatments were found more often in sprayed trees. These results provide evidence of insecticide-induced disruptions of species interaction.

Root and Skelsey (1969) argued that the development of selective insecticides might create new problems by allowing the development of species previously "held in check" by competition. As an illustration of this mechanism, the authors showed that the suppression of aphid populations with a carbamate insecticide led to a dramatic increase in collard leaf injury caused by flea beetles (Coleoptera: Alticini). Similar cases of secondary outbreaks caused by a reversal of the competitive hierarchy between herbivores have since then been documented in multiple cropping systems (Hardin et al., 1995). However, the mechanism unveiled in Chapter 2 differs with regard to the processes involved. In agroecosystems, insecticide-induced alterations of interspecific competition are, in most cases, the consequence of differential resistance to insecticides between competitors. In our study system, the competition between leaf-chewers and sessile herbivores is temporally separated and mediated by the host plant. Faeth (1986) suggested that the negative effect of chewing damage on leaf-miner populations may result from increased plant defences and foraging activity of parasitoids on damaged leaves. Insecticide treatments applied in spring strongly reduce the leaf-chewer population and hence chewing damage, relieving the summer-feeding sessile herbivores from damage-induced biotic pressures.

Similar processes have been involved in the release of secondary pests in other systems. For example, Szczepaniec et al. (2013) found that neonicotinoid treatments against ash borers favoured the development of spider mite outbreaks by reducing the activity of predatory arthropods and increasing foliage quality. However, in our study system, one can reasonably question whether the altered competition between leaf-chewers and sessile herbivores poses a realistic threat of secondary infestation. Among the leaf-mining and gall-inducing guilds of Central European deciduous oaks, only one species, the leaf-miner *Tischeria ekebladella* Bjerkander (Lepidoptera: Tischeriidae), is considered a potentially injurious pest (Csóka, 1997; Molnár et al., 2012). In Chapter 2, we emphasised that, although statistically significant, the positive effect of insecticides only explained a relatively small amount of the variation in the occurrence of sessile herbivores. Likewise, field studies investigating competition patterns in the same study system all point to the low ecological significance of the process (Cornelissen & Stiling, 2008; Faeth, 1986). Furthermore, insecticide is applied as a response

to sporadic outbreaks, such that spraying is far from being frequent enough to realistically induce resistance build-up. Therefore, while forestry insecticides can alter competition, this pathway seems to be of minor significance to the concerned species and the functioning of the ecosystem, at least at low levels of defoliation.

4.3.2 Losses of species in non-sensitive groups

In Chapter 3, we showed that parasitoids were significantly less diverse in trees sprayed with diflubenzuron and BTK, with 29 and 16 % fewer species relative to controls, respectively. Because parasitoids are obligatorily associated with other arthropod species, this pattern could be linked to the suppression of the spring caterpillar peak and the reduced diversity of several other groups, such as xylophagous beetles or epiphyte grazers (Appendix D, Fig. 4). Parasitoids are a particular group in insecticide impact assessment, as their obligate association with their host makes it challenging to distinguish trophic transfers from indirect effects. Host-mediated exposure to diflubenzuron and BTK appear to cause complex and species-specific effects in parasitoids, ranging from an absence of effect to 100 % mortality (Flexner et al., 1986; Granett & Weseloh, 1975; Madrid & Stewart, 1981; Weseloh et al., 1983). These discrepancies were suggested to be driven by relative timings of host intoxication and parasitisation and impacts of parasitism and insecticides on the host development rates (Flexner et al., 1986). By contrast, indirect effects caused by host scarcity are expected to be consistently negative. Many parasitoid species are characterised by low reproductive rates, narrow host ranges and long generation times (Barbosa, 1977; Kenis et al., 2005) and are hence expected to display a poor resilience to host scarcity.

In Chapter 3, we also reported significant reductions in the species diversity of several groups of arboreal arthropods in sprayed trees. One of the most dramatic impacts was observed on adult xylophagous beetles, which diversity in the diflubenzuron treatment was only half that of control, while a significant but less pronounced decline was also observed in the BTK treatment (Appendix D, Fig. 4). Such effects cannot be attributed to direct toxicity, as it is safe to assume that insects feeding exclusively within woody tissues at the larval stage avoid exposure to non-systemic larvicides applied to the foliage. I suggested that these patterns may instead be a consequence of the asymmetric impacts of insecticides during the acute phase. Previous research outcomes suggest that communities displaying marked differences in sensitivity to contaminants are more likely to experience indirect effects. The near-complete suppression of a sensitive and dominant species propagate to relatively tolerant species via interaction networks (Fleeger, 2020). In spring, when insecticides are typically

applied, oak canopy communities are heavily dominated by sensitive caterpillars, making them perfectly match this description.

The indirect effects of aerial applications on forest birds is a major cause for concern and have been the object of several studies during the last decades (Awkerman et al., 2011; Bell & Whitmore, 1997; Cooper et al., 1990; Holmes, 1998; Sample, Cooper, et al., 1993). In temperate oak forests, phytophagous caterpillars make up the bulk of the spring diet of insectivorous birds (Martinat et al., 1988; Perrins, 1991; Southwood et al., 2004). Compared to other insects, caterpillars constitute a rich and digestible diet, with high fat and low chitin contents making them particularly suitable to cover the high energy requirements of birds during the breeding season (Redford & Dorea, 1984). The role of caterpillars can be so critical that some species were shown to synchronise their nesting cycle with the caterpillar peak (Bañbura et al., 1999; Perrins, 1991). The use of insecticides against defoliators typically occur shortly before this peak and can hence alter the foraging patterns and breeding success of birds by brutally reducing the availability of their preferred prey (Awkerman et al., 2011; Holmes, 1998; Rodenhouse & Holmes, 1992; Sample, Cooper, et al., 1993). Resulting dietary shifts towards less dominant and nutritious prey may, in turn, further alter the structure of the arthropod community in unpredictable ways. Such processes can be anticipated based on the results from a diet study on multiple bird species deprived of abundant caterpillar prey by a diflubenzuron treatment (Sample, Cooper, et al., 1993). The authors showed that several species shifted their diet towards other insects taxa, some adopting a rather generalist strategy while others showed a marked preference towards certain taxa. Importantly, dietary shifts naturally occur at the end of spring in undisturbed oak forests due to the seasonal decline in caterpillar biomass (Sample, Cooper, et al., 1993). Our results suggest that insecticide treatment may intensify this process by causing an early drop of caterpillar biomass, increasing top-down pressure on the preferred alternative prey taxa. In this hypothesis, a dramatic decline in the diversity of adult xylophagous beetles could be indicative of their role as an alternative prey in our experiment.

Indirect effects feedback loops have not yet been tested in forests but have been documented in other study systems. In a mesocosm experiment, Allgeier et al. (2019) showed that BT products used for mosquito control disrupted the food web of an aquatic community. They found that BT treatments substantially reduced the abundance of chironomids, a cornerstone component of the ecosystem's food web, leading to increased predation of dragonflies on newts. Similar processes may come into play in oak canopy communities exposed to

defoliator-specific insecticides, and more attention should be given to such mechanisms in impact assessment studies.

4.4 Importance of large-scale and long-term studies

The effects of defoliator outbreaks and defoliation are typically not assessed together in field studies. Attempts to investigate the relative impacts of defoliation and insecticides have notably been impeded by the unpredictability of outbreaks and low statistical power (Manderino et al., 2014; Sample et al., 1996). In the drone experiment, we tried to account for outbreak effects by including trees with low or high defoliator density based on the monitoring of insect frass after budburst. However, this approach proved unsuccessful, as caterpillars abundances did not reach the expected levels. Likewise, while egg-mass counts predicted high densities of the gypsy moth in half of the blocks set up for the helicopter experiment, abundances remained low across all plots, likely due to an intense frost episode that hit the region shortly after the caterpillars hatched. It should be noted that the project supporting this thesis was funded during a relatively quiet period with regard to defoliator outbreaks in Bavarian oak forests. We thereby focused the site selection on stands showing signs of local gradations, which gave us a limited choice for both experiments.

On the one hand, the absence of outbreaks in the drone and helicopter experiments turned out to be an asset, as it allowed us to isolate the effects of insecticides by comparing treated and undisturbed trees. On the other hand, our results could have been markedly different in the presence of significant defoliation. For example, non-sensitive leaf-miners may benefit more from insecticide treatments when densities of defoliator are critical. Previous publications that investigated the competition between leaf-chewers and leaf-miners in oaks (Cornelissen & Stiling, 2008; Faeth, 1986; West, 1985), like Chapter 2, reported effects of low to moderate levels of chewing damage. It is safe to assume that severe defoliator outbreaks can affect leaf-miners much more harshly through complete defoliation or direct interference in early summer (Roslin & Roland, 2005). In such a situation, insecticide applications preserve the habitat of sessile herbivores, indirectly increasing population survival. Likewise, herbivores and epiphyte grazers surveyed in Chapter 3 would have probably been strongly affected by significant defoliation, especially sap-sucking insects, which population peak is congruent with the period of peak defoliation by the gypsy moth (Southwood et al., 2004). Because insecticides are explicitly applied to prevent defoliation, experiments allowing to

successfully address both disturbances' relative impacts would produce more relevant results to practice.

The stand-level experiment described in Chapter 4 was designed to capitalise on a large-scale gypsy moth outbreak that began in northern Bavaria in 2018. Overall, the project aims at bringing the methodological approaches developed in the present thesis into larger spatial and temporal scales. To this end, this project capitalises on a multidisciplinary approach bringing together experts in forest protection, forestry, and ecology. In this framework, the experiment was explicitly designed to address the relative ecological and economic impacts of gypsy moth outbreaks and their treatments with tebufenozide. The extensive monitoring of gypsy moth populations and defoliation carried out during the treatment year showed the experimental design is adequate to meet this goal (Appendix E, Fig. 5). While variability among high-density populations highlighted the unpredictability of outbreaks, the inclusion of many replicates largely compensated for it. We measured substantial defoliation in 8 of the 12 stands considered at high risk of defoliation. A considerable coordinated prognosis effort involving 11 regional forest offices provided gypsy moth egg-mass data on more than 25,000 oak trees across an approximately 15,000-km² study region (Appendix E, Supplementary information file S1). These data were instrumental to the success of the experimental design, allowing us to select highly infested stands and reduce the uncertainty regarding the occurrence of defoliation. The sheer magnitude of the survey effort exploited to design this experiment tells of the challenging nature of such undertaking. It highlights the extreme importance of involving forest management stakeholders in research projects from an early stage rather than opportunistically exploiting already treated plots. Clearly, such an effort could not have been handled by researchers alone.

Ultimately, large-scale studies remain undeniably more valuable than the small-scale approaches presented in chapters 1, 2 and 3, provided that meaningful replication is an achievable objective. Conducting spraying and ecological surveys on large plots allows producing results in a spatially realistic setting, making them readily exploitable by forest managers and policymakers. In such studies, it is crucial that sampling campaigns can be conducted over several consecutive years to address the medium- and long-term implications of defoliation and insecticide treatments. In the drone and helicopter experiments, we focused on short-term effects revolving around acute and short-term residual toxicity. Treatment application on single trees and small plots does not allow realistic assessment of resilience in affected species, as recolonisation from neighbouring untreated habitats can rapidly occur. However, this aspect of ecological sensitivity plays an essential role in systems

under pulsed stress. Indeed, quiet periods separating disturbance events (i.e. in our study system, periodic defoliator outbreaks and insecticide treatments) can support the differential recovery of species based on their resilience traits (Kefford et al., 2012). Realistically addressing species recovery requires large spray plots and long timescales. This is one of the primary objectives of the stand-level experiment. However, designing large-scale studies necessarily implies substantial financial support to overcome methodological difficulties. When funding is limited, the small-scale approaches described in this thesis should be considered, as they allow to address essential questions regarding the short-term impacts of insecticides and draft hypotheses for more extensive and better-funded projects. I recommend that researchers facing underfunding prioritise good practice in the design of experiments and high taxonomic resolution of the focal taxa, even at the expense of scale. Clearly, when resources are lacking, targeted approaches should prove more rewarding than ambitious but poorly designed experiments.

5 Conclusion

The various methodological approaches presented in this thesis all showed value to improve impact assessments of forestry insecticides in the field. The tree-level approach relying on spray drones allowed us to achieve a level of replication that is unprecedented for insecticide impact assessment in forests. Moreover, experiments conducted in single stands allow the comparisons of communities experiencing similar biotic and abiotic conditions, bridging the gap between laboratory and large-scale field studies.

We showed that increasing replication allows the detection of inconspicuous adverse effects, such as in leaf-rollers and leaf-miners. This approach is thereby valuable for studying the relationship between life history and exposure. Our results suggest that field exposure to forestry insecticides is primarily determined by the interaction between feeding guild, habitat use and phenology. In particular, diflubenzuron affected both the egg and larval stages of leaf-miners despite its poor absorption characteristics. These unexpected effects indicate that species should not be dropped out of study systems based on their expected tolerance unless explicitly demonstrated beforehand. These findings further indicate that exposure to insecticides varies over the life cycle of a species, emphasizing the importance of sampling completeness to reduce the risk of underestimating non-target effects.

The importance of sampling completeness was further confirmed by the insights that we drew from the analysis of insecticide impacts on the structure of arboreal communities. Using pyrethrum knockdown and DNA-metabarcoding, we were able to sample and identify to species a diverse assemblage of free-living arthropods, giving us a community perspective on insecticide impacts. We observed diversity losses in taxa tolerant to the insecticides, indicating that non-target effects cannot be merely inferred from the physiological and ecological sensitivity of species. These results instead suggest the existence of complex patterns involving indirect effects and feedback loops across food webs. These patterns should be further investigated, for which the use of comprehensive sampling and identification is strongly encouraged.

The methodological approaches outlined in the present thesis should contribute to fostering our knowledge of how insecticides affect forest ecosystems, with a focus on understanding the short-term dynamics that can trigger food web cascades and long-term effects. These cost-efficient approaches can be readily used in various study systems to produce meaningful results despite financial limitations. However, impact assessment in forests will remain most valuable on the back of adequately and sufficiently replicated studies conducted at realistic spatial and temporal scales. Such experiments have an undeniably high value for practice and can be achieved by fostering collaboration between forest stakeholders and scientists from various disciplines. Defoliator outbreaks and their management have a myriad of ecological, economic, and social implications, and integration within large-scale multidisciplinary projects is likely the best way forward for insecticide impact assessment.

6 Outlook: What does the future hold?

6.1 Insect outbreaks in future forests

Climate warming is anticipated to shape future forests by changing disturbance patterns associated with fire, extreme climatic events and insect outbreaks (Seidl et al., 2017). In particular, climate change has been linked with increased range, magnitude, and frequency of defoliator outbreaks in the boreal and temperate zones (reviewed in Pureswaran et al., 2018). Warmer temperatures allow insects to settle in previously inhospitable areas, potentially leading to host shifts as different forest types are being colonized. Besides, higher temperatures have a predominantly positive impact on insect physiology, including faster growth, better fitness, and higher survival (Pureswaran et al., 2018). Plants and natural enemies may also experience physiological changes, leading to phenological mismatches between herbivores, host trees and natural enemies, which can disrupt the periodicity of outbreaks and promote more frequent eruptions (Roques, 2015). Of particular concern is the shortening of generation times caused by enhanced growth rates or the early onset of the flight period. Shorter generation times have been shown to lead to greater investment in second generations and increases of voltinism in Lepidoptera (Altermatt, 2010).

Despite a large body of publications addressing the topic, the implications of climate-induced changes in defoliator outbreaks for future forests remain unpredictable, with considerable variation between defoliator species and forest types (Pureswaran et al., 2018). However, the magnitude and the diversity of the described impacts give legitimate cause for concern. The interaction between insect outbreaks and an increased frequency of extreme weather episodes, such as drought and heatwaves, could lead to a magnification of defoliation impacts on trees (Jactel et al., 2012).

6.2 Current and future trends in defoliator control

Current trends in forest protection indicate a progressive departure from the large-scale use of synthetic chemicals (Holmes & MacQuarrie, 2016). Modern management strategies increasingly rely on a diversity of practices tailored to specific situations and objectives. The aerial application of BTK has been the predominant strategy to suppress defoliator outbreaks for several decades already. Compared to synthetic insecticides, BTK is viewed as the lesser evil due to its natural origin and short persistence and benefit from a wider public acceptance (W-Y. Chang et al., 2009). However, we have shown that BTK treatments may still have measurable impacts on arthropod communities, and particular attention should be given to their indirect effects.

Beyond BTK, extensive research in insect pathology promoted the use of narrowly specific pathogens for highly targeted treatments (van Frankenhuyzen et al., 2016). Notable success stories include the discovery of *Entomophaga maimaiga* Humber, Shimazu, and Soper (Zygomycota: Entomophthorales) and its subsequent introduction as a biological control agent against the gypsy moth (Smitley et al., 1995), or the development of viral spray products for suppression treatments, such as baculoviruses against the balsam fir sawfly (Moreau et al., 2005) or the gypsy moth multicapsid nuclear polyhedrosis virus (MNPV; Reardon et al., 2012). Besides, the scope of forest protection is gradually moving from purely curative management towards diversified strategies, including proactive approaches targeting the pre-outbreak phases of population cycles (van Frankenhuyzen et al., 2016). The “Slow the Spread” program initiated in 1999 to contain the expansion of the gypsy moth in the US (Sharov et al., 2002) is a prime illustration of this paradigm shift. Over the last 15 years, more than 70 % of the sprayed area consisted of mating disruption treatments with pheromones on low-density populations (Liebhold et al., 2021; USDA Forest Service, 2020).

Nevertheless, chemicals will likely keep a place in forest protection. Diflubenzuron and neurotoxicants are still occasionally applied against sawflies, which resist BTK and tebufenozide (Forest Stewardship Council, 2019; Holmes & MacQuarrie, 2016; Möller, 2014). Because the low environmental stability of BTK sometimes leads to treatment failure (e.g. Martin et al., 2002), synthetic insecticides like tebufenozide are still preferred in some countries (Lemme et al., 2019). They are also used to protect high-value stands within the framework of integrated pest management (Holmes & MacQuarrie, 2016). Although the impacts of changing climate on future insect disturbance remain challenging to forecast, several models predict an intensification of defoliator damage in the coming decades

(Pureswaran et al., 2018). From this perspective, a renewed reliance on insecticides for forest protection is not to be excluded.

6.3 Towards the birth of forest ecotoxicology?

Despite the long history of insecticide treatments in forests, their side effects have received considerably less attention than in agricultural and aquatic ecosystems. The number of studies addressing non-target effects is remarkably small, and experimental protocols have hardly evolved since the 1990s. Most impact assessment studies, including those presented in the present thesis, are purely exploratory surveys based on comparisons of species assemblages in treated and untreated stands or before and after spraying. As for methodological shortcomings, this situation is arguably driven by a lack of funding, which may not evolve without the birth of an ecotoxicological community studying forest ecosystems.

These facts should, however, in no way be invoked to justify a lack of investment into pesticide impact research in forests. Forests are among the most diverse ecosystems on Earth. They are source habitats for many species that contribute to key ecosystem functions and services (Brockerhoff et al., 2017; Duelli & Obrist, 2003). Moreover, forests are home to rare or endangered species, which may be typically less resilient to chemical stress (Kefford et al., 2012). With the perspective of an intensification of defoliator outbreaks, forest ecosystems may become more frequently exposed to insecticides in the future. Besides, aerial applications are an essential component of nuisance and vector control strategies, and, unlike in forestry, their use kept increasing over the last decades (van den Berg et al., 2012). In Europe, the BT variant *israelensis* is widely used against mosquitoes over various natural ecosystems, including inundation forests (Allgeier, Kästel, et al., 2019). Recent epidemics of tropical vector-borne diseases and current predictions of intensified spread of invasive species suggest a probable increase in the frequency of such treatments in the near future (Bellini et al., 2020).

For the reasons outlined above, stimulating the interest of the ecotoxicological community and funding bodies towards forest ecosystems seems primordial. Exploratory studies conducted over the last five decades barely scratched the surface of the impacts of aerial spraying, such that both forest communities (especially in tree canopies) and their response to insecticides remain poorly known. In this regard, it is, at first, essential to continue conducting long-term and well-designed field studies to frame biologically sound hypotheses

as to the processes underlying insecticide side effects. One particularly critical aspect of this exploratory phase would be to sample and compile insecticide fate, exposure traits and species interaction data to allow a more mechanistic approach at a later stage. To this end, researchers in the field should be encouraged to diversify experimental methods and integrate state-of-the-art technologies into field experiments.

In Chapter 3, we took advantage of DNA-metabarcoding to unveil diversity losses in low sensitivity groups. However, we were only able to speculate on the causal mechanisms due to the exploratory nature of the experiment. DNA-barcoding could be further employed to foster our understanding of the observed patterns, for instance by characterizing the diet composition of vertebrate predators (e.g. Rytönen et al., 2019). Such efforts could be further combined with classic monitoring of the foraging and reproductive performance of predators (e.g. Rodenhouse & Holmes, 1992). Similarly, DNA-barcoding opened new avenues to study host-parasitoid networks, as it allows the detection and identification of endoparasitoids from within their host (Hrček & Godfray, 2015). Ecotoxicological approaches investigating exposure and resilience (Kefford et al., 2012; Rico & van den Brink, 2015) and indirect effects (Allgeier, Friedrich, et al., 2019; Riedl et al., 2018) should be transposed to forest systems to test ecotoxicological processes. Furthermore, current knowledge on the physiological sensitivity of forest species is lacking, and efforts should be dedicated to conducting assessments of relevant toxic endpoints beyond pest species. Last but not least, toxicity data could be used to estimate species physiological sensitivity across diverse assemblages using cross-species extrapolations. In this framework, models describing toxicological processes in model organisms are used as a basis to extrapolate the physiological sensitivity of untested species following relatedness-, trait- or genomic-based approaches (reviewed in van den Berg et al., 2021). These models could ultimately be integrated into modular designs with existing modelling procedures predicting insecticide fate, exposure, population response and food web effects (Fleeger, 2020; Roeben et al., 2020; van den Brink et al., 2013) in order to produce a comprehensive mechanistic framework of insecticide impacts in forests.

Modern science offers countless opportunities to support the development of forest ecotoxicology. Obtaining wider attention from research funding bodies might well be the main challenge to overcome to make it happen. In this perspective, I have great hopes that the recently implemented multidisciplinary experiment presented in Chapter 4 will produce meaningful results to help to stimulate the (belated) birth of forest ecotoxicology.

7 References

- Addison, J. A. (1996). Safety testing of tebufenozide, a new molt-inducing insecticide, for effects on nontarget forest soil invertebrates. *Ecotoxicology and Environmental Safety*, 33, 55–61.
- Alalouni, U., Schädler, M., & Brandl, R. (2013). Natural enemies and environmental factors affecting the population dynamics of the gypsy moth. *Journal of Applied Entomology*, 137(10), 721–738.
- Allgeier, S., Friedrich, A., & Brühl, C. A. (2019). Mosquito control based on *Bacillus thuringiensis israelensis* (Bti) interrupts artificial wetland food chains. *Science of The Total Environment*, 686, 1173–1184.
- Allgeier, S., Kästel, A., & Brühl, C. A. (2019). Adverse effects of mosquito control using *Bacillus thuringiensis* var. *israelensis*: Reduced chironomid abundances in mesocosm, semi-field and field studies. *Ecotoxicology and Environmental Safety*, 169, 786–796.
- Altermatt, F. (2010). Climatic warming increases voltinism in European butterflies and moths. *Proceedings of the Royal Society B: Biological Sciences*, 277(1685), 1281–1287.
- Amos-Binks, L. J., MacLean, D. A., Wilson, J. S., & Wagner, R. G. (2010). Temporal changes in species composition of mixedwood stands in northwest New Brunswick: 1946–2008. *Canadian Journal of Forest Research*, 40, 1–12.
- 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., McCullough, D. G., & Holle, B. V. (2011). Economic impacts of non-native forest insects in the continental United States. *PLOS ONE*, 6(9), e24587.
- Austarå, Ø., Orlund, A., Svendsrud, A., & Veidahl, A. (1987). Growth loss and economic consequences following two years defoliation of *pinus sylvestris* by the pine sawfly *Neodiprion sertifer* in West-Norway. *Scandinavian Journal of Forest Research*, 2(1–4), 111–119.
- Awkerman, J. A., Marshall, M. R., Williams, A. B., Gale, G. A., Cooper, R. J., & Raimondo, S. (2011). Assessment of indirect pesticide effects on worm-eating warbler populations in a managed forest ecosystem. *Environmental Toxicology and Chemistry*, 30(8), 1843–1851.

- Baird, D. J., & Hajibabaei, M. (2012). Biomonitoring 2.0: A new paradigm in ecosystem assessment made possible by next-generation DNA sequencing. *Molecular Ecology*, 21(8), 2039–2044.
- Baird, D. J., Rubach, M. N., & van den Brink, P. J. (2008). Trait-based ecological risk assessment (TERA): The new frontier? *Integrated Environmental Assessment and Management*, 4(1), 2–3.
- Bañbura, J., Lambrechts, M. M., Blondel, J., Perret, P., & Cartan-Son, M. (1999). Food handling time of blue tit chicks: Constraints and adaptation to different prey types. *Journal of Avian Biology*, 30(3), 263–270.
- Barber, N. A., Marquis, R. J., & Tori, W. P. (2008). Invasive prey impacts the abundance and distribution of native predators. *Ecology*, 89(10), 2678–2683.
- Barbosa, P. (1977). R and K strategies in some larval and pupal parasitoids of the gypsy moth. *Oecologia*, 29(4), 311–327.
- Bayerische Landesanstalt für Wald und Forstwirtschaft. (2014). *Monitoring Eichenschädlinge*. <https://www.lwf.bayern.de/waldschutz/monitoring/063818/index.php>
- Beck, L., Römbke, J., Ruf, A., Prinzing, A., & Woas, S. (2004). Effects of diflubenzuron and *Bacillus thuringiensis* var. *Kurstaki* toxin on soil invertebrates of a mixed deciduous forest in the Upper Rhine Valley, Germany. *European Journal of Soil Biology*, 40(1), 55–62.
- Bell, J. L., & Whitmore, R. C. (1997). Bird populations and habitat in *Bacillus thuringiensis* and Dimilin-treated and untreated areas of hardwood forest. *American Midland Naturalist*, 137(2), 239–250.
- Bellini, R., Michaelakis, A., Petrić, D., Schaffner, F., Alten, B., Angelini, P., Aranda, C., Becker, N., Carrieri, M., Di Luca, M., Fălcută, E., Flacio, E., Klobučar, A., Lagneau, C., Merdić, E., Mikov, O., Pajovic, I., Papachristos, D., Sousa, C. A., ... Zgomba, M. (2020). Practical management plan for invasive mosquito species in Europe: I. Asian tiger mosquito (*Aedes albopictus*). *Travel Medicine and Infectious Disease*, 35, 101691.
- Bellocq, M. I., Bendell, J. F., & Cadogan, B. L. (1992). Effects of the insecticide *Bacillus thuringiensis* on *Sorex cinereus* (masked shrew) populations, diet, and prey selection in a jack pine plantation in northern Ontario. *Canadian Journal of Zoology*, 70(3), 505–510.
- Berryman, A. A. (1987). The theory and classification of outbreaks. In P. Barbosa & J. C. Schultz (Eds.), *Insect Outbreaks*. Academic Press, San Diego, CA, US, pp. 3–30.
- Berryman, A. A. (1988). *Dynamics of Forest Insect Populations—Patterns, Causes, Implications*. Plenum Press, New York, NY, US.
- Berryman, A. A. (1996). What causes population cycles of forest Lepidoptera? *Trends in Ecology & Evolution*, 11(1), 28–32.

- Bianchi, F. J. J. A., Booij, C. J. H., & Tscharrntke, T. (2006). Sustainable pest regulation in agricultural landscapes: A review on landscape composition, biodiversity and natural pest control. *Proceedings of the Royal Society B: Biological Sciences*, 273(1595), 1715–1727.
- Biddinger, D. J., & Hull, L. A. (1999). Sublethal effects of selected insecticides on growth and reproduction of a laboratory susceptible strain of tufted apple bud moth (Lepidoptera: Tortricidae). *Journal of Economic Entomology*, 92(2), 314–324.
- Bjørnstad, O. N., Liebhold, A. M., & Johnson, D. M. (2008). Transient synchronization following invasion: Revisiting Moran's model and a case study. *Population Ecology*, 50(4), 379–389.
- Bjørnstad, O. N., Peltonen, M., Liebhold, A. M., & Baltensweiler, W. (2002). Waves of larch budmoth outbreaks in the European alps. *Science*, 298(5595), 1020–1023.
- Boulton, T. J., Otvos, I. S., Halwas, K. L., & Rohlf, D. A. (2007). Recovery of nontarget Lepidoptera on Vancouver Island, Canada: One and four years after a gypsy moth eradication program. *Environmental Toxicology and Chemistry*, 26(4), 738–748.
- Bradshaw, C. J. A., Leroy, B., Bellard, C., Roiz, D., Albert, C., Fournier, A., Barbet-Massin, M., Salles, J.-M., Simard, F., & Courchamp, F. (2016). Massive yet grossly underestimated global costs of invasive insects. *Nature Communications*, 7(12986), 1–8.
- Brockerhoff, E. G., Barbaro, L., Castagneyrol, B., Forrester, D. I., Gardiner, B., González-Olabarria, J. R., Lyver, P. O., Meurisse, N., Oxbrough, A., Taki, H., Thompson, I. D., van der Plas, F., & Jactel, H. (2017). Forest biodiversity, ecosystem functioning and the provision of ecosystem services. *Biodiversity and Conservation*, 26(13), 3005–3035.
- Brunk, I., Sobczyk, T., & Roth, M. (2019). Pest control in German forests: General patterns of biodiversity and possible impacts of BTK, diflubenzuron and lambda-cyhalothrin on non-target arthropods, birds and bats – A literature review. *Journal of Forest and Landscape Research*, 4, 1–26.
- Buhr, H. J. (2012). *Pflanzengallen*. <https://www.pflanzengallen.de/>
- Bull, D. L., & Ivie, G. W. (1978). Fate of diflubenzuron in cotton, soil, and rotational crops. *Journal of Agricultural and Food Chemistry*, 26(3), 515–520.
- Bussian, B. M., Pandelova, M., Lehnik-Habrink, P., Aichner, B., Henkelmann, B., & Schramm, K.-W. (2015). Persistent endosulfan sulfate is found with highest abundance among endosulfan I, II, and sulfate in German forest soils. *Environmental Pollution*, 206, 661–666.
- Butler, L., Chrislip, G. A., Kondo, V. A., & Townsend, E. C. (1997). Effect of diflubenzuron on nontarget canopy arthropods in closed, deciduous watersheds in a central Appalachian forest. *Journal of Economic Entomology*, 90(3), 784–794.

- Butler, L., Kondo, V. A., & Blue, D. (1997). Effects of tebufenozide (RH-5992) for gypsy moth (Lepidoptera: Lymantriidae) suppression on nontarget canopy arthropods. *Environmental Entomology*, 26(5), 1009–1015.
- Cadogan, B. L., & de Groot, P. (1995). Design of experimental efficacy trials in Canadian forests. In J. A. Armstrong & W. G. H. Ives (Eds.), *Forest insect pests in Canada*. Natural Resources Canada, Forestry Service, Ottawa, ON, Canada, pp. 479–483.
- Cadogan, B. L., & Scharbach, R. D. (2003). Design and evaluation of an aerial spray trial with true replicates to test the efficacy of *Bacillus thuringiensis* insecticide in a boreal forest. *Journal of Economic Entomology*, 96(2), 388–395.
- Campbell, R. W., & Sloan, R. J. (1977). Forest stand responses to defoliation by the gypsy moth. *Forest Science*, 23(2), 1–35.
- Canadian Council of Forest Ministers. (2021). *National Forestry Database—Forest Insects*. <http://nfdp.ccfm.org/en>
- Carson, R. (1962). *Silent Spring*. Houghton Mifflin, Boston, MA, US.
- Castro, A. A., Lacerda, M. C., Zanuncio, T. V., Ramalho, F. S., Polanczyk, R. S., Serrao, J. E., & Zanuncio, J. C. (2012). Effect of the insect growth regulator diflubenzuron on the predator *Podisus nigrispinus* (Heteroptera: Pentatomidae). *Ecotoxicology*, 21(1), 96–103.
- Chang, Wei-Yew, Lantz, V. A., Hennigar, C. R., & MacLean, D. A. (2012). Economic impacts of forest pests: A case study of spruce budworm outbreaks and control in New Brunswick, Canada. *Canadian Journal of Forest Research*, 42, 490–505.
- Chang, W-Y., Lantz, V. A., & MacLean, D. A. (2009). Public attitudes about forest pest outbreaks and control: Case studies in two Canadian provinces. *Forest Ecology and Management*, 257(4), 1333–1343.
- Chao, A., & Jost, L. (2012). Coverage-based rarefaction and extrapolation: Standardizing samples by completeness rather than size. *Ecology*, 93(12), 2533–2547.
- Clotfelter, E. D., Pedersen, A. B., Cranford, J. A., Ram, N., Snajdr, E. A., Nolan, V., & Ketterson, E. D. (2007). Acorn mast drives long-term dynamics of rodent and songbird populations. *Oecologia*, 154(3), 493–503.
- Cooke, B. J., & Lorenzetti, F. (2006). The dynamics of forest tent caterpillar outbreaks in Québec, Canada. *Forest Ecology and Management*, 226(1–3), 110–121.
- Cooper, R. J., Dodge, K. M., Martinat, P. J., Donahoe, S. B., & Whitmore, R. C. (1990). Effect of diflubenzuron application on eastern deciduous forest birds. *Journal of Wildlife Management*, 54(3), 486–493.
- Cooper, R. J., Dodge, K. M., Whitmore, R. C., & Smith, H. R. (1993). Response of ground-level wildlife food plants to canopy defoliation by the gypsy moth. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies*, 47, 268–275.

- Cornelissen, T., & Stiling, P. (2008). Clumped distribution of oak leaf miners between and within plants. *Basic and Applied Ecology*, 9(1), 67–77.
- Courtemanch, D. L., & Gibbs, K. E. (1980). Short-term and long-term effects of forest spraying of carbaryl (Sevin-4-oil) on stream invertebrates. *The Canadian Entomologist*, 112(3), 271–276.
- Csóka, G. (1997). Increased insect damage in Hungarian forest under drought impact. *Biologia*, 52, 159–162.
- Csóka, G. (1998). Oak defoliating insects in Hungary. In M. L. McManus & A. M. Liebhold (Eds.), *Proceedings: Population Dynamics, Impacts and Integrated Management of Forest Defoliated Insects*. General Technical Report NE-247. US Department of Agriculture, Forest Service, Radnor, PA, US, pp. 334–355.
- Csóka, G., Pödör, Z., Nagy, G., & Hirka, A. (2015). Canopy recovery of pedunculate oak, Turkey oak and beech trees after severe defoliation by gypsy moth (*Lymantria dispar*): Case study from western Hungary. *Central European Forestry Journal*, 61(3), 143–148.
- 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 Science*, 45(1), 74–84.
- Davis, F. R. (2014). *Banned: A History of Pesticides and the Science of Toxicology*. Yale University Press, New Haven, CT, US.
- Dhadialla, T. S., Carlson, G. R., & Le, D. P. (1998). New insecticides with ecdysteroidal and juvenile hormone activity. *Annual Review of Entomology*, 43(1), 545–569.
- Digweed, S. C. (2006). Oviposition preference and larval performance in the exotic birch-leaf-mining sawfly *Profenusa thomsoni*. *Entomologia Experimentalis et Applicata*, 120(1), 41–49.
- Doane, C. C., & McManus, M. L. (1981). *The gypsy moth: research toward integrated pest management*. Technical Bulletin No. 1584. U.S. Department of Agriculture, Forest Service, Washington, DC, US.
- Duelli, P., & Obrist, M. K. (2003). Regional biodiversity in an agricultural landscape: The contribution of seminatural habitat islands. *Basic and Applied Ecology*, 4(2), 129–138.
- Durkin, P. R. (2004a). *Control/eradication agents for the gypsy moth—Human health and ecological risk assessment for Bacillus thuringiensis var. kurstaki*. SERA Technical Report 03-43-05-02d. U.S. Department of Agriculture, Forest Service, Forest Health Protection, Arlington, VA, US.
- Durkin, P. R. (2004b). *Control/eradication agents for the gypsy moth—Human health and ecological risk assessment for diflubenzuron (Dimilin)*. SERA Technical Report 04-43-05-03b. US Department of Agriculture, Forest Service, Forest Health Protection, Arlington, VA, US.

- Durkin, P. R., & Klotzbach, J. (2004). *Control/eradication agents for the gypsy moth—Human health and ecological risk assessment for tebufenozide (Mimic)*. SERA Technical Report 04-43-05-06c. US Department of Agriculture, Forest Service, Forest Health Protection, Arlington, VA, US.
- Ellis, W. N. (2020). *Plant parasites of Europe – Leafminers, galls and fungi*. <https://bladminerders.nl/>
- ESRI. (2020). *ArcGIS Desktop: Release 10.7*.
- Faeth, S. H. (1986). Indirect interactions between temporally separated herbivores mediated by the host plant. *Ecology*, 67(2), 479–494.
- Fajvan, M. A., & Wood, J. M. (1996). Stand structure and development after gypsy moth defoliation in the Appalachian Plateau. *Forest Ecology and Management*, 89(1), 79–88.
- Fettig, C. J., Grosman, D. M., & Munson, A. S. (2013). Advances in insecticide tools and tactics for protecting conifers from bark beetle attack in the western United States. In S. Trdan (Ed.), *Insecticides—Development of Safer and More Effective Technologies*. IntechOpen, Rijeka, Croatia, pp. 472–792.
- Fischbacher, M., Naef-Daenzer, B., & Naef-Daenzer, L. (1998). Estimating caterpillar density on trees by collection of frass droppings. *Ardea*, 86(1), 121–129.
- Fleeger, J. W. (2020). How do indirect effects of contaminants inform ecotoxicology? A review. *Processes*, 8(12), 1659.
- Flexner, J. L., Lighthart, B., & Croft, B. A. (1986). The effects of microbial pesticides on non-target, beneficial arthropods. *Agriculture, Ecosystems and Environment*, 16(3–4), 203–254.
- Forest Stewardship Council. (2019). *List of approved derogations for use of ‘highly hazardous’ pesticides* (Vols. 30-001a EN). FSC International Center, Bonn, Germany.
- Gale, G. A., DeCecco, J. A., Marshall, M. R., McClain, W. R., & Cooper, R. J. (2001). Effects of gypsy moth defoliation on forest birds: An assessment using breeding bird census data. *Journal of Field Ornithology*, 72(2), 291–304.
- Gill, S. S., Cowles, E. A., & Pietrantonio, P. V. (1992). The mode of action of *Bacillus thuringiensis* endotoxins. *Annual Review of Entomology*, 37, 615–636.
- Glare, T. R., & O’Callaghan, M. (2000). *Bacillus thuringiensis: Biology, Ecology and Safety*. John Wiley & Sons, Chichester, UK.
- Gossner, M. M., Pašalić, E., Lange, M., Lange, P., Boch, S., Hessenmöller, D., Müller, J., Socher, S. A., Fischer, M., Schulze, E.-D., & Weisser, W. W. (2014). Differential responses of herbivores and herbivory to management in temperate european beech. *PLOS ONE*, 9(8), e104876.

- Gottschalk, K. W. (1990). Gypsy moth effects on mast production. In C. E. McGee (Ed.), *Proceedings of the workshop: Southern Appalachian mast management*. University of Tennessee, Knoxville, TN, US, pp. 42–50.
- Goulson, D. (2013). An overview of the environmental risks posed by neonicotinoid insecticides. *Journal of Applied Ecology*, 50(4), 977–987.
- Graf, J. F. (1993). The role of insect growth regulators in arthropod control. *Parasitology Today*, 9(12), 471–474.
- Granett, J., Robertson, J., & Retnakaran, A. (1980). Metabolic basis of differential susceptibility of two forest Lepidopterans to diflubenzuron. *Entomologia Experimentalis et Applicata*, 28(3), 295–300.
- Granett, J., & Weseloh, R. M. (1975). Dimilin toxicity to the gypsy moth larval parasitoid, *Apanteles melanoscelus*. *Journal of Economic Entomology*, 68(5), 577–580.
- Gray, D. R., & Mackinnon, W. E. (2007). Historical spruce budworm defoliation records adjusted for insecticide protection in New Brunswick, 1965–1992. *Journal of the Acadian Entomological Society*, 3, 1–6.
- Gross, H. L. (1992). Impact analysis for a jack pine budworm infestation in Ontario. *Canadian Journal of Forest Research*, 22, 818–831.
- Grosscurt, A. C. (1978). Diflubenzuron: Some aspects of its ovicidal and larvicidal mode of action and an evaluation of its practical possibilities. *Pest Management Science*, 9(5), 373–386.
- Hacker, H. (1997). Massenvermehrung des Schwammspinners (*Lymantria dispar* L.) in Mainfranken in den Jahren 1992 bis 1994. Untersuchungen zur Wirkung der Dimilin-Behandlung auf das Artenspektrum der Begleitfauna von Eichenwäldern. Beitrag II. *Beiträge zur bayerischen Entomofaunistik*, 2, 1–21.
- Hallmann, C. A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D., & Kroon, H. de. (2017). More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLOS ONE*, 12(10), e0185809.
- Hamel, D. R. (1977). The effects of *Bacillus thuringiensis* on parasitoids of the western spruce budworm, *Choristoneura occidentalis* (Lepidoptera: Tortricidae), and the spruce coneworm, *Dioryctria reniculelloides* (Lepidoptera: Pyralidae), in Montana. *The Canadian Entomologist*, 109(11), 1409–1415.
- Hardin, M. R., Benrey, B., Coll, M., Lamp, W. O., Roderick, G. K., & Barbosa, P. (1995). Arthropod pest resurgence: An overview of potential mechanisms. *Crop Protection*, 14(1), 3–18.

- Haynes, K. J., Bjørnstad, O. N., Allstadt, A. J., & Liebhold, A. M. (2013). Geographical variation in the spatial synchrony of a forest-defoliating insect: Isolation of environmental and spatial drivers. *Proceedings of the Royal Society B: Biological Sciences*, 280(1753), 20122373.
- Haynes, K. J., Liebhold, A. M., Fearer, T. M., Wang, G., Norman, G. W., & Johnson, D. M. (2009). Spatial synchrony propagates through a forest food web via consumer–resource interactions. *Ecology*, 90(11), 2974–2983.
- Haynes, K. J., Liebhold, A. M., & Johnson, D. M. (2009). Spatial analysis of harmonic oscillation of gypsy moth outbreak intensity. *Oecologia*, 159(2), 249–256. JSTOR.
- Haynes, K. J., Liebhold, A. M., & Johnson, D. M. (2012). Elevational gradient in the cyclicity of a forest-defoliating insect. *Population Ecology*, 54(2), 239–250.
- Haynes, K. J., Walter, J. A., & Liebhold, A. M. (2019). Population spatial synchrony enhanced by periodicity and low detuning with environmental forcing. *Proceedings of the Royal Society B: Biological Sciences*, 286(1903), 20182828.
- Hill, M. O. (1973). Diversity and evenness: A unifying notation and its consequences. *Ecology*, 54(2), 427–432.
- Holmes, S. B. (1998). Reproduction and nest behaviour of Tennessee warblers *Vermivora peregrina* in forests treated with Lepidoptera-specific insecticides. *Journal of Applied Ecology*, 35(2), 185–194.
- Holmes, S. B., & MacQuarrie, C. J. K. (2016). Chemical control in forest pest management. *The Canadian Entomologist*, 148(1), 270–295.
- Holmes, T. P., Aukema, J. E., Von Holle, B., Liebhold, A. M., & Sills, E. (2009). Economic impacts of invasive species in forests. *Annals of the New York Academy of Sciences*, 1162(1), 18–38.
- Horstmann, K. (1982). Auswirkung einer Bekämpfungsaktion mit Dimilin auf eine Eichenwickler-Population (Lepidoptera, Tortricidae) in Unterfranken. *Zeitschrift für Angewandte Entomologie*, 94(1-5), 490–497.
- Hrček, J., & Godfray, H. C. J. (2015). What do molecular methods bring to host–parasitoid food webs? *Trends in Parasitology*, 31(1), 30–35.
- Hunter, A. F. (1991). Traits that distinguish outbreaking and nonoutbreaking macrolepidoptera feeding on northern hardwood trees. *Oikos*, 60(3), 275–282.
- Hunter, A. F. (1995). The ecology and evolution of reduced wings in forest macrolepidoptera. *Evolutionary Ecology*, 9(3), 275–287.
- Hurlbert, S. H. (1984). Pseudoreplication and the design of ecological field experiments. *Ecological Monographs*, 54(2), 187–211.
- Ingrisch, S., & Köhler, G. (1998). *Die Heuschrecken Mitteleuropas*. Die Neue Brehm-Bücherei 629. Westarp Wissenschaften, Magdeburg, Germany.

- Iqbal, J., MacLean, D. A., & Kershaw, J. A. (2011). Impacts of hemlock looper defoliation on growth and survival of balsam fir, black spruce and white birch in Newfoundland, Canada. *Forest Ecology and Management*, 261(6), 1106–1114.
- Jacquet, J.-S., Orazio, C., & Jactel, H. (2012). Defoliation by processionary moth significantly reduces tree growth: A quantitative review. *Annals of Forest Science*, 69(8), 857–866.
- Jactel, H., Petit, J., Desprez-Loustau, M.-L., Delzon, S., Piou, D., Battisti, A., & Koricheva, J. (2012). Drought effects on damage by forest insects and pathogens: A meta-analysis. *Global Change Biology*, 18(1), 267–276.
- Jäkel, A., & Roth, M. (1999). Auswirkungen von Insektiziden (diflubenzuron, Bacillus thuringiensis var. Kurstaki) auf Nichtzielorganismen (edaphische Arthropodenfauna) in Kiefernforsten. In J. Pfadenhauer (Ed.), *Verhandlungen der Gesellschaft für Ökologie*, Band 29, pp. 237–246.
- Jansen, V. A. A. (1999). Phase locking: Another cause of synchronicity in predator–prey systems. *Trends in Ecology & Evolution*, 14(7), 278–279.
- Jepsen, J. U., Biuw, M., Ims, R. A., Kapari, L., Schott, T., Vindstad, O. P. L., & Hagen, S. B. (2013). Ecosystem impacts of a range expanding forest defoliator at the forest-tundra ecotone. *Ecosystems*, 16(4), 561–575.
- Johnson, D. M., Liebhold, A. M., & Bjørnstad, O. N. (2006). Geographical variation in the periodicity of gypsy moth outbreaks. *Ecography*, 29(3), 367–374.
- Johnstone, D. E. (1970). Notes on the Palaearctic grasshopper, *Meconema thalassinum* (De Geer), (Orthoptera: Tettigoniidae: Meconematinae) established in Long Island, New York. *Entomological News*, 81, 62–65.
- Jones, C. G., Ostfeld, R. S., Richard, M. P., Schaubert, E. M., & Wolff, J. O. (1998). Chain reactions linking acorns to gypsy moth outbreaks and lyme disease risk. *Science*, 279(5353), 1023–1026.
- Jost, L. (2007). Partitioning diversity into independent alpha and beta components. *Ecology*, 88(10), 2427–2439.
- KaDonna, R. (2010). *Phase 3 field guide—Crowns: Measurements and sampling, Version 5.0*. US Department of Agriculture, Forest Service, Southern Research Station, Knoxville, TN, US.
- Kallet, A., & Schlink, F. J. (1933). *100,000,000 Guinea Pigs: Dangers in Everyday Foods, Drugs, and Cosmetics*. Vanguard Press, New York, NY, US.
- Kasbohm, J. W., Vaughan, M. R., & Kraus, J. G. (1996). Effects of gypsy moth infestation on black bear reproduction and survival. *The Journal of Wildlife Management*, 60(2), 408–416.

- Kefford, B. J., Liess, M., Warne, M. St. J., Metzeling, L., & Schäfer, R. B. (2012). Risk assessment of episodic exposures to chemicals should consider both the physiological and the ecological sensitivities of species. *Science of the Total Environment*, 441, 213–219.
- Kenis, M., Herz, K., West, R. J., & Shaw, M. R. (2005). Parasitoid assemblages reared from geometrid defoliators (Lepidoptera: Geometridae) of larch and fir in the Alps. *Agricultural and Forest Entomology*, 7(4), 307–318.
- Kevan, P. G. (1975). Forest application of the insecticide fenitrothion and its effect on wild bee pollinators (Hymenoptera: Apoidea) of lowbush blueberries (*Vaccinium* spp.) in southern New Brunswick, Canada. *Biological Conservation*, 7(4), 301–309.
- Klemola, T., Andersson, T., & Ruohomäki, K. (2014). Delayed density-dependent parasitism of eggs and pupae as a contributor to the cyclic population dynamics of the autumnal moth. *Oecologia*, 175(4), 1211–1225.
- Klenner, M. F. (1996). Die Laufkäferfauna (Col., Carabidae) Diflubenzuron-behandelter und unbehalteter Eichenmischwälder der Westfälischen Bucht. *Gesunde Pflanzen*, 48(7), 248–252.
- Knížek, M., Forster, B., Grodzki, W., Chira, D., Mihalache, G., & Mihalciuc, V. (Eds.). (2001). *Methodology of Forest Insect and Disease Survey in Central Europe. Proceedings of the IUFRO WP 7.03.10 Workshop, September 24-28, 2000*. Forest Research and Management Institute, Section of Braşov, Buşteni, Romania.
- Koenig, W. D., Walters, E. L., & Liebhold, A. M. (2011). Effects of gypsy moth outbreaks on North American woodpeckers. *The Condor*, 113(2), 352–361.
- Koricheva, J., Klapwijk, M. J., & Björkman, C. (2012). Life-history traits and host plant use in defoliators and bark beetles: Implications for population dynamics. In P. Barbosa, D. K. Letourneau, & A. A. Agrawal (Eds.), *Insect Outbreaks Revisited*. Wiley-Blackwell, Chichester, UK, pp. 177–196.
- Kurwadkar, S., & Evans, A. (2016). Neonicotinoids: Systemic insecticides and systematic failure. *Bulletin of Environmental Contamination and Toxicology*, 97(6), 745–748.
- Lamb, P. D., Hunter, E., Pinnegar, J. K., Creer, S., Davies, R. G., & Taylor, M. I. (2019). How quantitative is metabarcoding: A meta-analytical approach. *Molecular Ecology*, 28(2), 420–430.
- Lemme, H., Lobinger, G., & Müller-Kroehling, S. (2019). Schwammspinner-Massenvermehrung in Franken. *LWF Aktuell*, 121, 37–43.
- Letourneau, D. K. (2012). Integrated pest management—Outbreaks prevented, delayed or facilitated? In P. Barbosa, D. K. Letourneau, & A. A. Agrawal (Eds.), *Insect Outbreaks Revisited*. Wiley-Blackwell, Chichester, UK, pp. 371–394.
- Liebhold, A. M., Elkinton, J. S., Williams, D. D., & Muzika, R.-M. (2000). What causes outbreaks of the gypsy moth in North America? *Population Ecology*, 42(3), 257–266.

- Liebhold, A. M., Haynes, K. J., & Bjørnstad, O. N. (2012). Spatial synchrony of insect outbreaks. In P. Barbosa, D. K. Letourneau, & A. A. Agrawal (Eds.), *Insect Outbreaks Revisited*. Wiley-Blackwell, Chichester, UK, pp. 113–125.
- Liebhold, A. M., Leonard, D., Marra, J. L., & Pfister, S. E. (2021). Area-wide management of invading gypsy moth (*Lymantria dispar*) populations in the USA. In J. Hendrichs, R. Pereira, & M. J. B. Vreysen (Eds.), *Area-wide integrated pest management: Development and field application*. CRC Press, Boca Raton, FL, US, pp. 551–560.
- Liebhold, A. M., & McManus, M. L. (1999). The evolving use of insecticides in gypsy moth management. *Journal of Forestry*, 97(3), 20–23.
- Lih, M. P., Stephen, F. M., Smith, K. G., Nagy, L. R., & Wallis, G. W. (1994). Effects of a gypsy moth eradication program on nontarget forest canopy insects and their bird predators. In D. J. Hilburn, K. J. R. Johnson, & A. D. Mudge (Eds.), *Proceedings of the 1994 Annual Gypsy Moth Review*. Oregon Department of Agriculture, Plant Pest and Disease Section, Salem, OR, US, pp. 193–200.
- I-M-Arnold, A., Grüning, M., Simon, J., Reinhardt, A.-B., Lamersdorf, N., & Thies, C. (2016). Forest defoliator pests alter carbon and nitrogen cycles. *Royal Society Open Science*, 3(10), 160361.
- Lovett, G. M., Christenson, L. M., Groffman, P. M., Jones, C. G., Hart, J. E., & Mitchell, M. J. (2002). Insect defoliation and nitrogen cycling in forests. *BioScience*, 52(4), 335–341.
- Lyytikäinen-Saarenmaa, P., Lyytikäinen-Saarenmaa, P., & Tomppo, E. (2002). Impact of sawfly defoliation on growth of Scots pine *Pinus sylvestris* (Pinaceae) and associated economic losses. *Bulletin of Entomological Research*, 92(2), 137–140.
- Maas, W., van Hes, R., Grosscurt, A. C., & Duel, D. H. (1981). Benzoyphenylurea insecticides. In R. Wegler (Ed.), *Chemie der pflanzenschutz und schadlingsbekämpfungsmitt*. Springer, Heidelberg, Germany, pp. 429–470.
- MacLean, D. A. (1980). Vulnerability of fir-spruce stands during uncontrolled spruce budworm outbreaks: A review and discussion. *The Forestry Chronicle*, 56, 213–221.
- Maclean, D. A. (2004). Predicting forest insect disturbance regimes for use in emulating natural disturbance. In A. H. Perera, L. J. Buse, & M. G. Weber (Eds.), *Emulating Natural Forest Landscape Disturbances—Concepts and Applications*. Columbia University Press, New York, NY, US, pp. 69–82.
- MacLean, D. A. (2016). Impacts of insect outbreaks on tree mortality, productivity, and stand development. *The Canadian Entomologist*, 148(S1), S138–S159.
- MacQuarrie, C. J. K., Lyons, D. B., Seehausen, M. L., & Smith, S. M. (2016). A history of biological control in Canadian forests, 1882–2014. *The Canadian Entomologist*, 148(S1), S239–S269.

- Madrid, F. J., & Stewart, R. K. (1981). Impact of diflubenzuron spray on gypsy moth parasitoids in the field. *Journal of Economic Entomology*, 74(1), 1–2.
- Majunke, C. (2016). *Prophylaxe und Therapie von Waldschäden früher und heute—Ein historischer Überblick*. Presented at 2. Tharandter Waldschutzkolloquium, Tharandt, Germany.
- Man, G. (2016). *Major forest insect and disease conditions in the united states: 2014 update: Vol. FS-1078*. US Department of Agriculture, Forest Service, Forest Health Protection, Washington, DC, US.
- Man, R., Kayahara, G. J., Rice, J. A., & MacDonald, G. B. (2008). Response of trembling aspen to partial cutting and subsequent forest tent caterpillar defoliation in a boreal mixedwood stand in northeastern Ontario, Canada. *Canadian Journal of Forest Research*, 38, 1349–1356.
- Manderino, R., Crist, T. O., & Haynes, K. J. (2014). Lepidoptera-specific insecticide used to suppress gypsy moth outbreaks may benefit non-target forest Lepidoptera. *Agricultural and Forest Entomology*, 16(4), 359–368.
- Martin, J.-C., Villemant, C., & Mazet, R. (2002). Utilisation de *Bacillus thuringiensis kurstaki* 3a-3b dans la lutte contre le bombyx disparate et problèmes posés par les migrations de chenilles. *IOBC/wprs Bulletin*, 25(5), 115–122.
- Martinat, P. J., Coffman, C. C., Dodge, K. M., Cooper, R. J., & Whitmore, R. C. (1988). Effect of diflubenzuron on the canopy arthropod community in a central Appalachian forest. *Journal of Economic Entomology*, 81(1), 261–267.
- Martinat, P. J., Jennings, D. T., & Whitmore, R. C. (1993). Effects of diflubenzuron on the litter spider and orthopteroid community in a central Appalachian forest infested with gypsy moth (Lepidoptera: Lymantriidae). *Environmental Entomology*, 22(5), 1003–1008.
- Mason, R. R. (1987). Nonoutbreak species of forest Lepidoptera. In P. Barbosa & J. C. Schultz (Eds.), *Insect Outbreaks*. Academic Press, San Diego, CA, US, pp. 31–57.
- Mason, R. R., Wickman, B. E., & Paul, H. G. (1997). Radial growth response of Douglas-fir and grand fir to larval densities of the Douglas-fir tussock moth and the western spruce budworm. *Forest Science*, 43(2), 194–205.
- Matyjaszczyk, E., Karmilowicz, E., & Skrzecz, I. (2019). How European Union accession and implementation of obligatory integrated pest management influenced forest protection against harmful insects: A case study from Poland. *Forest Ecology and Management*, 433, 146–152.
- McCravy, K. W., Dalusky, M. J., & Berisford, C. W. (2001). Effects of a broad spectrum and biorational insecticides on parasitoids of the Nantucket pine tip moth (Lepidoptera: Tortricidae). *Journal of Economic Entomology*, 94(1), 112–115.

- McManus, M. L. (2007). In the beginning: Gypsy moth in the United States. In P. C. Tobin & L. M. Blackburn (Eds.), *Slow the spread: A national program to manage the gypsy moth*. General Technical Report NRS-6. US Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA, US, pp. 3-13.
- McManus, M. L., & Csóka, G. (2007). History and impact of gypsy moth in North America and comparison to recent outbreaks in Europe. *Acta Silvatica and Lignaria Hungarica*, 3, 47-64.
- McMillin, J. D., & Wagner, M. R. (1997). Chronic defoliation impacts pine sawfly (Hymenoptera: Diprionidae) performance and host plant quality. *Oikos*, 79(2), 357-362.
- Medina, P., Smagghe, G., Budia, F., del Estal, P., Tirry, L., & Viñuela, E. (2002). Significance of penetration, excretion, and transovarial uptake to toxicity of three insect growth regulators in predatory lacewing adults. *Archives of Insect Biochemistry and Physiology*, 51(2), 91-101.
- Meier, P., & Zettel, J. (1997). Cold hardiness in *Entomobrya nivalis* (Collembola, Entomobryidae): Annual cycle of polyols and antifreeze proteins, and antifreeze triggering by temperature and photoperiod. *Journal of Comparative Physiology B*, 167(4), 297-304.
- Mellec, A., & Michalzik, B. (2008). Impact of a pine lappet (*Dendrolimus pini*) mass outbreak on C and N fluxes to the forest floor and soil microbial properties in a Scots pine forest in Germany. *Canadian Journal of Forest Research*, 38, 1829-1841.
- Metcalf, R. L., & Horowitz, A. R. (2014). Insect Control, 1. Fundamentals. In *Ullmann's Encyclopedia of Industrial Chemistry* (pp. 1-23). American Cancer Society.
- Miliczky, E. R., & Osgood, E. A. (1979). *The effects of spraying with Sevin-4-oil® on insect pollinators and pollination in a spruce-fir forest*. Technical Bulletin 90. Life Sciences and Agriculture Experiment Station, University of Maine, Orono, Maine, US.
- Miller, J. C. (1990). Field assessment of the effects of a microbial pest control agent on nontarget Lepidoptera. *American Entomologist*, 35(2), 135-139.
- Miller, J. C. (1992). Effects of a microbial insecticide, *Bacillus thuringiensis kurstaki*, on nontarget Lepidoptera in a spruce budworm-infested forest. *Journal of Research on the Lepidoptera*, 29(4), 267-276.
- Möller, K. (2014). Klimawandel und integrierter Waldschutz – Risikomanagement mit mehr Unbekanntem und weniger Möglichkeiten. *Eberswalder Forstliche Schriftenreihe*, 55, 59-65.
- Möller, K. (2020). Waldschutz in Zeiten von Klimawandel und Fake News. *Eberswalder Forstliche Schriftenreihe*, 69, 22-38.
- Molnár, B. P., Tröger, A., Toshova, T. B., Subchev, M., van Nieukerken, E. J., Koster, J. C. (Sjaak), Szócs, G., Tóth, M., & Francke, W. (2012). Identification of the female-produced

- sex pheromone of *Tischeria ekebladella*, an oak leafmining moth. *Journal of Chemical Ecology*, 38(10), 1298–1305.
- Montgomery, M. E., & Wallner, W. E. (1988). The gypsy moth: A westward migrant. In A. A. Berryman (Ed.), *Dynamics of forest insect populations: Patterns, causes, implications*. Plenum Press, New York, NY, US, pp. 353–375.
- Moran, P. A. P. (1953). The statistical analysis of the Canadian lynx cycle. II. Synchronization and meteorology. *Australian Journal of Zoology*, 1, 291–298.
- Moreau, G., Lucarotti, C. J., Kettela, E. G., Thurston, G. S., Holmes, S. B., Weaver, C., Levin, D. B., & Morin, B. (2005). Aerial application of nucleopolyhedrovirus induces decline in increasing and peaking populations of *Neodiprion abietis*. *Biological Control*, 1(33), 65–73.
- Morinière, J., Balke, M., Doczkal, D., Geiger, M. F., Hardulak, L. A., Haszprunar, G., Hausmann, A., Hendrich, L., Regalado, L., Rulik, B., Schmidt, S., Wägele, J.-W., & Hebert, P. D. N. (2019). A DNA barcode library for 5,200 German flies and midges (Insecta: Diptera) and its implications for metabarcoding-based biomonitoring. *Molecular Ecology Resources*, 19(4), 900–928.
- Mrema, E. J., Rubino, F. M., Brambilla, G., Moretto, A., Tsatsakis, A. M., & Colosio, C. (2013). Persistent organochlorinated pesticides and mechanisms of their toxicity. *Toxicology*, 307, 74–88.
- Muzika, R.-M., & Liebhold, A. M. (2000). A critique of silvicultural approaches to managing defoliating insects in North America. *Agricultural and Forest Entomology*, 2(2), 97–105.
- Naidoo, R., & Lechowicz, M. J. (2001). Effects of gypsy moth on radial growth of deciduous trees. *Forest Science*, 47(3), 338–348.
- Nealis, V. G., & van Frankenhuyzen, K. (1990). Interactions between *Bacillus thuringiensis* Berliner and *Apanteles fumiferane* Vier. (Hymenoptera: Braconidae), a parasitoid of Spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae). *The Canadian Entomologist*, 122(4), 585–594.
- New, T. R. (1987). Biology of the Psocoptera. *Oriental Insects*, 21(1), 1–109.
- Niquidet, K., Tang, J., & Peter, B. (2016). Economic analysis of forest insect pests in Canada. *The Canadian Entomologist*, 148(S1), S357–S366.
- Niwa, C. G., Stelzer, M. J., & Beckwith, R. C. (1987). Effects of *Bacillus thuringiensis* on parasites of western spruce budworm (Lepidoptera: Tortricidae). *Journal of Economic Entomology*, 80(4), 750–753.
- Nothnagle, P. J., & Schutlz, J. C. (1987). What is a forest pest? In P. Barbosa & J. C. Schultz (Eds.), *Insect Outbreaks*. Academic Press, San Diego, CA, US, pp. 59–81.
- Nykanen, H., & Koricheva, J. (2004). Damage-induced changes in woody plants and their effects on insect herbivore performance: A meta-analysis. *Oikos*, 104(2), 247–268.

- Official Journal of the European Union. (2009). *Directive 2009/128/EC of the European Parliament and of the Council of 21 October 2009 establishing a framework for Community action to achieve the sustainable use of pesticides*. L 309, 71–86.
- Ozanne, C. M. P. (2005). Techniques and methods for sampling canopy insects. In S. Leather (Ed.), *Insect sampling in forest ecosystems*. Blackwell Publishing, Oxford, UK, pp. 146–165.
- Page, M., Ryan, R. B., Rappaport, N., & Schmidt, F. (1982). Comparative toxicity of acephate, diflubenzuron, and malathion to larvae of the larch casebearer, *Coleophora laricella* (Lepidoptera, Coleophoridae) and adults of its parasites, *Chrysocharis laricinellae* (Hymenoptera, Eulophidae) and *Dicladocerus nearcticus*. *Environmental Entomology*, 11(3), 730–732.
- Patočka, J. (1980). *Die Raupen und Puppen der Eichenschmetterlinge Mitteleuropas*. Paul Parey, Hamburg, Germany.
- Peacock, J. W., Schweitzer, D. F., Carter, J. L., & Dubois, N. R. (1998). Laboratory assessment of the effects of *Bacillus thuringiensis* on native Lepidoptera. *Environmental Entomology*, 27(2), 450–457.
- Peakall, D. B., Bart, J. R., & Fowle, C. D. (1983). Impacts of aerial application of insecticides on forest birds. *C R C Critical Reviews in Environmental Control*, 13(2), 117–165.
- Perrins, C. M. (1991). Tits and their caterpillar food supply. *Ibis*, 133(s1), 49–54.
- Perry, W. B., Christiansen, T. A., & Perry, S. A. (1997). Response of soil and leaf litter microarthropods to forest application of diflubenzuron. *Ecotoxicology*, 6(2), 87–99.
- Petercord, R. (2013). Ohne Waldschutz keine forstliche Nachhaltigkeit. *LWF Wissen*, 72, 34–38.
- Pretzsch, H., Biber, P., Uhl, E., Dahlhausen, J., Rötzer, T., Caldentey, J., Koike, T., van Con, T., Chavanne, A., Seifert, T., Toit, B. du, Farnden, C., & Pauleit, S. (2015). Crown size and growing space requirement of common tree species in urban centres, parks, and forests. *Urban Forestry & Urban Greening*, 14(3), 466–479.
- Prien, S. (2016). Klassischer Forstschutz und Ökologischer Waldschutz. In S. Prien (Ed.), *Ökologischer Waldschutz—Für eine Biozidfreie Waldwirtschaft*. Eugen Ulmer Verlag, Stuttgart, Germany, pp. 15–30.
- Prinzing, A., Stork, N. E., Adis, J., & Didham, R. K. (1997). Spatial and temporal use of microhabitats as a key strategy for the colonization of tree bark by *Entomobrya nivalis* L. (Collembola: Entomobryidae). In *Canopy Arthropods*. Chapman & Hall, London, UK, pp. 453–476.
- Pschorn-Walcher, H. (1977). Biological control of forest insects. *Annual Review of Entomology*, 22, 1–22.

- Pureswaran, D. S., Roques, A., & Battisti, A. (2018). Forest insects and climate change. *Current Forestry Reports*, 4(2), 35–50.
- R Core Team. (2020). *R: A language and environment for statistical computing. Version 4.0.3*. <https://www.r-project.org/>
- Raffa, K. F., Grégoire, J.-C., & Staffan Lindgren, B. (2015). Natural history and ecology of bark beetles. In F. E. Vega & R. W. Hofstetter (Eds.), *Bark Beetles*. Academic Press, San Diego, CA, US, pp. 1–40.
- Raimondo, S., Turcáni, M., Patočka, J., & Liebhold, A. M. (2004). Interspecific synchrony among foliage-feeding forest Lepidoptera species and the potential role of generalist predators as synchronizing agents. *Oikos*, 107(3), 462–470.
- Ranacher, L., Sedmik, A., & Schwarzbauer, P. (2020). *Public perceptions of forestry and the forest-based bioeconomy in the European Union*. European Forest Institute, Joensuu, Finland.
- Rastall, K., Kondo, V. A., Strazanac, J. S., & Butler, L. (2003). Lethal effects of biological insecticide applications on nontarget Lepidopterans in two Appalachian forests. *Environmental Entomology*, 32(6), 1364–1369.
- Ratnasingham, S., & Hebert, P. D. N. (2013). A DNA-based registry for all animal species: The barcode index number (BIN) system. *PLOS ONE*, 8(7), e66213.
- Reardon, R., Podgwaite, J., & Zerillo, R. (2012). *Gypcheck environmentally safe viral insecticide for gypsy moth control*. Department of Agriculture, Forest Service, Forest Health Technology Enterprise Team, Morgantown, WV, US.
- Redford, K. H., & Dorea, J. G. (1984). The nutritional value of invertebrates with emphasis on ants and termites as food for mammals. *Journal of Zoology*, 203(3), 385–395.
- Redman, A. M., & Scriber, J. M. (2000). Competition between the gypsy moth, *Lymantria dispar*, and the northern tiger swallowtail, *Papilio canadensis*: Interactions mediated by host plant chemistry, pathogens, and parasitoids. *Oecologia*, 125(2), 218–228.
- Régnière, J., Delisle, J., Dupont, A., & Trudel, R. (2019). The impact of moth migration on apparent fecundity overwhelms mating disruption as a method to manage spruce budworm populations. *Forests*, 10(9), 775.
- Régnière, J., & Nealis, V. G. (2007). Ecological mechanisms of population change during outbreaks of the spruce budworm. *Ecological Entomology*, 32(5), 461–477.
- Régnière, J., Nealis, V. G., & Porter, K. (2009). Climate suitability and management of the gypsy moth invasion into Canada. *Biological Invasions*, 11(1), 135–148.
- Reisch, J. (1974). *Waldschutz und Umwelt*. Springer-Verlag, Berlin, Heidelberg.
- Retnakaran, A., Granett, J., & Robertson, J. (1980). Possible physiological mechanisms for the differential susceptibility of two forest Lepidoptera to diflubenzuron. *Journal of Insect Physiology*, 26(6), 385–390.

- Rico, A., & van den Brink, P. J. (2015). Evaluating aquatic invertebrate vulnerability to insecticides based on intrinsic sensitivity, biological traits, and toxic mode of action. *Environmental Toxicology and Chemistry*, 34(8), 1907–1917.
- Riedl, V., Agatz, A., Benstead, R., & Ashauer, R. (2018). A standardized tritrophic small-scale system (TriCosm) for the assessment of stressor-induced effects on aquatic community dynamics. *Environmental Toxicology and Chemistry*, 37(4), 1051–1060.
- Rieske, L. K., & Buss, L. J. (2001). Effects of gypsy moth suppression tactics on litter- and ground-dwelling arthropods in the central hardwood forests of the Cumberland Plateau. *Forest Ecology and Management*, 149(1–3), 181–195.
- Rodenhouse, N. L., & Holmes, R. T. (1992). Results of experimental and natural food reductions for breeding black-throated blue warblers. *Ecology*, 73(1), 357–372. JSTOR.
- Roeben, V., Oberdoerster, S., Rakel, K. J., Liesy, D., Capowicz, Y., Ernst, G., Preuss, T. G., Gergs, A., & Oberdoerster, C. (2020). Towards a spatiotemporally explicit toxicokinetic-toxicodynamic model for earthworm toxicity. *Science of The Total Environment*, 722, 137673.
- Röhle, H. (1986). Vergleichende Untersuchungen zur Ermittlung der Genauigkeit bei der Ablotung von Kronenradien mit dem Dachlot und durch senkrechtes Anvisieren des Kronenrandes (Hochblick-Messung). *Forstarchiv*, 57(1), 67–71.
- Rohrbaugh, P. W. (1934). Penetration and accumulation of petroleum spray oils in the leaves, twigs, and fruit of citrus trees. *Plant Physiology*, 9(4), 699–730.
- Root, R. B., & Skelsey, J. J. (1969). Biotic factors involved in crucifer aphid outbreaks following insecticide application. *Journal of Economic Entomology*, 62(1), 223–233.
- Roques, A. (2015). *Processionary Moths and Climate Change: An Update*. Springer Netherlands, Dordrecht, The Netherlands.
- Roslin, T., & Roland, J. (2005). Competitive effects of the forest tent caterpillar on the gallers and leaf-miners of trembling aspen. *Écoscience*, 12(2), 172–182.
- Rubach, M. N., Ashauer, R., Buchwalter, D. B., De Lange, H., Hamer, M., Preuss, T. G., Töpke, K., & Maund, S. J. (2011). Framework for traits-based assessment in ecotoxicology. *Integrated Environmental Assessment and Management*, 7(2), 172–186.
- Rytkönen, S., Vesterinen, E. J., Westerduin, C., Leviäkangas, T., Vatka, E., Mutanen, M., Välimäki, P., Hukkanen, M., Suokas, M., & Orell, M. (2019). From feces to data: A metabarcoding method for analyzing consumed and available prey in a bird-insect food web. *Ecology and Evolution*, 9(1), 631–639.
- Sample, B. E., Butler, L., & Whitmore, R. C. (1993). Effects of an operational application of Dimilin® on non-target insects. *The Canadian Entomologist*, 125(2), 173–179.
- Sample, B. E., Butler, L., Zivkovich, C., Whitmore, R. C., & Reardon, R. C. (1996). Effect of *Bacillus thuringiensis* Berliner var. *Kurstaki* and defoliation by the gypsy moth

- [*Lymantria dispar* (L.) (Lepidoptera: Lymantriidae)] on native arthropods in West Virginia. *The Canadian Entomologist*, 128(4), 573–592.
- Sample, B. E., Cooper, R. J., & Whitmore, R. C. (1993). Dietary shifts among songbirds from a diflubenzuron-treated forest. *The Condor*, 95(3), 616–624.
- Schneider, N. (2007). Staubläuse—Psocoptères—Psocoptera. In M. Meyer & E. Carrières (Eds.), *Inventaire de la biodiversité dans la forêt “Schnellert” (Commune de Berdorf)—Erfassung der Biodiversität im Waldgebiet “Schnellert” (Gemeinde Berdorf)*. Musée national d’histoire naturelle, Luxembourg, Luxembourg, pp. 255–257.
- Schoenmaker, A., Cusson, M., & van Frankenhuyzen, K. (2001). Interactions between *Bacillus thuringiensis* and parasitoids of late-instar larvae of the spruce budworm (Lepidoptera: Tortricidae). *Canadian Journal of Zoology*, 79, 1697–1703.
- Schowalter, T. D. (2012). Insect herbivore effects on forest ecosystem services. *Journal of Sustainable Forestry*, 31(6), 518–536.
- Schwenke, W. (1973). Waldschutz und DDT-Verbot. *Anzeiger für Schädlingskunde, Pflanzen- und Umweltschutz*, 46(4), 49–52.
- Scriber, J. M. (2004). Non-target impacts of forest defoliator management options: Decision for no spraying may have worse impacts on non-target Lepidoptera than *Bacillus thuringiensis* insecticides. *Journal of Insect Conservation*, 8(2), 241–261.
- Seibold, S., Gossner, M. M., Simons, N. K., Blüthgen, N., Müller, J., Ambarlı, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J. C., Linsenmair, K. E., Nauss, T., Penone, C., Prati, D., Schall, P., Schulze, E.-D., Vogt, J., Wöllauer, S., & Weisser, W. W. (2019). Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature*, 574(7780), 671–674.
- Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., Lexer, M. J., Trotsiuk, V., Mairota, P., Svoboda, M., Fabrika, M., Nagel, T. A., & Reyer, C. P. O. (2017). Forest disturbances under climate change. *Nature Climate Change*, 7(6), 395–402.
- Sharov, A. A., Leonard, D., Liebhold, A. A., Roberts, E. A., & Dickerson, W. (2002). “Slow the spread”: A national program to contain the gypsy moth. *Journal of Forestry*, 100(5), 30–36.
- Short, I., & Champion, J. (2014). Coppice-with-standards: An old silvicultural system with new potential? *Forestry & Energy Review*, 4(1), 42–44.
- Sibley, P. K., Kaushik, N. K., & Kreutzweiser, D. P. (1991). Impact of a pulse application of permethrin on the macroinvertebrate community of a headwater stream. *Environmental Pollution*, 70(1), 35–55.

- Simmons, M. J., Lee, T. D., Ducey, M. J., Elkinton, J. S., Boettner, G. H., & Dodds, K. J. (2014). Effects of invasive winter moth defoliation on tree radial growth in eastern Massachusetts, USA. *Insects*, 5(2), 301–318.
- Smagghe, G., Carton, B., Wesemael, W., Ishaaya, I., & Tirry, L. (1999). Ecdysone agonists – mechanism of action and application on *Spodoptera* species. *Pesticide Science*, 55(3), 386–389.
- Smagghe, G., & Degheele, D. (1994). Action of a novel nonsteroidal ecdysteroid mimic, tebufenozide (RH-5992), on insects of different orders. *Pest Management Science*, 42(2), 85–92.
- Smith, D. I., & Lockwood, J. A. (2003). Horizontal and trophic transfer of diflubenzuron and fipronil among grasshoppers (*Melanoplus sanguinipes*) and between grasshoppers and darkling beetles (Tenebrionidae). *Archives of Environmental Contamination and Toxicology*, 44(3), 377–382.
- Smith, R. F. (1986). Efficacy of selected insecticides against *Liriomyza trifolii* (Burgess) (Diptera: Agromyzidae), a leafminer of *Chrysanthemum*. *The Canadian Entomologist*, 118(8), 761–766.
- Smitley, D. R., Bauer, L. S., Hajek, A. E., Sapio, F. J., & Humber, R. A. (1995). Introduction and establishment of *Entomophaga maimaiga*, a fungal pathogen of gypsy moth (Lepidoptera: Lymantriidae) in Michigan. *Environmental Entomology*, 24(6), 1685–1695.
- Sobek, S., Tschardt, T., Scherber, C., Schiele, S., & Steffan-Dewenter, I. (2009). Canopy vs. understory: Does tree diversity affect bee and wasp communities and their natural enemies across forest strata? *Forest Ecology and Management*, 258(5), 609–615.
- Southwood, T. R. E., Wint, G. R. W., Kennedy, C. E. J., & Greenwood, S. R. (2004). Seasonality, abundance, species richness and specificity of the phytophagous guild of insects on oak (*Quercus*) canopies. *European Journal of Entomology*, 101(1), 43–50.
- Straw, N. A. (1996). The impact of pine looper moth, *Bupalus piniaria* L. (Lepidoptera; Geometridae) on the growth of Scots pine in Tentsmuir Forest, Scotland. *Forest Ecology and Management*, 87(1), 209–232.
- Sundaram, A., Sundaram, K. M. S., Nott, R., Curry, J., & Sloane, L. (1997). Persistence of *Bacillus thuringiensis* deposits in oak foliage, after aerial application of Foray® 48b using rotary and pressure atomizers. *Journal of Environmental Science and Health, Part B*, 32(1), 71–105.
- Sundaram, K. M. S. (1995). Persistence and fate of tebufenozide (RH-5992) insecticide in terrestrial microcosms of a forest environment following spray application of two Mimic® formulations. *Journal of Environmental Science and Health, Part B*, 30(3), 321–358.
- Szczepaniec, A., Raupp, M. J., Parker, R. D., Kerns, D., & Eubanks, M. D. (2013). Neonicotinoid insecticides alter induced defenses and increase susceptibility to spider mites in distantly related crop plants. *PLoS One*, 8(5), e62620.

- Tack, A. J. M., Gripenberg, S., & Roslin, T. (2012). Cross-kingdom interactions matter: Fungal-mediated interactions structure an insect community on oak. *Ecology Letters*, *15*(3), 177–185.
- Tanhuanpää, M., Ruohomäki, K., Kaitaniemi, P., & Klemola, T. (1999). Different impact of pupal predation on populations of *Epirrita autumnata* (Lepidoptera; Geometridae) within and outside the outbreak range. *Journal of Animal Ecology*, *68*(3), 562–570.
- Tcheslavskaia, K. S., Thorpe, K. W., Brewster, C. C., Sharov, A. A., Leonard, D. S., Reardon, R. C., Mastro, V. C., Sellers, P., & Roberts, E. A. (2005). Optimization of pheromone dosage for gypsy moth mating disruption. *Entomologia Experimentalis et Applicata*, *115*(3), 355–361.
- Thompson, D. G. (2011). Ecological impacts of major forest-use pesticides. In F. Sánchez-Bayo, P. J. van den Brink, & R. M. Mann (Eds.), *Ecological impacts of toxic chemicals*. Bentham eBooks, Sharjah, EAU, pp. 88–110.
- Twery, M. J. (1991). Effects of defoliation by gypsy moth. In K. W. Gottschalk, M. J. Twery, & S. I. Smith (Eds.), *Proceedings, U.S. Department of Agriculture interagency gypsy moth research review 1990*. General Technical Report NE-146. U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Radnor, PA, US, pp. 27–39.
- USDA Forest Service. (2020). *Gypsy Moth Digest 2.0.03*.
<https://apps.fs.usda.gov/nicportal/gmdigest/cfm/dsp/dspGypsyMothDigestHome.cfm>
- van den Berg, H., Zaim, M., Yadav, R. S., Soares, A., Ameneshewa, B., Mnzava, A., Hii, J., Dash, A. P., & Ejov, M. (2012). Global trends in the use of insecticides to control vector-borne diseases. *Environmental Health Perspectives*, *120*(4), 577–582.
- van den Berg, S. J. P., Maltby, L., Sinclair, T., Liang, R., & van den Brink, P. J. (2021). Cross-species extrapolation of chemical sensitivity. *Science of The Total Environment*, *753*, 141800.
- van den Brink, P. J., Baird, D. J., Baveco, H. (JM), & Focks, A. (2013). The use of traits-based approaches and eco(toxico)logical models to advance the ecological risk assessment framework for chemicals. *Integrated Environmental Assessment and Management*, *9*(3), e47–e57.
- van Frankenhuyzen, K. (2000). Application of *Bacillus thuringiensis* in forestry. In J.-F. Charles, A. Delécluse, & C. Nielsen-Le Roux (Eds.), *Entomopathogenic Bacteria: From Laboratory to Field Application*. Springer Netherlands, Dordrecht, The Netherlands, pp. 371–382.
- van Frankenhuyzen, K., Lucarotti, C., & Lavallée, R. (2016). Canadian contributions to forest insect pathology and to the use of pathogens in forest pest management. *The Canadian Entomologist*, *148*(S1), S210–S238.
- Villemant, C. (2010). Le Bombyx disparate en Europe et en Afrique du Nord—Historique des gradations, dynamique des populations et lutte. In O. Himmi (Ed.), *Entomologie et*

- developpement durable, Tome I. Actes de la CIFE VI. Vol. 47.* Mohammed V University, Rabat, Morocco, pp. 97–106.
- Wagner, D. L., Peacock, J. W., Carter, J. L., & Talley, S. E. (1996). Field assessment of *Bacillus thuringiensis* on nontarget Lepidoptera. *Environmental Entomology*, 25(6), 1444–1454.
- Wagner, R. G., Flynn, J., & Gregory, R. (1998). Public perceptions of risk and acceptability of forest vegetation management alternatives in Ontario. *The Forestry Chronicle*, 74(5), 720–727.
- Wallner, W. E., Dubois, N. R., & Grinberg, P. S. (1983). Alteration of parasitism by *Rogas lymantriae* (Hymenoptera: Braconidae) in *Bacillus thuringiensis*-stressed gypsy moth (Lepidoptera: Lymantriidae) hosts. *Journal of Economic Entomology*, 76(2), 275–277.
- Wang, C., Strazanac, J. S., & Butler, L. (2000). Abundance, diversity, and activity of ants (Hymenoptera: Formicidae) in oak-dominated mixed Appalachian forests treated with microbial pesticides. *Environmental Entomology*, 29(3), 579–586.
- Webb, R. E., Shapiro, M., Podgwaite, J. D., Reardon, R. C., Tatman, K. M., Venables, L., & Kolodny-Hirsch, D. M. (1989). Effect of aerial spraying with Dimilin, Dipel, or Gypchek on two natural enemies of the gypsy moth (Lepidoptera: Lymantriidae). *Journal of Economic Entomology*, 82(6), 1695–1701.
- Wepprich, T., Adrion, J. R., Ries, L., Wiedmann, J., & Haddad, N. M. (2019). Butterfly abundance declines over 20 years of systematic monitoring in Ohio, USA. *PLOS ONE*, 14(7), e0216270.
- Weseloh, R. M. (1984). Effects of the feeding inhibitor Plictran and low *Bacillus thuringiensis* Berliner doses on *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae): Implications for *Cotesia melanoscelus* (Ratzeburg) (Hymenoptera: Braconidae). *Environmental Entomology*, 13(5), 1371–1376.
- Weseloh, R. M. (1985). Changes in population size, dispersal behavior, and reproduction of *Calosoma sycophanta* (Coleoptera: Carabidae), associated with changes in gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae), abundance. *Environmental Entomology*, 14(3), 370–377.
- Weseloh, R. M., Andreadis, T. G., Moore, R. E. B., Anderson, J. F., Dubois, N. R., & Lewis, F. B. (1983). Field confirmation of a mechanism causing synergism between *Bacillus thuringiensis* and the gypsy moth parasitoid *Apanteles melanoscelus*. *Journal of Invertebrate Pathology*, 41, 99–103.
- West, C. (1985). Factors underlying the late seasonal appearance of the lepidopterous leaf-mining guild on oak. *Ecological Entomology*, 10(1), 111–120.
- Westwood, R., Saunders, D., Westwood, A. R., & Holliday, N. J. (2019). Effects of tebufenozide on the assemblage of moths (Lepidoptera) in an operational spruce budworm (Lepidoptera: Tortricidae) suppression programme. *The Canadian Entomologist*, 151(5), 651–676.

- Whitney, C. (2012). The silent decade: Why it took ten years to ban DDT in the United States. *The Virginia Tech Undergraduate Historical Review*, 1, 10–26.
- Williams, R. (2010). *Oak galls in Britain*. Vanellus Publications.
- Wimmer, M. J., Smith, R. R., Wellings, D. L., Toney, S. R., Faber, D. C., Miracle, J. E., Carnes, J. T., & Rutherford, A. B. (1993). Persistence of diflubenzuron on Appalachian forest leaves after aerial application of Dimilin. *Journal of Agriculture and Food Chemistry*, 41, 2184–2190.
- Winter, K., & Glatz, K. (2000). Auswirkungen einer Frostspannerbekämpfung auf die Bodenfauna eines Eichenwaldes. *Journal of Pest Science*, 73, 155–162.
- Work, T. T., & McCullough, D. G. (2000). Lepidopteran communities in two forest ecosystems during the first gypsy moth outbreaks in northern Michigan. *Environmental Entomology*, 29(5), 884–900.
- Wulf, A., & Graser, E. (1996). Gypsy moth outbreaks in Germany and neighboring countries. *Nachrichtenblatt Des Deutschen Pflanzenschutzdienstes*, 48(12), 265–269.
- Zúbrik, M., Kunca, A., Kulfan, J., Rell, S., Nikolov, C., Galko, J., Vakula, J., Gubka, A., Leontovyč, R., Konôpka, B., Lalík, M., Longauerová, V., Sitková, Z., Liška, J., Zach, P., Barta, M., & Holuša, J. (2021). Occurrence of gypsy moth (*Lymantria dispar* L.) in the Slovak Republic and its outbreaks during 1945–2020. *Central European Forestry Journal*, 67, 55–71.

Appendix A.

A methodological analysis of insecticide impact assessment studies in forests

Literature search

Non-target impact studies were retrieved from scientific literature databases Web of Science, Scopus and Google Scholar. The search was performed on article title, abstract and article keywords in Web of Science and Scopus, as whole text search in Google Scholar. I used the following search string:

“((insecticid* OR diflubenzuron OR tebufenozide OR “Bacillus thuringiensis” OR fenitrothion OR pyrethr*) AND (forest* OR woodland) AND (*arthropod* OR insect* OR lepidopter* OR coleopter* OR formicid* OR orthopter* OR araneae OR spider) AND ("non-target" OR nontarget OR "side effect"))”

The search was repeated in German and French language to increase the comprehensiveness of the results.

Inclusion criterion

The following criteria were used to further filter relevant studies for the analysis:

- **Field experiment** (excluding laboratory, mesocosm or semi-field experiments)
- **Forest ecosystems** (excluding studies on the effects of spray drift to other ecosystems)
- **Insecticides applied by aircraft** (excluding studies using ground sprays, soil injections or soil drenches)
- **Non-target effects** (excluding efficacy studies, including pest-parasitoid experiments)
- **Terrestrial arthropod surveys** (excluding studies on vertebrates, soil organisms and aquatic fauna)

A total of 44 studies corresponding to 32 experiments were retained for the analysis (Table A1).

Table A1. Methodological data of the selected studies, including publication records, dominant tree species, target (pest) species, insecticide(s), number of true replicates, use of blocking (T = true; F = false). The “sister publications” indicate different publications based on the same experiment.

Author	Year	Publication	Country	Dominant tree species	Target species	Insecticide	No. of rep.	Blocking	Sister publications
Leza et al.	2020	International Journal of Pest Management	ES	<i>Quercus ilex</i>	<i>Lymantria dispar</i>	BTK Diflubenzuron Deltamethrin alpha-cyPermethrin etofenprox	1*	F	-
Westwood et al.	2019	The Canadian Entomologist	CA	Mixed softwood	<i>Choristoneura fumiferana</i>	Tebufenozide	6	F	Saunders 2003
Maderino et al.	2014	Agricultural and Forest Entomology	US	<i>Quercus sp.</i> <i>Carya sp.</i>	<i>Lymantria dispar</i>	BTK	5	F	Wayland et al. 2015
Kwon	2008	Archives of Environmental Contamination and Toxicology	KR	<i>Pinus densiflora</i> <i>Pinus thunbergii</i>	<i>Monochamus sp.</i>	Fenitrothion	2	T	-
Boulton et al.	2007	Environmental Toxicology and Chemistry	CA	<i>Quercus garryana</i>	<i>Lymantria dispar</i>	BTK	1*	F	Boulton et al. 2004
Addison et al.	2006	Canadian Journal of Forest Research	CA	<i>Pseudotsuga menziesii</i>	<i>Choristoneura freemani</i>	BTK	1*	F	-
Lynkiene	2006	Baltic Forestry	LT	<i>Pinus sylvestris</i>	<i>Panolis flammea</i>	cypermethrin	1*	F	-
Głowacka	2005	Folia Forestalia Polonica, Series A	PL	<i>Pinus sylvestris</i>	<i>Lymantria monacha</i> <i>Dendrolimus pini</i> <i>Panolis flammea</i>	Diflubenzuron Teflubenzuron Novaluron	1	F	-
Schönfeld et al.	2005	Forstliche Forschungsberichte München	DE	<i>Quercus sp.</i> <i>Carpinus betulus</i>	<i>Lymantria dispar</i>	Diflubenzuron	1*	F	-
Wanner	2005	Journal of Pest Science	DE	<i>Pinus sylvestris</i>	<i>Lymantria monacha</i>	Teflubenzuron Lambda-cyhalothrin	2	F	-
Lynkiene	2004	Miškininkystė	LT	<i>Pinus sylvestris</i>	<i>Panolis flammea</i>	BTK Cypermethrin	1	F	-
Rastall et al.	2003	Environmental Entomology	US	<i>Quercus alba</i> <i>Acer rubrum</i> <i>Carya sp.</i>	<i>Lymantria dispar</i>	BTK MNPV	6	F	Strazanac & Butler 2005 Wang et al. 2000
Rieske & Buss	2001	Forest Ecology and Management	US	<i>Quercus sp.</i> <i>Acer sp.</i>	<i>Lymantria dispar</i>	BTK Diflubenzuron	4	T	-
Winter & Glatz	2000	Journal of Pest Science	DE	<i>Quercus sp.</i> <i>Carpinus betulus</i>	<i>Operophtera brumata</i>	BTK Alpha-cypermethrin	1	F	-
Luciano & Lentini	1999	IOBC/wprs Bulletin	IT	<i>Quercus suber</i>	<i>Lymantria dispar</i>	BTK	1	F	-
Jäkel & Roth	1998	Proceedings Soil Zoological Problems in Central Europe	DE	<i>Pinus sylvestris</i>	<i>Lymantria monacha</i> <i>Dendrolimus pini</i>	BTK Diflubenzuron	1	F	Jäkel & Roth 1999
Butler et al.	1997	Environmental Entomology	US	<i>Quercus sp.</i>	<i>Lymantria dispar</i>	Tebufenozide	3	F	-
Butler et al.	1997	Journal of Economic Entomology	US	Mixed hardwood	<i>Lymantria dispar</i>	Diflubenzuron	2	F	Barrows et al. 1994 Griffith et al. 2000 Cochran & Poling 1995 Perry et al. 1997

* Pseudoreplicated studies

Table A1. Methodological data of the selected studies (continued).

Author	Year	Publication	Country	Dominant tree species	Target species	Insecticide	No. of rep.	Blocking	Sister publications
Hacker	1997	Beiträge zur bayerischen Entomofaunistik	DE	<i>Quercus sp.</i>	<i>Lymantria dispar</i>	Diflubenzuron	1	F	-
Sample et al.	1996	The Canadian Entomologist	US	<i>Quercus sp.</i> <i>Carya sp.</i> <i>Pinus sp.</i>	<i>Lymantria dispar</i>	BTK	12	F	Butler et al. 1995
Wagner et al.	1996	Environmental Entomology	US	<i>Quercus sp.</i> <i>Acer rubrum</i> <i>Liriodendron tulipifera</i>	<i>Lymantria dispar</i>	BTK	5	T	-
Głowacka	1995	Folia Forestalia Polonica, Series A	PL	<i>Pinus sylvestris</i>	<i>Lymantria monacha</i>	BTK Diflubenzuron Deltamethrin Alpha-cypermethrin Etofenprox	10	F	-
Kienner	1994	Gesunde Pflanzen	DE	<i>Quercus sp.</i>	<i>Operophtera brumata</i> <i>Tortrix viridana</i>	Diflubenzuron	6	T	-
Lih et al.	1994	Proceeding 1994 Annual Gypsy Moth Review	US	<i>Quercus sp.</i>	<i>Lymantria dispar</i>	BTK	1*	F	-
Sample et al.	1993	The Canadian Entomologist	US	<i>Quercus sp.</i> <i>Carya sp.</i> <i>Pinus sp.</i>	<i>Lymantria dispar</i>	Diflubenzuron	1*	F	-
Walsh et al.	1993	Journal of Applied Entomology	UK	<i>Pinus contorta</i>	<i>Panolis flammea</i>	Fenitrothion	1	F	-
Miller et al.	1992	Journal of Research on the Lepidoptera	US	<i>Pseudotsuga menziesii</i>	<i>Choristoneura occidentalis</i>	BTK	1*	F	-
Miller et al.	1990	American Entomologist	US	<i>Quercus garryana</i>	<i>Lymantria dispar</i>	BTK	3	F	-
Martinat et al.	1988	Journal of Economic Entomology	US	<i>Acer rubrum</i> <i>Quercus sp.</i>	<i>Lymantria dispar</i>	Diflubenzuron	4	F	Martinat et al. 1993
Everts et al.	1983	Archives of Environmental Contamination and Toxicology	IC	ND	<i>Glossina sp.</i>	Deltamethrin Permethrin	2	F	-
Marshall	1979	Recent Advances in Acarology	CA	<i>Pseudotsuga menziesii</i>	<i>Orgyia pseudotsugata</i>	Diflubenzuron	2	T	-
Hoffmann et al.	1949	Ecological Monographs	US	<i>Acer rubrum</i> <i>Quercus alba</i>	<i>Lymantria dispar</i>	DDT	2	F	-

* Pseudoreplicated studies

Appendix B: Chapter 1

Assessing insecticide effects in forests: a tree-level approach using Unmanned Aerial Vehicles

This chapter was published as a research article in the *Journal of Economic Entomology* 112(6): 2686-2694 (2019).

The article is available upon request (please contact benjamin.leroy@tum.de) and online from the publisher's website (<https://doi.org/10.1093/jee/toz235>).

Appendix C: Chapter 2

Side-effects of insecticides on leaf-miners and gall-inducers depend on species ecological traits and competition with leaf-chewers

This chapter was published as a research article in *Environmental Toxicology and Chemistry* 40(4): 1171-1187 (2021).

The article is available upon request (please contact benjamin.leroy@tum.de) and online from the publisher's website (<https://doi.org/10.1002/etc.4969>).

Appendix D: Chapter 3

Metabarcoding of canopy arthropods reveals negative impacts of forestry insecticides on community structure across multiple taxa

The article is available upon request (please contact benjamin.leroy@tum.de).

Appendix E: Chapter 4

Relative impacts of gypsy moth outbreaks and insecticide treatments on forest resources and ecosystems: an experimental approach

This chapter was published as a registered report in *Ecological Solutions and Evidence* 2(1): e12045 (2021).

The article is available upon request (please contact benjamin.leroy@tum.de) and online from the publisher's website (<https://doi.org/10.1002/2688-8319.12045>).