

ROBIN GIELEN

Diversity and ecological role of  
pathogenic fungi in insect populations



DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

**425**

DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS  
425

**ROBIN GIELEN**

Diversity and ecological role of pathogenic  
fungi in insect populations



UNIVERSITY OF TARTU  
Press

Department of Zoology, Institute of Ecology and Earth Sciences,  
Faculty of Science and Technology, University of Tartu, Estonia

Dissertation was accepted for the commencement of the degree of *Doctor philosophiae* in zoology and ecology at the University of Tartu on 30.08.2023 by the Scientific Council of the Institute of Ecology and Earth Sciences, University of Tartu

Supervisors: Prof. Toomas Tammaru, University of Tartu, Estonia  
Dr. Kadri Põldmaa, University of Tartu, Estonia

Opponent: Dr. Nicolai V. Meyling, University of Copenhagen, Denmark

Commencement: Room 127, J. Liivi 2, Tartu, on 14 November 2023 at 10.15 a.m.

Publication of this thesis is granted by the Institute of Ecology and Earth Sciences,  
University of Tartu

ISSN 1024-6479 (print)  
ISBN 978-9916-27-346-3 (print)  
ISSN 2806-2140 (pdf)  
ISBN 978-9916-27-347-0 (pdf)

Copyright: Robin Gielen, 2023

University of Tartu Press  
[www.tyk.ee](http://www.tyk.ee)

# CONTENTS

LIST OF PUBLICATIONS .....	6
1. INTRODUCTION.....	7
1.1 Drivers of insect population dynamics.....	7
1.2 Predators of insects .....	8
1.3 Pathogens of insects .....	9
1.4 Entomopathogenic fungi as insect mortality agents.....	11
1.5 Aims of the thesis.....	14
2. MATERIAL AND METHODS .....	16
2.1 Studied insects .....	16
2.2 Study design.....	18
2.2.1 Using existing data .....	18
2.2.2 Insect rearing in semi-natural conditions.....	18
2.2.3 Survey of natural Lepidoptera populations.....	19
2.3 Identification of the fungi .....	20
2.4 Data analysis .....	20
3. RESULTS AND DISCUSSION .....	21
3.1 Diversity and host specialization of entomopathogenic fungi infecting herbivorous Lepidoptera.....	21
3.2 Mortality of herbivorous insects attributable to fungal entomopathogens .....	27
3.3 Do entomopathogenic fungi have a regulatory role in insect populations? .....	28
3.4 Do entomopathogenic fungi create selective pressures on insect traits?.....	29
4. CONCLUSIONS.....	31
SUMMARY IN ESTONIAN .....	32
ACKNOWLEDGEMENTS .....	35
REFERENCES.....	36
PUBLICATIONS .....	43
CURRICULUM VITAE .....	114
ELULOOKIRJELDUS.....	116

## LIST OF PUBLICATIONS

This thesis is the summary of the following papers, which are referred to in the thesis by their Roman numerals I–V.

- I Gielen, R.**, Meister, H., Tammaru, T., Põldmaa, K. 2021. Fungi recorded on folivorous Lepidoptera: high diversity despite moderate prevalence. *Journal of Fungi* 7 (1). <https://doi.org/10.3390/jof7010025>
- II Gielen, R.**, Põldmaa, K., Tammaru, T. 2022. In search of ecological determinants of fungal infections: A semi-field experiment with folivorous moths. *Ecology and Evolution* 12 (5). <https://doi.org/10.1002/ece3.8926>.
- III Gielen, R.**, Robledo, G., Zapata, A.I., Tammaru, T., Põldmaa, K. 2022. Entomopathogenic fungi infecting lepidopteran larvae: a case from Central Argentina. *Life* 12 (7). <https://doi.org/10.3390/life12070974>.
- IV Gielen, R.**, Teder, T., Põldmaa, K., Tammaru, T. 2023. Assemblage of entomopathogenic fungi infesting immature stages of Noctuidae (Lepidoptera): High diversity but low effect on host populations. *European Journal of Entomology* 120. <https://doi.org/10.14411/eje.2023.023>
- V Gielen, R.**, Ude, K., Kaasik, A., Põldmaa, K., Teder, T., Tammaru, T. Entomopathogenic fungi as a mortality agent in insect populations: a quantitative review. *Manuscript*

Author's contribution to the studies (\* denotes a moderate contribution, \*\* a high contribution, \*\*\* a leading role)

	I	II	III	IV	V
Original idea	**	**	**	*	**
Study design	***	***	***	**	***
Data collection	***	***	***	***	**
Data analysis	***	***	***	***	**
Manuscript preparation	***	***	***	***	***

# 1. INTRODUCTION

## 1.1 Drivers of insect population dynamics

Many insects are characterized by strong fluctuations in the density of their populations which may span over several orders of magnitude (Price et al., 2011; Speight et al., 2008). While density-independent factors (primarily, weather-related phenomena) have often a strong impact on the demography of insect populations, completely stochastic and high order (chaotic) dynamics is uncommon in natural populations of insects. This suggests that insect populations are still governed by basic feedback architectures (Berryman, 2003). Today, both bottom-up and top-down forces are acknowledged to have an impact on population dynamics, distribution and evolution of herbivorous insects; however, we still do not understand how does the relative weight of these forces vary across biomes, habitats and ecological guilds of insects (Vidal and Murphy, 2018).

Bottom-up effects are frequently detected in studies on herbivorous insects. Food plants can affect the insects' population dynamics via the quality or (more rarely) the quantity of the food or through indirect effects, like chemical or mechanical defense, or just by their distribution and abundance (Price et al., 2011; Vidal and Murphy, 2018; Wilkinson and Sherratt, 2016); the bottom-up effects appear to be stronger in food specialists compared to food generalists (Vidal and Murphy, 2018). Bottom-up processes are also among the most widely acknowledged explanations for why herbivores do not destroy all vegetation (Wilkinson and Sherratt, 2016). It is generally accepted that plant-related factors primarily influence herbivore survival in early developmental stages whereas natural enemies have greater impact in the later stages (Cornell and Hawkins, 1995; Speight et al., 2008). At a more quantitative level, however, recent studies (Roslin et al., 2017; Vidal and Murphy, 2018) have concluded that bottom-up forces are still typically substantially weaker than top-down forces, which emphasizes the importance of natural enemies as the primary determinants of the abundance of insects.

High fecundity, an individual-level trait shared by the majority of insect species, inevitably results in high mortality rates at the level of the population (Price et al., 2011). The most common cause of death for immature herbivores is indeed the action of their natural enemies, i.e. the organisms using insects as their food source (Cornell and Hawkins, 1995). Natural enemies are thought to play a regulatory role in the dynamics of the food web which is supported, among other, by the diverse adaptations against natural enemies, population models, and numerous cases of successful biological control of insect herbivores (Price et al., 2011; Speight et al., 2008).

## 1.2 Predators of insects

Insects are subjected to predation from a wide variety of vertebrates, including birds, fish and mammals (Price et al., 2011; Speight et al., 2008). It is difficult to assess the predation pressure imposed by a single species on a population of insects because the predators frequently are generalists that feed on a multitude of prey species. However, diverse studies have shown that late instar larval and pupal mortality of Lepidoptera is largely due to avian predators (Nixon and Roland, 2012; Rimmel et al., 2009). Daily mortality imposed by birds alone on lepidopteran larvae has been estimated at 5% (ranging from 0–30%) in the temperate zone (Rimmel et al., 2009), which would integrate into the gross mortality rate of 40–50% (Nixon and Roland, 2012; Rimmel et al., 2009) and 15–30% (Ruiz-Guerra et al., 2012) over the entire immature development in the temperate and the tropical zones respectively. Small mammals are considered an important cause of death for late instar larvae and especially pupae in low-density populations in temperate habitats (Liebhold et al., 2000; Nixon and Roland, 2012). For example, predation by small mammals has been shown to cause an average of 20% mortality of hymenopteran pupae in Japan, being more intense in autumn (Pinkantayong et al., 2015).

Furthermore, egg and early instar larvae succumb almost exclusively to arthropod predators (Alalouni et al., 2013; Nixon and Roland, 2012), mainly because arthropod predation is more sensitive to prey size (Hajek and Eilenberg, 2018). The mean arthropod predation has been found to be 13.5% (median 8.8%) per day; it differs strongly between the study systems and has significant spatial variation within study areas (Rimmel et al., 2011; Sang and Teder, 2011). Most arthropod predators, including ants, bugs, beetles, wasps and spiders, rely on both sight and smell to locate their prey. They are less mobile or less adept at controlling their mobility than vertebrates, which causes them to concentrate more on the habitat prey are usually found, such as the host plant, rather than searching for the individuals per se (Hajek and Eilenberg, 2018; Rimmel et al., 2011).

In addition to predation, arthropods kill insects through parasitism. Oxford English Dictionary (2023) defines a parasite as “an organism that lives on, in, or with an organism of different species and obtains food, shelter, or other benefits at the expense of the host organism – which it may directly or indirectly harm”. An important group of parasites, in the context of insect population dynamics, is formed by parasitoids – insects (mainly representing various groups of Hymenoptera and Diptera) which live freely as adults but have larvae developing parasitically inside the bodies of their hosts (Hawkins, 1994; Hochberg and Ives, 2000; Speight et al., 2008). Differently from parasites in the strict sense, parasitoids are destined to eventually kill their hosts.

All immature stages of herbivorous insects are vulnerable to parasitoid attack, though it may be cautiously generalized that younger instar larvae suffer the most (Hajek and Eilenberg, 2018; Hochberg and Ives, 2000; Mills, 2010). Quantitatively, the effect of parasitoids on the populations of their hosts is highly

variable, being strongly dependent on host feeding niche and parasitoid species richness (Hawkins, 1994). Parasitoids are abundant and diverse, with the effect of parasitoids on insect populations being thus comparable to that of predators (Hajek and Eilenberg, 2018; Price et al., 2011). As a result, parasitoid-related mortality is typically around 15% over the immature development (Stireman and Singer, 2003), though cases of very high mortality are not exceptional (Mills, 2010; Teder et al., 2013). Because predators do not distinguish between parasitized and non-parasitized larvae, the impacts of predation and parasitism are not necessarily additive (Nixon and Roland, 2012; Peterson et al., 2009). There is much evidence that parasitoids can regulate host populations (although Berryman, 2003; Liebhold et al., 2000 provide an opposing viewpoint), though the density-dependence primarily forms a second-order feedback or manifests itself in a delayed manner.

As natural enemies are typically responsible for most of the mortality in insect populations (Cornell and Hawkins, 1995; Price et al., 2011), they have the potential to impose selective pressures on various traits of insects. Selective pressures arise as soon as the mortality is not random but varies, for example, among seasons, habitats or host plants, or depends on the traits of potential prey (Hawkins et al., 1997; Rimmel et al., 2011, 2009). For instance, in the temperate zone, avian predation peaks during nesting period in early summer and is positively correlated with larval body size, which likely explains why late season larvae of bivoltine moths reach larger body sizes despite lower food quality (Rimmel et al., 2011; Teder et al., 2010). Similar to this, in the temperate zone, larval mortality has been shown to be 2.2 times higher in deciduous forests compared to coniferous ones, mostly due to differences in bird communities (Rimmel et al., 2009). Given that there are no major latitudinal differences in the rates of avian and mammalian predation (Roslin et al., 2017), we expect that the potential of vertebrate predators to create selective pressures should be comparable across climate zones. The potential of parasitoids to impose selective pressures on their hosts should be of the same magnitude, as exemplified by the impact of parasitoids on the evolution of host plant use (Stireman and Singer, 2003), or creating selective pressure against large body size (Teder et al., 1999).

### **1.3 Pathogens of insects**

Many animals succumb to various diseases, and insects are not an exception either. Nevertheless, pathogens of insects have rarely received the same magnitude of attention as parasitoids and predators. Indeed, pathogens of insects are undoubtedly the most diverse group of insect mortality agents, belonging to groups as different as viruses, bacteria, protists, fungi and nematodes (Roy and Cottrell, 2013; Speight et al., 2008; Vega and Kaya, 2012). However, due to scarcity of focused research efforts and the fact that pathogens are not so easy to spot as parasitoids and predators (Vega and Kaya, 2012), the mortality caused by

pathogens is generally underestimated in studies on the demography of insect populations (Hawkins et al., 1997; Meyling and Hajek, 2010; Mora-Aguilera et al., 2017). In fact, much of the mortality recorded as being caused by unidentified factors should be attributed to pathogens (Alalouni et al., 2013). Even if entomopathogens are known to cause dramatic epizootics that lead to rapid decline in insect populations (Bonsall, 2004; Pell et al., 2010; Vega and Kaya, 2012), respective ecological interactions are poorly known in general, especially in natural populations (Hawkins et al., 1997; Meyling and Hajek, 2010; Mora-Aguilera et al., 2017). Somewhat more is known about agroecosystems, in which pathogens have been studied in the context of biocontrol of agricultural pests (Bonsall, 2004; Hajek and Eilenberg, 2018; Roy and Cottrell, 2013).

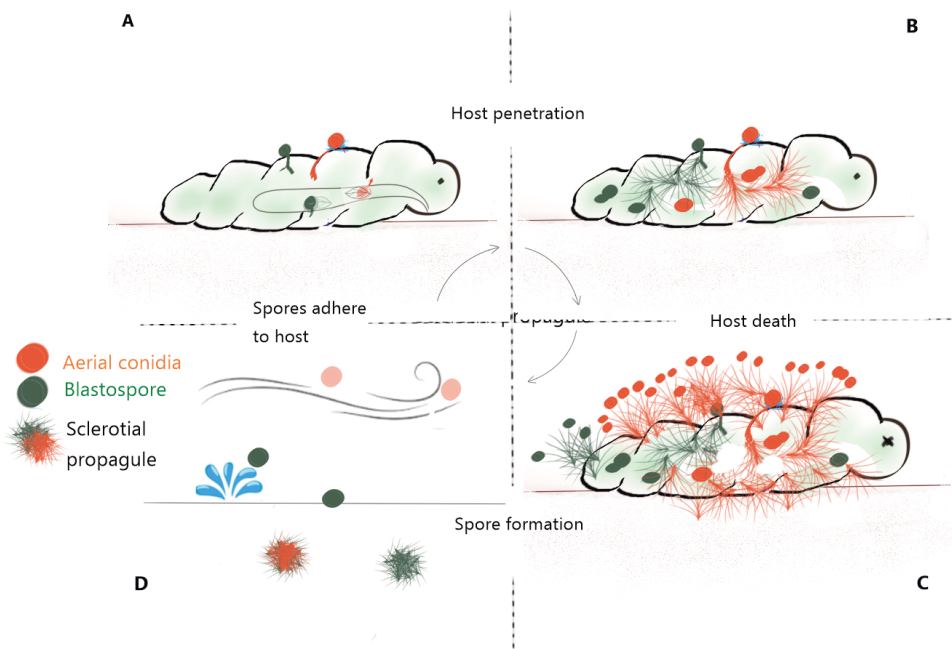
In terms of ecological research on pathogens, viruses seem to have received most attention (Hajek and Eilenberg, 2018; Vega and Kaya, 2012). Viruses tend to lead to high mortality in a density-dependent fashion, at least under high population densities (Il'inykh, 2007), as shown for gypsy moth populations infected by nuclear polyhedrosis virus in North America (Liebhold et al., 2000). In this system, there are dramatic epidemics that cause a sharp decline in population densities of the insect (Bonsall, 2004; Pell et al., 2010; Vega and Kaya, 2012). The impact of viruses on insect population dynamics may become complicated by extreme resistance which has been shown to emerge after some generations (Lacey et al., 2015). Susceptibility of insects to viral agents is also dependent on abiotic factors (relative humidity, UV light etc.; Harrison and Hoover, 2012) which means that it is common for viral pathogens to remain dormant in insect populations during harsh weather conditions (Podgwaite and Mazzone, 1986).

Bacteria are always present in dead insects because they constitute a normal component of the gut microbiota (Kleespies et al., 2008). For this reason, it is not always easy to attribute the death of an insect to bacteria. Data on *Bacillus thuringiensis*, a bacterium with proven entomopathogenic lifestyle, suggest an approximate of 7–8% as the rate of bacteria-induced mortality in insect populations (Kleespies et al., 2008; Zimmermann et al., 2016). However, in laboratory bioassays, up to 80% mortality has been shown (Secil et al., 2012). Similarly to viruses, bacterial virulence is strongly linked to the host environment and the specific strain (Jurat-Fuentes and Jackson, 2012). However, as in the case of viruses, insects are able to acquire resistance against certain strains of bacterial entomopathogens, who mostly persist in populations in the latent stage, rarely inducing epizootics (Jurat-Fuentes and Jackson, 2012; Lacey et al., 2015).

Among other pathogens, nematodes act more as vectors for bacteria, and only for insects dwelling in the soil, water or litter (Deka et al., 2021; Koppenhöfer, 2007). Nematodes have been shown to be able to lead to up to 100% mortality in laboratory conditions and up to 50% in semi-natural conditions (Abbas, 2022), although data on the mortality in natural populations are scarce (Lewis and Clarke, 2012).

## 1.4 Entomopathogenic fungi as insect mortality agents

A sizeable group of insect pathogens belongs to the fungal kingdom (Lacey et al., 2015; Vega and Kaya, 2012). There are at least 1,000 species of fungi from more than a hundred genera known to act as pathogens of insects (Hajek and Eilenberg, 2018; Vega et al., 2012). The evolutionary success of the entomopathogenic lifestyle may be related to the fact that, in contrast to other pathogens, certain fungi have the ability to penetrate insect's cuticle which serves as the insect's main defense against microbial antagonists (Samson et al., 2013; Vega and Kaya, 2012). Therefore, fungi are able to infect a broader range of insects, including phloem suckers, which cannot be infected by other microbes (Samson et al., 2013).



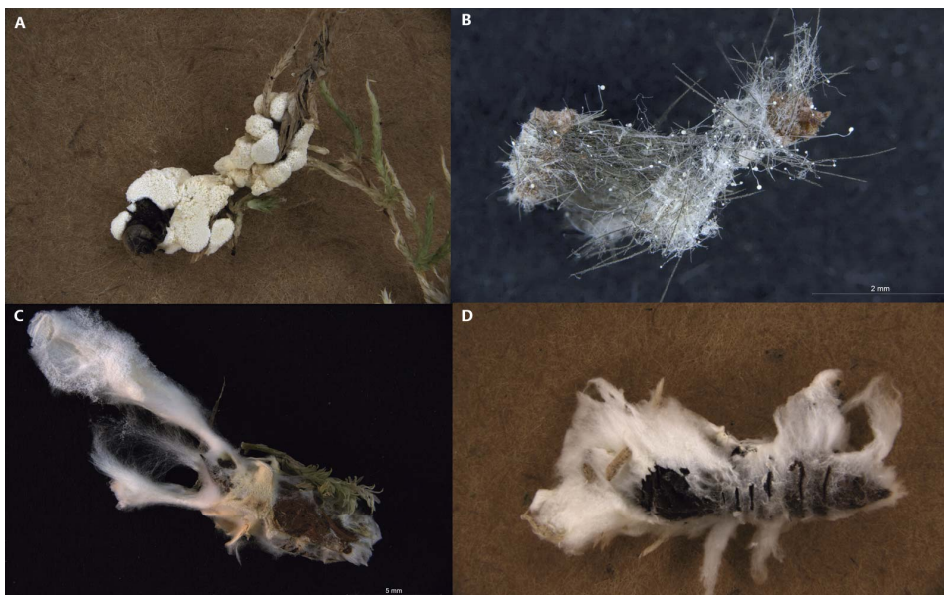
**Figure 1.** Schematic presentation of the life cycle of entomopathogenic fungi. Three types of propagules are present: hydrophobic air dispersed spores (conidia; orange), durable hydrophilic blastospores (green), or melanized hyphal aggregates called sclerotia. A – spore germination; B – fungal growth inside the insect; C – fungal structures producing spores; D – spore dispersal.

Life cycle of entomopathogenic fungi (EPF) can broadly be divided into four phases: spore germination, fungal growth within the host, spore formation and spore dispersal (Figure 1; Samson et al., 2013; Vega et al., 2005; Vega and Kaya, 2012). In the following, I will discuss the differences in the life cycles of the two most studied orders in this respect – Entomophthorales (Entomophthoromycota) and Hypocreales (Ascomycota). Spore germination starts with its attachment to

the insect cuticle. Species from the order Entomophthorales rely on producing mucilaginous coat around the spore, which aids in adhesion to the cuticle (Eilenberg et al., 1986). Furthermore, species from the order Hypocreales, also tend to use electrostatic mechanisms and proteins which successfully bind to hydrophobic surfaces (Boucias et al., 1988; Holder and Keyhani, 2005; Wang and St Leger, 2007), such as the insects cuticle. From there onward, the spore germinates, forming a germ tube and in some cases also an appressorium, mucilage and/or enzymes to aid in cuticular penetration (Samson et al., 2013; Vega et al., 2012). When the cuticle is breached, the fungus – in the form of hyphal bodies or yeast-like blastospores – starts utilizing available nutrients in the insect’s hemo-coel, for its growth and reproduction. Further development of the fungus may lead to the death of the host insect according to two different scenarios. First, in the case of the growth strategy, the insect dies of malnutrition and extensive fungal growth within its tissues. The alternative is the toxin strategy, where fungus produces secondary metabolites to overwhelm the insect’s immune system and in process kills the insect (Hajek, 1997; Vega et al., 2012). Roughly, the first scenario is characteristic of the Entomophthorales and the second of the Hypocreales. Temperature, host size and stage, and fungal dose all affect how long it takes for the host to die after conidial inoculation (Hajek, 1997). After the death of the host, the fungus emerges from the less melanized intersegmental folds (Bidochka and Small, 2005) and envelops the insect in mycelium, producing air-dispersed (Hypocreales) or actively discharged (Entomophthorales) conidia externally on the cadavers (Jackson et al., 2010). When environmental conditions are unsuitable, fungi produce blastospores (Hypocreales), (micro)sclerotia (Hypocreales) or resting spores (Entomophthorales) to survive longer periods in the cadaver or soil (Boomsma et al., 2014; Hajek, 1997; Jackson et al., 2010). Reproductive structures of the EPF (Figure 2) are often easy to observe on the dead host individuals, which greatly contributes to the feasibility of studying fungal diseases of insects, as compared to the typically much more cryptic pathogens from other groups.

Parasitism on insects has arisen repeatedly in various lineages in the course of the evolution of fungi (Humber, 2008; Shang et al., 2016; St. Leger and Wang, 2020). Phylogenetic and genetic data have demonstrated that switching to consuming insects most likely happened as a host transition in fungi associated with plants which ‘looked for’ a more nutrient-rich (e.g. in nitrogen) food source (Barelli et al., 2016). The fact that numerous EPF frequently also colonize plant tissues as endophytes lends support to this (Amatuzzi et al., 2017; Barelli et al., 2016; Vega, 2018). As fungi are vulnerable to external environmental factors like UV light and low relative humidity (Hajek and Eilenberg, 2018), spending part of their lifecycle as endophytes or saprotrophs may be a useful adaptation. As EPF are not restricted to feeding on living insects, it is common for generalist EPF to continue feeding on the killed host as saprotrophs (Roy and Cottrell, 2013; Samson et al., 2013). As a result, it is not always possible to draw a sharp line between entomopathogens and opportunistic pathogens, who spend their lives as saprotrophs, being, however, able to infect a weakened insect (Vey 1971; Sharma and Marques, 2018). Applying Koch's postulates, a set of four criteria intended

to prove a link between a microbe and a disease is an indirect way to determine a fungal feeding strategy. This may nevertheless fail to reveal the real infection patterns in natural conditions.



**Figure 2** Images of insect (lepidopteran) larvae and pupae infested by fungi. A – *Beauveria pseudobassiana* on a last instar *Cabera pusaria* larva; B – *Aspergillus flavus* on a third instar *Hypercompe indecisa* larva; C – *Samsoniella cf. hepiali* on a pupa of *Hypomecis atomaria*; D – *Akanthomyces muscarius* on a pupa of *Acrionicta rumicis*.

Even though the entomopathogenic strategy has evolved in many major fungal lineages, there is higher concentration of respective species in two phyla: Ascomycota and Entomophthoromycota (Boomsma et al., 2014; Samson et al., 2013). Entomophthoromycota are mostly obligate pathogens of adult insects. They have restricted host ranges, while still being found infecting insects from 10 orders. These fungi are biotrophic, meaning they can only grow while their host is still alive and feeding them (Araújo and Hughes, 2016; Samson et al., 2013). As opposed to this, EPF from Ascomycota are mostly hemibiotrophic generalists, transitioning from a parasitic, biotrophic phase in the hemocoel to a saprotrophic phase after the host has died (Araújo and Hughes, 2016; St. Leger and Wang, 2020).

The prevalence of fungi in the host population, as well as their abundance, virulence and persistence in the surrounding environment, will determine their ability to control insect populations. The first task of an insect ecologist focusing on EPF is thus to estimate the prevalence of fungi in hosts and their abundance in the environment (Hesketh et al., 2010). Even though we have accumulated knowledge throughout a century of studies on EPF (Samson et al., 2013; Vega and Kaya, 2012), mostly carried out with the focus on application of EPF in

biocontrol, we are still lacking systematic knowledge about the role of entomopathogens in the dynamics of natural insect populations (Boomsma et al., 2014; Hesketh et al., 2010; Meyling and Hajek, 2010). This becomes apparent in major studies including life-table analyses (Hawkins et al., 1997; Peterson et al., 2009) and case studies on insect mortality with a global scope (Roslin et al., 2017) in which fungi are grouped together with other pathogens, or not mentioned at all.

A fundamental question of ecology is to identify the diversity of interactions the study subject has with others players in the ecosystem (Speight et al., 2008; Vega and Kaya, 2012). For EPF the number of host species determines its abundance and distribution in nature (Vega et al., 2012). Research on EPF has nevertheless primarily focused on their physiological host range (Hesketh et al., 2010; Santos et al., 2020), defined as pathogen's virulence to insects in laboratory experiments under favourable conditions (Hajek and Goettel, 2007). Such experiments typically overestimate the ecological host range of the EPF, i.e. the host range realized in natural communities (Hajek and Goettel, 2007; Sharma and Marques, 2018). The effects of various environmental factors, ranging from abiotic ones (temperature, humidity, UV) to various ecological interactions (host availability, host conditions, food plant, etc.) can constrain the ecological host range (Samson et al., 2013). Additionally, since EPF are a crucial component of the communities of insect natural enemies, studies of the dynamics of hosts' natural populations should shed light on their broader ecological significance. Moreover, we still know very little about the selective pressures that EPF exert on the life histories of their hosts and how the host and the pathogen interact ecologically in natural settings.

## 1.5 Aims of the thesis

The main objective of the current thesis was to evaluate the diversity of EPF associated with natural populations of herbivorous insects, and to describe the patterns of mortality attributable to these antagonists, to be discussed in the context of both population dynamics and evolutionary ecology of the host insects.

The specific aims of this thesis were:

1. To shed light on the levels of mortality caused by fungi in natural insect populations (I–V). To facilitate the understanding of the role of fungi in insect population dynamics, it is crucial to measure the probability to die due to a fungal disease for different developmental stages of the insect. Differences may exist depending on the taxonomic affiliation of the fungi, similar to how various vertebrate groups (small mammals vs. birds) act differently as predators of insects. Therefore, describing the taxonomic diversity of the assemblage of EPF is a task inseparable from evaluating the overall infestation rates of the insects.

2. To investigate whether an insect's physical condition affects its ability to resist fungal infection (**II, IV**). Physical condition of a herbivorous insect is mainly influenced by the quality of its food, which implies that condition-dependence in resistance could amplify bottom-up effects in the regulation of insect populations.
3. To determine whether there are latitudinal differences in mortality caused by entomopathogenic fungi (**II, III & IV**). As fungi are quite constrained by environmental factors, climatic conditions should play a significant role in insect-fungus relationships, which should be detectable in comparisons across latitudes.
4. To identify how entomopathogenic fungi interact with herbivorous insect's living space (**II, IV & V**). If fungal prevalence is not homogeneous in the space-time continuum, locating the differences would provide insight into the spatial aspects of population dynamics of the insect, and would help us to identify associated selective pressures.
5. To determine whether the fungal-induced mortality is dependent on the insect's food plant (**II, III & V**). The "bodyguard" hypothesis (Elliot et al., 2000; Vega, 2018; Vega and Kaya, 2012) states that plants may provide the enemies of their enemies, in this case fungi infecting herbivorous insects, with suitable living space, increasing thereby the likelihood that generalist herbivores choosing such plants for consumption will become infected.

## **2. MATERIAL AND METHODS**

### **2.1 Studied insects**

Lepidoptera served as a model for my field studies because their ecology is well known compared to many other insects, and because our lab at the University of Tartu has ample experience with working with these animals. Ecologically speaking, Lepidoptera serve as the main food source for many diurnal and nocturnal vertebrate insectivores, host countless specialized parasitoids, and play significant roles as pests and pollinators, acting as both agents and targets of natural selection (Goldstein, 2017). Butterflies and moths make up a sizeable proportion of the terrestrial biodiversity, and therefore provide an essential platform for exploring ecological and evolutionary issues related to population dynamics and evolutionary ecology (Goldstein, 2017; Speight et al., 2008). Furthermore, there are around 100 EPF species known to infect Lepidoptera (Araújo and Hughes, 2016). My studies were conducted with twelve species from the families Erebidae, Geometridae and Noctuidae (Table 1), the three largest families in terms of the number of species (Goldstein, 2017).

**Table 1** Species of Lepidoptera and their larval host plants used in this thesis.

Species	Family	Fed with	Used in paper
<i>Cabera pusaria</i> L.	Geometridae	<i>Alnus glutinosa</i> , <i>A. incana</i> , <i>Betula pendula</i> , <i>B. pubescens</i>	I, II
<i>Chiasmia clathrata</i> L.		<i>Lathyrus pratensis</i>	I
<i>Hypomecis atomaria</i> L.		<i>Betula pendula</i> , <i>B. pubescens</i> , <i>Rubus idaeus</i> , <i>Salix alba</i> , <i>Trifolium repens</i> , <i>Vaccinium myrtillus</i>	I, II
<i>Hypomecis punctinalis</i> Scopoli		<i>Betula pendula</i> , <i>Tilia cordata</i> , <i>Quercus robur</i>	I
<i>Acronicta rumicis</i> L.	Noctuidae	<i>Betula pendula</i> , <i>B. pubescens</i> , <i>Rubus idaeus</i> , <i>Vaccinium myrtillus</i>	II
<i>Anicla infecta</i> Ochseneheimer		<i>Erigeron bonariensis</i> , <i>E. sumatrensis</i> , <i>Pascalina glauca</i> , <i>Prosopis alba</i> , <i>Zea mays</i>	III
<i>Dargida albilinea</i> Hübner		<i>Erigeron bonariensis</i> , <i>E. sumatrensis</i> , <i>Pascalina glauca</i> , <i>Prosopis alba</i> , <i>Zea mays</i>	III
<i>Globia algae</i> Esper		<i>Typha latifolia</i>	IV
<i>Globia sparganii</i> Esper		<i>Typha latifolia</i>	IV
<i>Nonagria typhae</i> Thunberg		<i>Typha latifolia</i>	IV
<i>Orthosia gothica</i> L.		<i>Betula pendula</i>	I
<i>Hypercompe indecisa</i> Walker	Erebidae	<i>Erigeron bonariensis</i> , <i>E. sumatrensis</i> , <i>Pascalina glauca</i> , <i>Prosopis alba</i> , <i>Zea mays</i>	III

## 2.2 Study design

### 2.2.1 Using existing data

I first studied EPF which had been found parasitizing insects used in ecological experiments conducted between the years 2014 and 2017 at the University of Tartu (**Paper I**). In those experiments (Meister et al., 2017a, 2017b, 2018), larvae of several moth species had been reared in plastic vials in the laboratory. Dead pupae which developed visible signs of fungal infections had been stored for further analyses.

The larvae had been fed with plants collected from the surroundings of Tartu, Estonia, so that despite the laboratory setting, the recorded fungi can be assumed to represent local natural assemblages. Larvae pupated in moist *Sphagnum* moss, and were kept overwinter in thermoregulated chambers at 0°C. Adult moths were allowed to eclose in spring under room temperature. The samples were studied in order to record the diversity and prevalence of fungi in laboratory conditions, and to compare these findings with observations done outdoors.

To determine how general are the patterns recorded in our empirical studies, and to evaluate the level of the knowledge about the ecology of EPF in general, we performed an analysis of published empirical case studies reporting the prevalence of EPF in natural insect populations (**Paper V**). We used case studies in which insect sampling had been carried out in the field and the incidence of fungal infection had been recorded at the level of individual insects. Respective papers were collected through systematic screening of major literature databases (Google Scholar, Web of Science). To obtain a metric of fungal prevalence at the spatio-temporal scale, the meta-analytically corrected statistics of the prevalence of EPF were compared between insect orders, fungal orders, geographic regions and growth forms of the hosts' food plants.

### 2.2.2 Insect rearing in semi-natural conditions

The effects of biotic factors on the probability to get infested by EPF in natural populations were investigated using two different types of rearing experiments. Additionally, the experimental settings facilitated recording the diversity of the EPF associated with the lepidopteran hosts. First, newly hatched larvae of a geometrid moth were reared to pupation in mesh bags on tree branches in forests of central Estonia (58°N, 26°E), the experiment was repeated in two consecutive years (**Paper I**). The advantage of the mesh-bag rearing is in the possibility to observe and keep track of the insects on food plant under the same conditions as experienced by their conspecifics in nature. The disadvantage of this method is however in creating the green-house effect in the bag and/or problems during heavy rain, which makes the bag wet and sticky, increasing the probability that the larvae become stuck onto the bag surface and die of starvation.

Second, in order to determine whether the mortality imposed by EPF and their assemblages are linked to host species, spatial location, food plant of the host or

the host's physical condition, newly hatched larvae of three moth species were individually reared until adulthood in plastic vials in outdoor conditions (a 'semi-field' experiment) in the Southern Estonian village of Rõka (58° S, 27° E, **paper II**). The area is characterized by hemiboreal mixed forest stands with *Picea abies* and *Pinus sylvestris* as the dominant tree species. Each individual was fed throughout its immature development with single food plant individual/species collected from a designated location in the study area. In the last instar, half of the larvae were subjected to starvation treatment, precluding their access to food every other day. Dead larvae and pupae with visual signs of fungal infection were collected and preserved for further studies. The experiment was replicated also in central Argentina (31°S, 64°W, **paper III**), where, due to adverse weather conditions, newly hatched larvae of three moth species were reared indoors on variety of food plants. Córdoba, the region in which the experiment was performed lies on the northern boundary of the pampas, characterized as borderline of temperate and humid sub-tropical climate. Due to time constraints, we were unable to rear individuals until adulthood and instead focused only on larval mortality caused by the fungi. Even though the setting of this sort of experiments is not fully natural, it allowed us to keep track of individual insects (and to manipulate certain parameters) while feeding the insects on local plants still provided the opportunity to record the local assemblage of fungal antagonists characteristic of the study area.

### 2.2.3 Survey of natural Lepidoptera populations

The experiments with the 'semi-field' design were complemented by a field survey of infestation rates in a natural system exceptionally well suited for this purpose. In particular, larvae and pupae of three noctuid moths endophytically feeding on common cattail (*Typha latifolia*) were collected from various locations across southeastern Estonia over the course of two years (**Paper IV**). The main advantage of this system is the ease of obtaining unbiased samples of immature insects: by carefully dissecting the stems of the host plants, both live larvae and pupae as well as carcasses of dead insects can be collected (Teder et al., 1999; Teder and Tammaru, 2002; Teder et al., 2013). Furthermore, *T. latifolia* frequently grows in dense stands in distinct patches, making it possible to define local populations of the associated insects. The aim of the study was to obtain data on fungal prevalence in natural populations of moths and see if the infestation rate and species diversity differ between locations, and depends on the time of collection and characteristics of the plot (plant height, plant density, age of the plot, herbivore density etc.).

## 2.3 Identification of the fungi

Dead insects were inspected for visible fungal structures. When present, the fungi were inoculated to 2% malt extract agar (Oxoid, Cambridge, UK) in 9 cm diameter Petri dishes. For identifying the fungi, the colonies and morphological structures developed in culture were examined while sparing some material for DNA barcoding. DNA extraction, PCR, and sequencing procedures were carried out following the protocols outlined by Põldmaa et al. (2019). The ITS region of the ribosomal RNA gene was sequenced using the Standard-Seq service at MacroGen Europe BV (Amsterdam). Along with the comparison of morphological features, assigning the obtained DNA barcodes to the UNITE species hypotheses (SH, see Kõljalg et al., 2020) served as the main identification strategy. The advantage of the SH system is that regardless of the change or lack of a Latin binomial, unique persistent identifiers, assigned to all SHs in the form of DOIs, allow for unambiguous communication about the identity of studied organisms. Dried specimens and isolates were deposited, respectively, in fungal collections TUF and TFC at the Natural History Museum, University of Tartu. Information on collecting sites and dates for all specimens as well as associated isolates, sequences, images and metadata, were uploaded to UNITE and published using the PlutoF workbench.

## 2.4 Data analysis

In addition to describing species richness of the EPF and recording mortality ascribed to them, we searched for factors explaining the prevalence of EPF. For this purpose, generalized linear models (GLM) were used to determine whether fungal infection is influenced by the following factors: moth species (**II**, **III**), hatching date (**II**), population density (**IV**), pupal weight (**II**, **IV**), starvation treatment (**II**), parasite prevalence (**IV**), food plant species (**II**, **III**), plant vigor (**IV**), plant density (**IV**), age of the plant community (**IV**), study site (**II**, **IV**), and study year (**IV**). These analyses were done using total sets of data specific to particular studies and also separately by insect life stages (**II**) and for the most abundant fungal family (**II**), genera (**IV**) and species (**II**, **IV**).

Multinomial regression was used to compare the species composition of EPF between insect life stages (**II**). For this purpose, several species were combined into ecologically sound groups for the analyses.

Furthermore, to identify the differences in infection rates between 1) insect orders, 2) fungal orders, and 3) geographical locations we fitted a binomial GLMM with a likelihood ratio test to the aggregated data with data source and observation-level random effects (**V**). We tested whether different fungal orders are equally represented among the regions, and growth forms of the host plant of the insect hosts (grass, shrub, tree, or rhizosphere) (**V**).

### 3. RESULTS AND DISCUSSION

#### 3.1 Diversity and host specialization of entomopathogenic fungi infecting herbivorous Lepidoptera

The assemblage of fungi infecting herbivorous Lepidoptera was found to be diverse, encompassing species from ten phyla according to recent taxonomic treatments (Samson et al., 2013; Araújo and Hughes, 2016; Tedersoo et al., 2018). In the course of the empirical work conducted in the framework of this thesis project, we encountered species from two of these phyla, Ascomycota and Mucoromycota. Moreover, Mortierellomycota, recently elevated to phylum level (Tedersoo et al., 2018) was also represented among our collections. All in all, 45 species of EPF were identified on the basis DNA barcodes – 26, 23, 8 and 10 species in papers I–IV, respectively (Table 2).

Additionally, published data on 122 fungal species infecting insects, from four fungal phyla, were retrieved in the framework of the meta-analytic study (V).

I conclude that the diversity of EPF associated with natural populations of moths is high. However, revealing this diversity is only possible through studies focusing on the entire assemblage of fungi which appear to be surprisingly scarce (see Amatuzzi et al., 2017; Poitevin et al., 2018; Sharma and Marques, 2018 for some examples). The majority of the fungi discovered in our experimental studies performed in Estonia and Argentina belonged to the phylum Ascomycota, followed by some representatives from Mortierellomycota and Mucoromycota. Most of the encountered fungal species are usually considered to be opportunistic pathogens or saprotrophs, with discussions of their entomopathogenicity arising only recently (Santos et al., 2020; Sharma and Marques, 2018; Zhu et al., 2022). Discerning pathogens from saprotrophs proves to be extremely difficult, especially for fungi with hemibiotrophic strategies.

**Table 2.** Species of entomopathogenic fungi identified in the course of the empirical work of this thesis project. All sequences were assigned to species hypotheses in UNITE version 9 applying distance threshold 1.5%, unless indicated otherwise.

UNITE Species Hypothesis	Species name	Order	Phylum	Article	SH in articles I–IV
SH4360527.09FU <sup>1</sup>	<i>Cladosporium</i> sp.	Capnodiales	Ascomycota	<b>I &amp; II</b>	SH1572792.08FU SH2320203.08FU
SH1240491.09FU	<i>Aureobasidium pullulans</i> (de Bary) G. Arnaud	Dothideales		<b>I</b>	SH1872652.08FU
SH3214790.09FU <sup>1</sup>	<i>Aspergillus</i> sp. 1	Eurotiales		<b>III &amp; IV</b>	SH1532328.08FU SH3214790.09FU
SH2500109.09FU <sup>1</sup>	<i>Aspergillus</i> sp. 2			<b>II</b>	SH1649133.08FU
SH1294045.09FU	<i>Penicillium bialowiezense</i> K.M. Zalesky			<b>II &amp; IV</b>	SH2189921.08FU SH2071955.09FU
SH1228265.09FU	<i>Penicillium godlewskii</i> K.W.Zaleski			<b>II</b>	SH2189963.08FU
SH1225643.09FU	<i>Penicillium velutinum</i> J.F.H. Beyma			<b>II</b>	SH2189995.08FU
SH1228198.09FU	<i>Penicillium</i> sp. 1			<b>II</b>	SH1537860.08FU
SH0884485.09FU	<i>Penicillium polonicum</i> K.M. Zalesky			<b>II</b>	SH2189908.08FU SH1529984.08FU
SH1225804.09FU	<i>Penicillium thomii</i> Maire			<b>I</b>	SH2189918.08FU SH2189912.08FU
SH1229201.09FU	<i>Penicillium</i> sp. 2			<b>I &amp; II</b>	SH2283940.08FU
SH1259052.09FU	<i>Akanthomyces muscarius</i> (Petch) Spatafora, Kepler & B. Shrestha	Hypocreales		<b>I, II &amp; IV</b>	SH1886969.08FU SH2006624.09FU
SH2006785.09FU <sup>2</sup>	<i>Beauveria bassiana</i> (Bals.-Criv.) Vuill.			<b>IV</b>	SH2006785.09FU

UNITE Species Hypothesis	Species name	Order	Phylum	Article	SH in articles I–IV
SH4059696.09FU <sup>1</sup>	<i>Beauveria pseudobassiana</i> S.A. Rehner & Humber			<b>II &amp; IV</b>	SH2173947.08FU SH4059696.09FU
SH1259367.09FU	<i>Cordyceps bifusispora</i> O.E. Erikss			<b>I</b>	SH1887323.08FU
SH1259218.09FU	<i>Cordyceps farinosa</i> (Holmsk.) Kepler, B. Shrestha & Spatafora			<b>I</b>	SH1524463.08FU
SH1259045.09FU	<i>Cordyceps militaris</i> (L.) Fr.			<b>II</b>	SH2173962.08FU
SH1079735.09FU	<i>Fusarium chlamydosporum</i> ecies complex			<b>III</b>	SH1610186.08FU
SH1079718.09FU	<i>Fusarium keratoplasticum</i> Geiser, O'Donnell, D.P.G. Short & Ning Zhang			<b>III</b>	–
SH1079840.09FU	<i>Fusarium</i> cf. <i>langsethiae</i>			<b>IV</b>	SH1699024.09FU SH3187143.09FU SH3194426.09FU
SH0994959.09FU	<i>Fusarium oxysporum</i> Schltdl			<b>III</b>	–
SH1079277.09FU	<i>Fusarium proliferatum</i> (Matsush.) Nirenberg ex Gerlach & Nirenberg			<b>III</b>	SH1623679.08FU
SH1071658.09FU	<i>Fusarium</i> sp. 1 <sup>3</sup>			<b>I</b>	SH2228332.08FU
SH1071658.09FU	<i>Fusarium</i> sp. 2 <sup>3</sup>			<b>II</b>	SH1546416.08FU

UNITE Species Hypothesis	Species name	Order	Phylum	Article	SH in articles I–IV
SH1079201.09FU	<i>Fusarium</i> sp. 3 <sup>4</sup>			<b>I, II &amp; IV</b>	SH1919083.08FU SH2229701.08FU SH1698094.09FU
SH1060460.09FU	<i>Fusarium</i> sp. 4			<b>I &amp; III</b>	SH2456045.08FU SH1610157.08FU SH1458596.08FU SH1656686.08FU
SH1259385.09FU	<i>Lecanicillium praecognitum</i> Gorczak & Kisto			<b>I</b>	SH1524455.08FU
SH0940258.09FU	<i>Leptobacillium leptobactrum</i> (W. Gams) Zare & W. Gams			<b>II</b>	SH1529400.08FU
SH1400837.09FU <sup>2</sup>	<i>Mariannaea</i> sp.			<b>I &amp; II</b>	SH1506679.08FU
SH3321817.09FU <sup>1</sup>	<i>Metapochonia bulbilosa</i> (W. Gams & Malla) Kepler, S.A. Rehner & Humber			<b>I</b>	SH1930500.08FU
SH4059091.09FU <sup>1</sup>	<i>Samsoniella</i> sp.			<b>II</b>	SH2173953.08FU
SH0913400.09FU	<i>Sarocladium strictum</i> (W. Gams) Summerb.			<b>II</b>	SH1541921.08FU
SH4180515.09FU <sup>1</sup>	<i>Simplicillium aogashimaense</i> Nonaka, Kaifuchi & Masuma			<b>I</b>	SH1988378.08FU
SH0940247.09FU	<i>Simplicillium filiforme</i> R.M.F. Silva, R.J.V. Oliveira, Souza- Motta, J.L. Bezerra & G.A. Silva			<b>II</b>	SH1529405.08FU
SH1279229.09FU	<i>Simplicillium lamellicola</i> (F.E.V. Sm.) Zare & W. Gams			<b>II</b>	SH1584062.08FU

UNITE Species Hypothesis	Species name	Order	Phylum	Article	SH in articles I–IV
SH4180574.09FU <sup>1</sup>	<i>Simplicillium lanosoniveum</i> (J.F.H. Beyma) Zare & W. Gams			<b>I</b>	SH1988383.08FU
SH0955239.09FU	<i>Tilachlidium brachiatum</i> (Batsch) Petch			<b>I</b>	SH1513367.08FU
SH3095020.09FU <sup>1</sup>	<i>Trichoderma</i> cf. <i>longibrachiatum</i>			<b>I</b>	SH1568015.08FU
SH3106886.09FU <sup>1</sup>	<i>Trichoderma</i> sp.			<b>I &amp; II</b>	SH2303517.08FU SH2303501.08FU SH2303512.08FU
SH2616920.09FU <sup>1</sup>	<i>Trichoderma polysporum</i> (B.S. Lu, Druzhin. & Samuels) Jaklitsch & Voglmayr			<b>II</b>	–
SH1301428.09FU	<i>Alternaria</i> sp.	Pleosporales		<b>II &amp; III</b>	SH1526648.08FU
SH1299116.09FU	<i>Entomortierella jenkinii</i> (A.L. Sm.) Telagathoti, Probst & Peintner	Mortierellales	Mortierello- mycota	<b>II</b>	SH1629839.08FU
SH0887892.09FU	<i>Podtla humilis</i> (Linnem. ex W. Gams) Vandepol & Bonito			<b>I</b>	SH2444324.08FU
SH1270678.09FU	<i>Mucor hiemalis</i> Wehmer	Mucorales	Mucoro- mycota	<b>I</b>	SH1989679.08FU
	<i>Umbelopsis</i> sp		Umbelopsidale	<b>I</b>	

<sup>1</sup> at 0.5 % threshold, <sup>2</sup> At 1.0 % distance threshold, <sup>3</sup> *Fusarium solani* species complex, <sup>4</sup> *Fusarium tricinctum* species complex

Our studies revealed that EPF from Ascomycota are not strictly species-specific, but rather can be described as restricted to a particular insect life stage. This is suggested by the pattern that fungal assemblages differed substantially between developmental stages of the insects (**II**, **V**) but not between insect species (**I–V**). Furthermore, we did not find (**I–IV**) evidence of EPF solely infecting one host species, in any of these cases in which sample sizes allowed us to evaluate the level of host specialization. Indeed, as fungi lack the ability to actively search for hosts, they might not benefit from strong host specialization (Meyling and Hajek, 2010). In **paper II**, we found insect larval infections being dominated by opportunistic EPF species, whereas infections of pupae were dominated by obligate EPF, frequently reported in the scientific literature on EPF. Insect larvae constitute easier prey for the trophically less specialized opportunistic pathogens – like *Fusarium*, *Penicillium* and *Aspergillus* spp. – because of their aggregation in the time-space continuum and weaker exoskeleton. Furthermore, as herbivorous larvae of Lepidoptera consume large quantities of plant material, the infection through oral ingestion of the pathogen is most probable during this life stage (Araújo and Hughes, 2016). Oral ingestion may prove to be an easy way in since the insect’s cuticle has been suggested to be the strongest barrier for opportunistic pathogens to overcome (St. Leger and Wang, 2020).

In contrast, our empirical samples did not include some groups which could have been expected, notably the well-known entomopathogenic order Entomophthorales. This could stem from either 1) our target host group – larvae of folivorous Lepidoptera – not being preferred by them; 2) our study areas lacking these fungi; or 3) our methodology (fungal isolation) being inappropriate for them. It is true that species from order Entomophthorales are known to be mainly specialists of adult Diptera (Araújo and Hughes, 2016). However, the possibility that our target insect group is not among the hosts of these fungi, is refuted by the fact that entomophthorean fungi have frequently been isolated from juvenile Lepidoptera. For example, *Entomophaga aulicae* has been recorded from *Panolis flammea* (Noctuidae) in United Kingdom (Hicks and Watt, 2000), from *Favonius quercus* (Lycaenidae) in Bulgaria (Georgieva et al., 2014), *Furia gastropache* from *Malacosoma disstria* (Lasiocampidae) in the northeastern USA (Filotas et al., 2003); there are discussions of the potential of *Entomophaga maimaiga* to regulate *Lymantria dispar* (Erebidae) populations in Europe (Zúbrik et al., 2016). Similarly, literature data show that Lepidoptera harbour by no means lower fungal diversity than other insect orders (Figure 1 in **paper V**).

The second possibility – our study areas simply lack fungi from other phyla – is the least likely, because all main phylogenetic and functional groups of fungi are present in the soils of all ecosystems studied so far (Tedersoo et al., 2014). Furthermore, species from the order Entomophthorales, are considered to dominate the diversity of EPF in the temperate zone (Hajek, 1997), which is also supported by **paper V**. The most likely explanation is that members of Entomophthorales cannot be cultured on regular culture media as they require living cells for growth (as demonstrated for the genus *Neozygites*; Grundschober et al., 1998). Since no indication of these fungi was ever found on dead insects when

those were examined under a microscope, their absence may still have other causes. However, I cannot refute the possibility that some Entomophthorales species initially infected the studied insects, but the eventually observed fungal species had grown over these.

### 3.2 Mortality of herbivorous insects attributable to fungal entomopathogens

Despite the large diversity of fungi able to kill insects, the mortality caused by fungal pathogens in nature was found to be relatively low in Lepidoptera (I–IV), and in insects in general (V), ranging between 2–4% for larvae (II & III) and 2–17% in pupae (I–IV, Table 3). These values are also consistent with the meta-analytically weighed mean of 8.2% (V) for all insects. The latter result is based on the analysis of data from 79 case studies yielding 1273 observations of interactions between 104 insect and 122 fungal species (V). However, the observations were heavily biased towards higher latitudes, mainly originating from Europe and the USA.

**Table 3** Prevalence of entomopathogenic fungi in insect populations (I–V)

Paper	Insect	Stage	Fungal prevalence	No of fungal species	Study setting
I	Lepidoptera	Pupae	2.8%	23	Lab
		Pupae	17.3%	10	Mesh bag
II		Larvae	2.9%	13	Reared in Nature
		Pupae	4.7%	17	
III		Larvae	3.8%	8	Reared indoors
IV		Pupae	8%	10	Nature survey
V	Insecta	All	8.2% (0.8–11%)	122	Case studies

Our findings on Lepidoptera are in good agreement with earlier observations made on this order as well as other insects (V), suggesting that our conclusions could be widely generalized. EPF seem to be omnipresent, as in no subset of our empirical data their prevalence was zero (I–IV). Even though the proportion of insect populations that die from fungal infections is typically low (below 10%), the overall prevalence appears to be roughly invariable across insect and fungal taxa, as well as across geographic locations. Furthermore, life-table studies on insect mortality factors (Hawkins et al., 1997; Peterson et al., 2009; Pinto et al., 2022) do not suggest the mean mortality caused by pathogens to exceed 10%, supporting our findings.

A notable proportion of published case studies, done mainly in agricultural settings (Akner et al., 2020; Townsend et al., 1995), with some exceptions

(Zúbrik et al., 2016), report epidemics caused by EPF (V), something we did not find support for in our empirical work. Most likely, this discrepancy results from study and publishing bias – cases of epidemic infestations understandably attract more research attention, especially because studies on EPF are preferentially conducted in applied contexts (Mora-Aguilera et al., 2017). This is supported by the fact that 5.4% of observations, but 33% of papers, describe fungal infections which have caused mortality higher than 70% (V). Even though laboratory testing has shown great potential of fungal entomopathogens to control insect populations (Chen et al., 2021; Santos et al., 2020; Zúbrik et al., 2016), such studies are often focused on the physiological susceptibility of the insect as the experiments use high dosages and are performed in conditions favorable for the fungi (Hesketh et al., 2010; Roy and Cottrell, 2013). High mortality due to EPF appears still to be rare in nature.

### **3.3 Do entomopathogenic fungi have a regulatory role in insect populations?**

The results of this thesis do not indicate that entomopathogens might play a significant role in regulating the dynamics of insect populations. Even though mortality rates have occasionally been found to be considerable (Akıner et al., 2020; Chen et al., 2021), our empirical work did not find levels of mortality that were high enough to suggest any significant top-down effects. More importantly, the prevalence of EPF was only weakly (II & III) if at all (IV) explained by any of the environmental predictors considered. Even if the question of density-dependent mortality was directly touched just by one of our studies (IV), the overall weakness of environmental determinants creates the impression that getting a fungal disease is largely a matter of chance, with the high diversity of the EPF indirectly supporting the same conclusion.

Another way how EPF could be involved in the regulation of insect populations is through some interaction with bottom-up effects (Cory and Ericsson, 2010). If inferior quality of host plants could also increase the prevalence of EPF, this could open another channel for bottom-up effects to operate. We found no evidence supporting this scenario in either our semi-field experiment (II) or in the field survey (IV). Even if food does not necessarily serve as an infection pathway, it still affects the physiological condition and thus immune response of the insect. However, insect physiological condition, manipulated through food restriction, had an effect on pupal weights but did not result in statistically significant increase or decrease in fungal prevalence (II). Furthermore, plant vigor (IV) failed to attain statistical significance providing no support for bottom-up effects via plant individual quality.

Latitudinal differences in EPF prevalence have been suggested for the well-studied orders Entomophthorales and Hypocreales (Hajek, 1997; Vega and Kaya, 2012). This was also confirmed by our meta-analytical results which showed that

the infection rate of the Hypocreales increases towards the equator and that of the Entomophthorales towards the poles (V). However, total mortality caused by EPF did not differ among latitudes implying that the pathogen species composition changes but not the overall fungal-induced mortality. Even more generally, both our empirical (II, III) and meta-analytical (V) work suggests that the nature of the interactions between EPF and insects does not differ radically among the biomes allowing us to cautiously conclude that the ecological understanding gained from the study of temperate ecosystems is more widely applicable.

### 3.4 Do entomopathogenic fungi create selective pressures on insect traits?

In case the probability to die as a consequence of fungal disease would depend on some traits of the host, including those which determine where and when does some activity of the host occurs, we should see fungal-mediated selective pressures acting on the values of the traits involved. As an example, we assumed the prevalence EPF to increase with the season progressing as a consequence of both deteriorating food quality and the likely accumulation of fungal propagules in the environment. In our semi-field experiment (II), however, we could not show calendar date to have the expected effect on the prevalence of EPF. We could not show that the interaction with EPF creates a selective pressure on moth phenology.

Small-scale spatial differences in mortality risk could select for microhabitat preferences, or overall mobility patterns of insects. No convincing evidence for such differences was found in the thesis project. Neither food plants collected from different locations (within one kilometer, II) nor differences between *Typha* stands across southeast Estonia (IV) revealed any statistically significant variation in fungal prevalence between the areas. It is clear that conspecific plants growing at different locations may harbor fungal assemblages for reasons unrelated to the characteristics of the plants, such as a recent outbreak of a particular species. Even more, as microclimatic conditions are of utmost importance for successful infection (Hajek, 1997; Vega and Kaya, 2012), sites within just a few kilometers are supposed to vary in infection prevalence. In future, site specific climatic factors – such as temperature, relative humidity, vegetation density etc. – should be incorporated into studies on the prevalence of EPF.

If, however, the risk of succumbing to a fungal disease will depend on the food plant the insect is feeding on, the EPF can be a factor involved in the evolution of the host range of the herbivore. Our studies may be the first to document EPF prevalence being influenced by insect's food plant (II, III & V). In **paper II** we found a clear link between insects feeding on birch and infection with *Akanthomyces muscarius*. All 14 detected cases were from insects reared on this host plant (several locations and several insect species), whereas none were from alternative hosts. This fungus is indeed known to occur as an endophyte, having been recorded in maple and oak leaves in Italy (Nicoletti and Becchimanzi, 2020),

in beech branches in Germany and in spruces in Finland and Sweden (data from UNITE database; Kõljalg et al., 2020). Furthermore, we found a similar pattern in Argentina where only insects feeding on *Pascalina glauca* succumbed to *Fusarium* species (III). In addition, studies from Estonia (Bahram et al., 2021) and China (Yu et al., 2021) have found many potential EPF like *Alternaria*, *Aspergillus*, *Cladosporium*, *Fusarium*, *Lecanicillium*, *Mucor*, *Mortierella*, *Penicillium* and *Trichoderma* – also observed in our studies – living as endophytes in the leaves of trees, increasing the possibility of EPF infections through host plant ingestion. This makes the “bodyguard hypothesis” quite likely to be applicable. According to this hypothesis, plants provide suitable habitat or microclimate for the persistence of pathogens of their natural enemies (Elliot et al., 2000; Vega and Kaya, 2012; Vega, 2018). This supported by our conclusion that plant growth form appeared to have an effect on EPF prevalence (V): the incidence of fungal infection was more probable with insects feeding on plants classified as trees.

Being ingested with food is the most obvious pathway of infecting insects for pathogens which do not possess means for actively searching their hosts, like nematodes for example (Vega and Kaya, 2012). This is true for viruses and bacteria, but might also hold for EPF in the case of juvenile herbivorous insects, such as lepidopteran larvae, who consume large quantities of plant material. As entomopathogens have at least in some lineages arisen from plant pathogens or endophytes (Humber, 2008; St. Leger and Wang, 2020), it is of no surprise to find a link between particular fungal and food plant species (II, III, V). Plants providing services for the enemies of their enemies is well known to involve volatile compounds (Heil, 2014) and for myrmecochorous plants (Giladi, 2006). In case of fungi, plants provide them a refuge from adverse environmental factors (Elliot et al., 2000; Barelli et al., 2016; Vega, 2018).

## 4.CONCLUSIONS

The following conclusions can be drawn from my thesis:

- There is a wide variety of fungi that infect insects. Around ten percent of known EPF species infect Lepidoptera. Despite recent advances in the systematics of EPF, many other aspects, like the specialization of pathogens to different life stages of the hosts, have been largely neglected. Our studies show that EPF infecting Lepidoptera are more specialized on certain developmental stages of the hosts than host species.
- The present thesis broadens the array of taxa traditionally considered to include entomopathogenic fungi proposing several species to act as pathogens of insects. While ten phyla were known to incorporate species of entomopathogens, Ascomycota and Entomophthoromycota have received most of attention in taxonomic and ecological studies. Therefore, investigating the other phyla may provide valuable information for understanding insect-fungus interactions.
- Fungal induced mortality is generally low in natural insect populations. Since fungi typically only cause 10% of the mortality of insects and there was no evidence of density-dependence, they hardly have a significant effect on insect population dynamics.
- Even though mortality attributable to EPF was found not to differ on the latitudinal scale, the infection rate attributable to Hypocreales increases towards the equator and that of the Entomophthorales towards the poles.
- Little is known about the selective pressures that entomopathogenic fungi exert on insect populations. We found that EPF may create selective pressures on the evolution of host plant range of herbivorous insects. The elegant case of the incidence of *Akanthomyces muscarius* being restricted to larvae feeding on birch should indicate selection against using this host plant species.
- Evolutionary ecology of insect-fungus interactions remains poorly known: even though my studies outlined some paths which may be worth examining, much remains to be done in this field.

## SUMMARY IN ESTONIAN

### Patogeensete seente liigirikkus ja ökoloogiline roll putukapopulatsioonides

Ökoloogia üks põhiülesandeid on seletada populatsioonide arvukuse erinevusi ajas ja ruumis ning mõista neid erinevusi põhjustavad tegureid. Populatsioonide arvukust mõjutavad biotilised tegurid jaotatakse “alt üles” mõjudeks (*bottom-up*), kui mõjutajaks on madalam troofiline tase (uuritava toit) või “ülevalt alla” mõjudeks (*top-down*), kui mõju tuleb kõrgema troofilise taseme poolt (kes uuritavat toiduks kasutab). Herbivoorsete putukate puhul on alt üles mõjud kahtlemata olulised, mõjutab ju putukate viljakust toidutaim läbi oma kvaliteedi, kvantiteedi või ka läbi erinevate kaitsekohastumuste nagu keemilised ühendid, mehaaniline kaitse jms. Viimase aja teadustööd on siiski näidanud, et toidu mõju putuka kohasusele pole nii suur kui varasemalt on arvatud. Pigem hoiab putukate arvukust kontrolli all siiski nende suur suremus, mida põhjustavad putukate looduslikud vaenlased: kiskjad, parasitoidid ja patogeenid.

Kiskjate, nii selgroogsete kui selgrootute, kui ka parasitoidide poolt põhjustatud suremuse mõju putukate populatsioonide arvukusele ja selle dünaamikale on põhjalikult uuritud. Samas pole patogeenide puhul piisavat selgust isegi mitte põhinäitajate osas: me ei tea, kui palju nad populatsioonis suremust põhjustavad. Patogeenide ökoloogilise rolli uurimine on keeruline, kuna nende hulka kuuluvad väga erinevad organismid alustades viirustest ja bakteritest ning lõpetades ümarusside ja seentega, mis eeldab ka mitmekesisiste taksonispetsiifiliste uurimismeetodite rakendamist.

Käesolev doktoritöö keskendub entomopatogeensete (edaspidi EP) seente mitmekesisuse ja nende patogeenide poolt põhjustatud suremuse uurimisele looduslikes populatsioonides, tulemusi tõlgendatakse putukate populatsioonidünaamika ja evolutsioonilise ökoloogia vaatevinklist. Töö algas varem kogutud valimite (putukaökoloogiliste katsete käigus tuvastatud seeninfektsiooni juhud liblikanukkudel, **I artikkel**) uurimisega, millele lisaks otsisin kokku ja analüüsisin olemasolevat kirjandust, mis dokumenteerib EPS poolt põhjustatud letaalseid infektsioone (edaspidi, seenetamist) looduslikes populatsioonides (**V**). Töö järgmises etapis viisin läbi katseid looduslähedastes tingimustes Eestis (**II**) ja Argentiinas (**III**), kus kasvasin liblikaid võimalusel munast valmikuni ning dokumenteerisin seenetamist ning erinevaid seenetamist potentsiaalselt mõjutavaid parameetreid. Kõrvutamaks looduslähedastes oludes läbi viidud katseid andmetega manipuleerimata loodusest, seirasin hundinuial (*Typha latifolia*) elavate öölaste seenetamist Kagu-Eestis kahe aasta jooksul (**IV**).

EP seeni on praeguseks tuvastatud üle 1000 liigi, millest paljud on globaalse levikuga. See arv on kindlasti alahinnatud, kuna seeneriik on väga mitmekesine oma 18 hõimkonnaga ja siiani puudulikult uuritud. Lisaks juba teada olevale kümnele hõimkonnale, mis sisaldavad entomopatogeenseid seeni, täiendab minu doktoritöö seda nimistut hiljuti eristatud hõimkonnaga kõduhallikseened

(*Mortierellomycota*); ka tuvastati töö raames esmakordselt et mitmete seeneliikide entomopatogeensus.

Empiirilises töös liblikatega selgus EP seente suur liigirikkus, erinevates osatöodes (I–IV) tuvastati EP seeni vastavalt 25, 23, 8 ja 10 liiki. Tulemus on uudne, kuna konkreetsete putukapopulatsioonidega seotud EP seente kogu mitmekesisust dokumenteerivaid töid on maailmas leida vaid käputäis. Suurt interaktsioonide hulka näitab ka kirjanduse analüüs (V), kus 79 asjakohasest uuringust (dokumenteerisid EPS-putukas interaktsioone looduslikes populatsioonides) leiti andmeid kokku 122 seeneliigi kohta, mis nakatasid 104 putukaliiki.

Ühtegi tõendit EP seente spetsialiseerumisest kindlale liblikaliigile meie tödest välja ei tulnud. Pigem näib EP seente liigiline koosseis sõltuvat peremehe arengujärgust (II). Röövikute patogeenide kooslustes olid valdavad pigem oportunistlikeks patogeenideks peetavad seened. Need on seened, kes enamuse oma elust veedavad lagundajatena ning hakkavad patogeeniks ainult sobivatel tingimustel (nõrgestatud või haavatud putukas). Liblikate röövikud söövad palju taimset massi, suurendades patogeeni sissesöömise tõenäosust, kuna viimased võivad kasvada ka endofüütidena taimedes. Suukaudne nakatamine on oportunistidele tihti ainsaks võimaluseks, sest erinevalt spetsialiseerunud seenpatogeenidest ei suuda nad tungida läbi putuka kitiinkesta.

Töös dokumenteeritud patogeenide suur liigirikkus viitab ökoloogiliste interaktsioonide paljususele ja mitmekesisusele putukate ja seente vahel. Seetõttu on oodatav, et EP seentel võiks olla oluline roll putukate populatsioonidünaamikas. Käesoleva töö raames ei suutnud me siiski näidata EP seentel putukapopulatsioonide reguleerivat rolli, kuna seenpatogeenide põhjustatud suurem liblikatel oli pigem tagasihoidlik, jäädes meie katsete põhjal liblikate puhul 2–17% piiridesse (I–IV). Ka kirjanduse analüüs andis sarnase tulemuse: üldine EP seentele omistatava suuremuse mediaan jääb putukate looduslikes populatsioonides 8% kanti (V). Selline suuremuse protsent ei toeta võimalust, et seentel on oluline “ülevallt alla” mõju putukate populatsioonidünaamikale. Samuti ei erinenud EP seentega nakkuste protsent troopika, subtroopika ja parasvöötme vahel, kuigi erinevate seeneseltside põhjustatud suurem oli laiuskraaditi erinev. Näiteks leidsime kinnitust varasemale arvamusele, et helekottseenelaadsed (*Hypocreales*) põhjustavad suuremat suuremust troopikas, samas kui putukahallikulaadsetele (*Entomophthorales*) omistatav suurem kasvab koos laiuskraadidega. Leidsime seega erinevuse EP seente koosluste taksonoomilises koosseisus, analoogselt sellega, mida nägime putukate erinevaid arengujärke võrreldes.

Üheski doktoritöö raames tehtud katses ei täheldatud siiski seeninfektsiooni täielikku puudumist, mis viitab sellele, et seenpatogeenid on putukapopulatsioonides alati olemas. Usutavasti ei ole seenpatogeeniga nakatumine piiratud seeneoste olemasoluga putuka keskkonnas ning putuka seenega nakatumist või mittenakatamist määravad mingid isendi või keskkonna parameetrid. Kuna seene seisukohast edukas nakatamine lõppeb putuka surmaga, looks selliste parameetrite olemasolu valikusurve putukate tunnustele. Kui näiteks seenega nakatumise tõenäosus muutub vastavalt aastaajale, peaks vastav valikusurve mõjutama

putuka fenoloogiat. Doktoritöö raames siiski ei leitud seost EP seenega nakatumise ja kuupäeva vahel (II). Sarnaselt ei leidnud me erinevusi ruumis ei väiksel (kilomeetri piires; II) ega ka suuremal (Kagu-Eesti; IV) skaalal. Asukoha mõju võiks tuleneda nakkustekitaja varasemast levikust piirkonnas või näiteks sobivast mikrokliimast, mida erinevad taimekooslused võivad pakkuda. See tähendaks taimede kaudset mõju EP seentega nakatumisele. Katseliselt me siiski “alt üles” mõju ei näinud. Kuigi toidutaimede manipuleeritud kvaliteet mõjutas putuka edukust (II), ei olnud see korreleeritud EP seentega nakatumisega. Sarnaselt ei omanud ka taime kvaliteedinäitajad (IV) mõju EP seentega nakatumisele.

Kui EP seentega nakatumise tõenäosus sõltuks toidutaimede liigist, toimiks valikusurve selle taime toiduks kasutamise vastu. Käesoleva doktoritöö raames tehtud uurimus on üks esimesi maailmas, kus on näidatud seost kindla seeneliigiga nakatumise ja toidutaimede liigi vahel. Nimelt leidsime, et helekottseenelaadse seenega *Akanthomyces muscarius* nakatusid vaid need liblikad, kes toitustid kasel (II). Selline seos ei sõltunud toidutaimesendi asukohast ega putuka liigist. On teada mõned EP seened, kes suudavad elada taimedes endofüütidena ning varasemalt on oletatud, et sellised endofüütsed vormid suudavad võimaluse avanedes üle minna entomopatoogeensele toitumisele. Selline asjade käik toetaks nn turvamehe hüpoteesi (*bodyguard hypothesis*), mille kohaselt loovad taimed oma vaenlaste vaenlastele soodsaid tingimusi, panustades niimoodi oma kaitsesse. Sama hüpoteesi toetab kaudset ka meie leid (V), et EP seentega nakatumise osakaal on kõrgem puudel kui rohhtaimedel toituvatel putukatel. Kuna entomopatoogeensus seentes on vähemalt korra tekkinud taimepatogeenide kohastumisest paremale (lämmastiku-rikkamale) toidule, ei ole üllatav, et EP seened ja (putukate toidu)-taimed on omavahelistes suhetes (II, III, V).

## ACKNOWLEDGEMENTS

I thank professor Toomas Tammaru for taking on the not always an easy job of supervising and pushing me forward in the field of science. He is an exemplary scientist and man whose intelligence and witty humor has never ceased to amaze me. I thank Kadri Põldmaa for supporting me from the first meeting, as a second year bachelor student with stubborn research interests, until the far ends of doctoral studies. Through many highs and lows they are the two people without whom this piece of writing would not have seen the sunlight. Thank you both for your patience, understanding and the opportunity to be your “academic son”.

I would like to thank also my colleagues mainly from disciplines of mycology and entomology, for advice, constructive criticism or just for creating a fine scientific atmosphere. Thank you for being there when I had questions, celebratory drinks or just an empty stomach (in no particular order): Toomas Esperk, Leonard O. Opere, Tiit Teder, Kelly Kittus, Robert B. Davis, John Clarke, Ants Kaasik, Sille Holm, Mari-Liis Viljur, Stenio I. A. Foerster, Vineesh Nedumpally, Daniel Valdma, Auli Veske, Erki Õunap, Pille Gerhold, Virve Sõber, Juhan Javoš, Nidal Fetnassi, Jane Oja, Kadri Pärtel, Siim-Kaarel Sepp, Tanel Vahter, Inga Hiiesalu, Kati Kungas, Maarja Öpik, Leho Tedersoo, Heidi Tamm, Irma Zettur, Irja Saar and Margret Sisask. Thank you for helping me rear insects Kadri Ude, Piia Tomingas and Mihkel Annusver.

Also I would like to thank colleagues from Argentina who welcomed me to their beautiful country: Andrea A. Coccuci, Alicia N. Sersic, Ana Ibañez, Juliana V. Izquierdo, Maria Sosa Pivatto, Santiago M. Costas, Florencia Soteras, Magali Bruni, Adrián Giaquinta, Valentina Borda, Francisco Kuhar, Adriana I. Zapata, Hernan M. Beccacece and Gerardo Robledo. You are always welcome in Estonia if travels should bring you here.

A special thanks to my sisters of other academic mothers: Marili Sell, Susanna Vain, Iris Reinula, Mari-Ann Lind, Linda Ruusalepp. Of course a thank you must be said to my biological family Katiliina, Edwin, Iris and Minna, for never-ending support and also my friends from TÜLKR and elsewhere. Finally my utmost gratitude goes to Sten-Oliver, Pääsu, Martin, Jarmo, Lauri, Adam, Kati, Linda, Sandra, Paula, Liisi, Epp, Kertu Liis, Ott and Matis for staying by my side even though I sometimes complained too much about science.

## REFERENCES

- Abbas, M.S.T., 2022. Pathogenicity of entomopathogenic nematodes to dipteran leaf miners, house flies and mushroom flies. *Egyptian Journal of Biological Pest Control* 32, 76. <https://doi.org/10.1186/s41938-022-00566-y>
- Akıner, M.M., Öztürk, M., Güney, İ., Usta, A., 2020. Natural infection potential and efficacy of the entomopathogenic fungus *Beauveria bassiana* against *Orosanga japonica* (Melichar). *Egyptian Journal of Biological Pest Control* 30, 68. <https://doi.org/10.1186/s41938-020-00269-2>
- 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, 721–738. <https://doi.org/10.1111/jen.12072>
- Amatuzzi, R.F., Cardoso, N., Poltronieri, A.S., Poitevin, C.G., Dalzoto, P., Zawadeneak, M.A., Pimentel, I.C., 2017. Potential of endophytic fungi as biocontrol agents of *Duponchelia fovealis* (Zeller) (Lepidoptera:Crambidae). *Brazilian Journal of Biology* 78, 429–435. <https://doi.org/10.1590/1519-6984.166681>
- Araújo, J.P.M., Hughes, D.P., 2016. Chapter One – Diversity of entomopathogenic fungi: which groups conquered the insect body?, in: Lovett, B., St. Leger, R.J. (Eds.), *Advances in Genetics, Genetics and Molecular Biology of Entomopathogenic Fungi*. Academic Press, pp. 1–39. <https://doi.org/10.1016/bs.adgen.2016.01.001>
- Bahram, M., Küngas, K., Pent, M., Pölme, S., Gohar, D., Pöldmaa, K., 2021. Vertical stratification of microbial communities in woody plants. *Phytobiomes Journal PBIOMES-06-21-0038-R*. <https://doi.org/10.1094/PBIOMES-06-21-0038-R>
- Barelli, L., Moonjely, S., Behie, S.W., Bidochka, M.J., 2016. Fungi with multifunctional lifestyles: endophytic insect pathogenic fungi. *Plant Molecular Biology* 90, 657–664. <https://doi.org/10.1007/s11103-015-0413-z>
- Berryman, A.A., 2003. On principles, laws and theory in population ecology. *Oikos* 103, 695–701.
- Bidochka, M.J., Small, C.L., 2005. Phylogeography of *Metarhizium*, an insect pathogenic fungus, in: *Insect-Fungal Associations: Ecology and Evolution*. Oxford University Press, pp. 28–49.
- Bonsall, M.B., 2004. The impact of diseases and pathogens on insect population dynamics. *Physiological Entomology* 29, 223–236. <https://doi.org/10.1111/j.0307-6962.2004.00389.x>
- Boomsma, J.J., Jensen, A.B., Meyling, N.V., Eilenberg, J., 2014. Evolutionary interaction networks of insect pathogenic fungi. *Annual Review of Entomology* 59, 467–485. <https://doi.org/10.1146/annurev-ento-011613-162054>
- Boucias, D.G., Pendland, J.C., Latge, J.P., 1988. Nonspecific factors involved in attachment of entomopathogenic Deuteromycetes to host insect cuticle. *Applied and Environmental Microbiology* 54, 1795–1805.
- Chen, W., Xie, W., Cai, W., Thaochan, N., Hu, Q., 2021. Entomopathogenic fungi biodiversity in the soil of three provinces located in southwest China and first approach to evaluate their biocontrol potential. *Journal of Fungi* 7, 984. <https://doi.org/10.3390/jof7110984>
- Cornell, H.V., Hawkins, B.A., 1995. Survival patterns and mortality sources of herbivorous insects: some demographic trends. *The American Naturalist* 145, 563–593. <https://doi.org/10.1086/285756>

- Cory, J.S., Ericsson, J.D., 2010. Fungal entomopathogens in a tritrophic context. *Bio-Control* 55, 75–88. <https://doi.org/10.1007/s10526-009-9247-4>
- Deka, B., Baruah, C., Babu, A., 2021. Entomopathogenic microorganisms: their role in insect pest management. *Egyptian Journal of Biological Pest Control* 31, 121. <https://doi.org/10.1186/s41938-021-00466-7>
- Eilenberg, J., Bresciani, J., Latgé, J.-P., 1986. Ultrastructural studies of primary spore formation and discharge in the genus *Entomophthora*. *Journal of Invertebrate Pathology* 48, 318–324. [https://doi.org/10.1016/0022-2011\(86\)90060-1](https://doi.org/10.1016/0022-2011(86)90060-1)
- Elliot, Sabelis, Janssen, Geest, V.D., Beerling, Franssen, 2000. Can plants use entomopathogens as bodyguards? *Ecology Letters* 3, 228–235. <https://doi.org/10.1046/j.1461-0248.2000.00137.x>
- Filotas, M.J., Hajek, A.E., Humber, R.A., 2003. Prevalence and biology of *Furia gastropachae* (Zygomycetes: Entomophthorales) in populations of forest tent caterpillar (Lepidoptera: Lasiocampidae). *The Canadian Entomologist* 135, 359–378. <https://doi.org/10.4039/n02-004>
- Georgieva, M., Takov, D., Georgiev, G., Pilarska, D., Pilarski, P., Mirchev, P., Humber, R., 2014. Studies on non-target phyllophagous insects in oak forests as potential hosts of *Entomophaga maimaiga* (Entomophthorales: Entomophthoraceae) in Bulgaria. *Acta Zoologica Bulgarica* 66, 115–120.
- Giladi, I., 2006. Choosing benefits or partners: a review of the evidence for the evolution of myrmecochory. *Oikos* 112, 481–492. <https://doi.org/10.1111/j.0030-1299.2006.14258.x>
- Goldstein, P.Z., 2017. Diversity and significance of Lepidoptera: a phylogenetic perspective, in: Footitt, R.G., Adler, P.H. (Eds.), *Insect Biodiversity*. John Wiley & Sons, Ltd, Chichester, UK, pp. 463–495. <https://doi.org/10.1002/9781118945568.ch13>
- Grundschober, A., Tuor, U., Aebi, M., 1998. In vitro cultivation and sporulation of *Neozygites parvispora* (Zygomycetes: Entomophthorales). *Systematic and Applied Microbiology* 21, 461–469. [https://doi.org/10.1016/S0723-2020\(98\)80057-X](https://doi.org/10.1016/S0723-2020(98)80057-X)
- Hajek, A., Goettel, M., 2007. Guidelines for evaluating effects of entomopathogens on non-target organisms, in: Lacey, L.A., Kaya, H.K. (Eds.), *Field Manual of Techniques in Invertebrate Pathology*. Springer, Dordrecht, pp. 816–833. [https://doi.org/10.1007/978-1-4020-5933-9\\_40](https://doi.org/10.1007/978-1-4020-5933-9_40)
- Hajek, A.E., 1997. Ecology of terrestrial fungal entomopathogens, in: Jones, J.G. (Ed.), *Advances in Microbial Ecology*, *Advances in Microbial Ecology*. Springer US, Boston, MA, pp. 193–249. [https://doi.org/10.1007/978-1-4757-9074-0\\_5](https://doi.org/10.1007/978-1-4757-9074-0_5)
- Hajek, A.E., Eilenberg, J., 2018. *Natural enemies: an introduction to biological control*. Cambridge University Press.
- Harrison, R., Hoover, K., 2012. Chapter 4. Baculoviruses and other occluded insect viruses, in: *Insect Pathology*. pp. 73–131. <https://doi.org/10.1016/B978-0-12-384984-7.00004-X>
- Hawkins, B.A., 1994. *Pattern and process in host-parasitoid interactions*. Cambridge University Press, Cambridge. <https://doi.org/10.1017/CBO9780511721885>
- Hawkins, B.A., Cornell, H.V., Hochberg, M.E., 1997. Predators, parasitoids, and pathogens as mortality agents in phytophagous insect populations. *Ecology* 78, 2145–2152. [https://doi.org/10.1890/0012-9658\(1997\)078\[2145:PPAPAM\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1997)078[2145:PPAPAM]2.0.CO;2)
- Heil, M., 2014. Herbivore-induced plant volatiles: targets, perception and unanswered questions. *New Phytologist* 204, 297–306. <https://doi.org/10.1111/nph.12977>

- Hesketh, H., Roy, H.E., Eilenberg, J., Pell, J.K., Hails, R.S., 2010. Challenges in modelling complexity of fungal entomopathogens in semi-natural populations of insects. *BioControl* 55, 55–73. <https://doi.org/10.1007/s10526-009-9249-2>
- Hicks, B.J., Watt, A.D., 2000. Fungal disease and parasitism in *Panolis flammea* during 1998: evidence of change in the diversity and impact of the natural enemies of a forest pest. *Forestry: An International Journal of Forest Research* 73, 31–36. <https://doi.org/10.1093/forestry/73.1.31>
- Hochberg, M.E., Ives, A.R., 2000. Parasitoid population biology. Princeton University Press, United Kingdom.
- Holder, D.J., Keyhani, N.O., 2005. Adhesion of the entomopathogenic fungus *Beauveria (Cordyceps) bassiana* to substrata. *Applied and Environmental Microbiology* 71, 5260–5266. <https://doi.org/10.1128/AEM.71.9.5260-5266.2005>
- Humber, R.A., 2008. Evolution of entomopathogenicity in fungi. *Journal of Invertebrate Pathology, Special Issue for SIP 2008* 98, 262–266. <https://doi.org/10.1016/j.jip.2008.02.017>
- Il'inykh, A.V., 2007. Epizootiology of baculoviruses. *Biology Bulletin* 34, 434–441. <https://doi.org/10.1134/S1062359007050020>
- Jackson, M.A., Dunlap, C.A., Jaronski, S.T., 2010. Ecological considerations in producing and formulating fungal entomopathogens for use in insect biocontrol. *BioControl* 55, 129–145. <https://doi.org/10.1007/s10526-009-9240-y>
- Jurat-Fuentes, J., Jackson, T., 2012. Chapter 8. Bacterial entomopathogens, in: *Insect Pathology*. pp. 265–349. <https://doi.org/10.1016/B978-0-12-384984-7.00008-7>
- Kepler, R.M., Luangsa-Ard, J.J., Hywel-Jones, N.L., Quandt, C.A., Sung, G.-H., Rehner, S.A., Aime, M.C., Henkel, T.W., Sanjuan, T., Zare, R., Chen, M., Li, Z., Rossman, A.Y., Spatafora, J.W., Shrestha, B., 2017. A phylogenetically-based nomenclature for Cordycipitaceae (Hypocreales). *IMA Fungus* 8, 335–353. <https://doi.org/10.5598/ima fungus.2017.08.02.08>
- Kleespies, R.G., Huger, A.M., Zimmermann, G., 2008. Diseases of insects and other arthropods: results of diagnostic research over 55 years. *Biocontrol Science and Technology* 18, 439–482. <https://doi.org/10.1080/09583150802011618>
- Kõljalg, U., Nilsson, H.R., Schigel, D., Tedersoo, L., Larsson, K.-H., May, T.W., Taylor, A.F.S., Jeppesen, T.S., Frøslev, T.G., Lindahl, B.D., Põldmaa, K., Saar, I., Suija, A., Savchenko, A., Yatsiuk, I., Adojaan, K., Ivanov, F., Piirmann, T., Pöhönen, R., Zirk, A., Abarenkov, K., 2020. The taxon hypothesis paradigm—on the unambiguous detection and communication of taxa. *Microorganisms* 8, 1910. <https://doi.org/10.3390/microorganisms8121910>
- Koppenhöfer, A.M., 2007. Nematodes, in: Lacey, L.A., Kaya, H.K. (Eds.), *Field Manual of Techniques in Invertebrate Pathology: Application and Evaluation of Pathogens for Control of Insects and Other Invertebrate Pests*. Springer Netherlands, Dordrecht, pp. 249–264. [https://doi.org/10.1007/978-1-4020-5933-9\\_11](https://doi.org/10.1007/978-1-4020-5933-9_11)
- Lacey, L.A., Grzywacz, D., Shapiro-Ilan, D.I., Frutos, R., Brownbridge, M., Goettel, M.S., 2015. Insect pathogens as biological control agents: Back to the future. *Journal of Invertebrate Pathology* 132, 1–41. <https://doi.org/10.1016/j.jip.2015.07.009>
- Lewis, E.E., Clarke, D.J., 2012. Chapter 11 – Nematode parasites and entomopathogens, in: Vega, F.E., Kaya, H.K. (Eds.), *Insect Pathology (Second Edition)*. Academic Press, San Diego, pp. 395–424. <https://doi.org/10.1016/B978-0-12-384984-7.00011-7>
- Liebold, A., Elkinton, J., Williams, D., Muzika, R.-M., 2000. What causes outbreaks of the gypsy moth in North America? *Population Ecology* 42, 257–266. <https://doi.org/10.1007/PL00012004>

- Meister, H., Esperk, T., Välimäki, P., Tammaru, T., 2017a. Evaluating the role and measures of juvenile growth rate: latitudinal variation in insect life histories. *Oikos* 126, 1726–1737. <https://doi.org/10.1111/oik.04233>
- Meister, H., Hämäläinen, H.R., Valdma, D., Martverk, M., Tammaru, T., 2018. How to become larger: ontogenetic basis of among-population size differences in a moth. *Entomologia Experimentalis et Applicata* 166, 4–16. <https://doi.org/10.1111/eea.12634>
- Meister, H., Tammaru, T., Sandre, S.-L., Freitak, D., 2017b. Sources of variance in immunological traits: evidence of congruent latitudinal trends across species. *Journal of Experimental Biology* 220, 2606–2615. <https://doi.org/10.1242/jeb.154310>
- Meyling, N.V., Hajek, A.E., 2010. Principles from community and metapopulation ecology: application to fungal entomopathogens. *BioControl* 55, 39–54. <https://doi.org/10.1007/s10526-009-9246-5>
- Mills, N., 2010. Egg parasitoids in biological control and integrated pest management, in: Consoli, F.L., Parra, J.R.P., Zucchi, R.A. (Eds.), *Egg Parasitoids in Agroecosystems with Emphasis on Trichogramma*, Progress in Biological Control. Springer Netherlands, Dordrecht, pp. 389–411. [https://doi.org/10.1007/978-1-4020-9110-0\\_15](https://doi.org/10.1007/978-1-4020-9110-0_15)
- Mora-Aguilera, G., Cortez-Madrigal, H., Acevedo-Sánchez, G., 2017. Epidemiology of entomopathogens: basis for rational use of microbial control of insects. *Southwestern Entomologist* 42, 153–169. <https://doi.org/10.3958/059.042.0116>
- Nicoletti, R., Becchimanzi, A., 2020. Endophytism of *Lecanicillium* and *Akanthomyces*. *Agriculture* 10, 205. <https://doi.org/10.3390/agriculture10060205>
- Nixon, A.E., Roland, J., 2012. Generalist predation on forest tent caterpillar varies with forest stand composition: an experimental study across multiple life stages. *Ecological Entomology* 37, 13–23. <https://doi.org/10.1111/j.1365-2311.2011.01330.x>
- Oxford English Dictionary, 2023. parasite, n.
- Pell, J.K., Hannam, J.J., Steinkraus, D.C., 2010. Conservation biological control using fungal entomopathogens. *BioControl* 55, 187–198. <https://doi.org/10.1007/s10526-009-9245-6>
- Peterson, R.K.D., Davis, R.S., Higley, L.G., Fernandes, O.A., 2009. Mortality risk in insects. *Environmental Entomology* 38, 2–10. <https://doi.org/10.1603/022.038.0102>
- Pinkantayong, P., Suzuki, S., Kubo, M., Muramoto, K., Kamata, N., 2015. A hierarchical Bayesian model to estimate the unobservable predation rate on sawfly cocoons by small mammals. *Ecology and Evolution* 5, 733–742. <https://doi.org/10.1002/ece3.1394>
- Pinto, J.R.L., Fernandes, O.A., Higley, L.G., Peterson, R.K.D., 2022. Do patterns of insect mortality in temperate and tropical zones have broader implications for insect ecology and pest management? *PeerJ* 10, e13340. <https://doi.org/10.7717/peerj.13340>
- Podgwaite, J.D., Mazzone, H.M., 1986. Latency of insect viruses, in: Maramorosch, K., Murphy, F.A., Shatkin, A.J. (Eds.), *Advances in Virus Research*. Academic Press, pp. 293–320. [https://doi.org/10.1016/S0065-3527\(08\)60266-3](https://doi.org/10.1016/S0065-3527(08)60266-3)
- Poitevin, C.G., Porsani, M.V., Poltronieri, A.S., Zawadneak, M.A.C., Pimentel, I.C., 2018. Fungi isolated from insects in strawberry crops act as potential biological control agents of *Duponchelia fovealis* (Lepidoptera: Crambidae). *Applied Entomology and Zoology* 53, 323–331. <https://doi.org/10.1007/s13355-018-0561-0>
- Pöldmaa, K., Bills, G., Lewis, D.P., Tamm, H., 2019. Taxonomy of the *Sphaerostilbella broomeana*-group (Hypocreales, Ascomycota). *Mycological Progress* 18, 77–89. <https://doi.org/10.1007/s11557-018-01468-w>
- Price, P.W., Denno, R.F., Eubanks, M.D., Finke, D.L., Kaplan, I., 2011. *Insect ecology: behavior, populations and communities*, 1st edition. ed. Cambridge University Press, Cambridge.

- Recherches sur la réaction hémocytaire anticryptogamique de type granulome chez les insectes, 1971. Université Toulouse III – Paul Sabatier, Toulouse.
- Rommel, T., Davison, J., Tammaru, T., 2011. Quantifying predation on folivorous insect larvae: The perspective of life-history evolution. *Biological Journal of the Linnean Society* 104, 1–18. <https://doi.org/10.1111/j.1095-8312.2011.01721.x>
- Rommel, T., Tammaru, T., Mägi, M., 2009. Seasonal mortality trends in tree-feeding insects: a field experiment. *Ecological Entomology* 34, 98–106. <https://doi.org/10.1111/j.1365-2311.2008.01044.x>
- Roslin, T., Hardwick, B., Novotny, V., Petry, W.K., Andrew, N.R., Asmus, A., Barrio, I.C., Basset, Y., Boesing, A.L., Bonebrake, T.C., Cameron, E.K., Dáttilo, W., Donoso, D.A., Drozd, P., Gray, C.L., Hik, D.S., Hill, S.J., Hopkins, T., Huang, S., Koane, B., Laird-Hopkins, B., Laukkanen, L., Lewis, O.T., Milne, S., Mwesige, I., Nakamura, A., Nell, C.S., Nichols, E., Prokurat, A., Sam, K., Schmidt, N.M., Slade, A., Slade, V., Suchanková, A., Teder, T., van Nouhuys, S., Vandvik, V., Weissflog, A., Zhukovich, V., Slade, E.M., 2017. Higher predation risk for insect prey at low latitudes and elevations. *Science* 356, 742–744. <https://doi.org/10.1126/science.aaj1631>
- Roy, H.E., Cottrell, T.E., 2013. Forgotten natural enemies: interactions between coccinellids and insect-parasitic fungi. *European Journal of Entomology* 105, 391–398. <https://doi.org/10.14411/eje.2008.049>
- Ruiz-Guerra, B., Renton, K., Dirzo, R., 2012. Consequences of fragmentation of tropical moist forest for birds and their role in predation of herbivorous insects. *Biotropica* 44, 228–236. <https://doi.org/10.1111/j.1744-7429.2011.00795.x>
- Samson, R.A., Evans, H.C., Latge, J.-P., 2013. *Atlas of entomopathogenic fungi*. Springer Science & Business Media, Berlin/Heidelberg, Germany.
- Sang, A., Teder, T., 2011. Dragonflies cause spatial and temporal heterogeneity in habitat quality for butterflies. *Insect Conservation and Diversity* 4, 257–264. <https://doi.org/10.1111/j.1752-4598.2011.00134.x>
- Santos, A.C. da S., Diniz, A.G., Tiago, P.V., Oliveira, N.T. de, 2020. Entomopathogenic *Fusarium* species: a review of their potential for the biological control of insects, implications and prospects. *Fungal Biology Reviews* 34, 41–57. <https://doi.org/10.1016/j.fbr.2019.12.002>
- Secil, E.S., Sevim, A., Demirbag, Z., Demir, I., 2012. Isolation, characterization and virulence of bacteria from *Ostrinia nubilalis* (Lepidoptera: Pyralidae). *Biologia* 67, 767–776. <https://doi.org/10.2478/s11756-012-0070-5>
- Shang, Y., Xiao, G., Zheng, P., Cen, K., Zhan, S., Wang, C., 2016. Divergent and convergent evolution of fungal pathogenicity. *Genome Biology and Evolution* 8, 1374–1387. <https://doi.org/10.1093/gbe/evw082>
- Sharma, L., Marques, G., 2018. *Fusarium*, an entomopathogen—a myth or reality? *Pathogens* 7. <https://doi.org/10.3390/pathogens7040093>
- Speight, M.R., Hunter, M.D., Watt, A.D., 2008. *Ecology of insects: concepts and applications*. Wiley.
- St. Leger, R.J., Wang, J.B., 2020. *Metarhizium*: jack of all trades, master of many. *Open Biology* 10, 200307. <https://doi.org/10.1098/rsob.200307>
- Stireman, J., Singer, M., 2003. Determinants of parasitoid-host associations: insights from a natural Tachinid-Lepidopteran community. *Ecology* 84, 296–310. [https://doi.org/10.1890/0012-9658\(2003\)084\[0296:DOPHAI\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[0296:DOPHAI]2.0.CO;2)
- Teder, T., Esperk, T., Remmel, T., Sang, A., Tammaru, T., 2010. Counterintuitive size patterns in bivoltine moths: late-season larvae grow larger despite lower food quality. *Oecologia* 162, 117–125. <https://doi.org/10.1007/s00442-009-1439-1>

- Teder, T., Tammaru, T., 2002. Cascading effects of variation in plant vigour on the relative performance of insect herbivores and their parasitoids: Cascading effects and population dynamics. *Ecological Entomology* 27, 94–104. <https://doi.org/10.1046/j.0307-6946.2001.00381.x>
- Teder, T., Tammaru, T., Kaasik, A., 2013. Exploitative competition and coexistence in a parasitoid assemblage. *Population Ecology* 55, 77–86. <https://doi.org/10.1007/s10144-012-0341-6>
- Teder, T., Tammaru, T., Pedmanson, R., 1999. Patterns of host use in solitary parasitoids (Hymenoptera, Ichneumonidae): field evidence from a homogeneous habitat. *Ecography* 22, 79–86. <https://doi.org/10.1111/j.1600-0587.1999.tb00456.x>
- Tedersoo, L., Bahram, M., Põlme, S., Kõljalg, U., Yorou, N.S., Wijesundera, R., Ruiz, L.V., Vasco-Palacios, A.M., Thu, P.Q., Suija, A., Smith, M.E., Sharp, C., Saluveer, E., Saitta, A., Rosas, M., Riit, T., Ratkowsky, D., Pritsch, K., Põldmaa, K., Piepenbring, M., Phosri, C., Peterson, M., Parts, K., Pärtel, K., Otsing, E., Nouhra, E., Njouonkou, A.L., Nilsson, R.H., Morgado, L.N., Mayor, J., May, T.W., Majuakim, L., Lodge, D.J., Lee, S.S., Larsson, K.-H., Kohout, P., Hosaka, K., Hiiesalu, I., Henkel, T.W., Harend, H., Guo, L., Greslebin, A., Grelet, G., Geml, J., Gates, G., Dunstan, W., Dunk, C., Drenkhan, R., Dearnaley, J., De Kesel, A., Dang, T., Chen, X., Buegger, F., Brearley, F.Q., Bonito, G., Anslan, S., Abell, S., Abarenkov, K., 2014. Global diversity and geography of soil fungi. *Science* 346, 1256688. <https://doi.org/10.1126/science.1256688>
- Tedersoo, L., Sánchez-Ramírez, S., Kõljalg, U., Bahram, M., Döring, M., Schigel, D., May, T., Ryberg, M., Abarenkov, K., 2018. High-level classification of the Fungi and a tool for evolutionary ecological analyses. *Fungal Diversity* 90, 135–159. <https://doi.org/10.1007/s13225-018-0401-0>
- Townsend, R.J., Glare, T.R., Willoughby, B.E., 1995. The fungi *Beauveria* spp. cause epizootics in grass grub populations in Waikato. *Proceedings of the New Zealand Plant Protection Conference* 48, 237–241. <https://doi.org/10.30843/nzpp.1995.48.11488>
- Vega, F.E., 2018. The use of fungal entomopathogens as endophytes in biological control: a review. *Journal of Forest Research* 110, 4–30. <https://doi.org/10.1080/00275514.2017.1418578>
- Vega, F.E., Blackwell, M. (Eds.), 2005. *Insect-fungal associations: ecology and evolution*. Oxford University Press, Oxford, New York.
- Vega, F.E., Kaya, H.K., 2012. *Insect pathology*, 2nd edition. ed. Academic Press, Cambridge, MA, USA.
- Vega, F.E., Meyling, N.V., Luangsa-ard, J.J., Blackwell, M., 2012. Chapter 6 – Fungal entomopathogens, in: Vega, F.E., Kaya, H.K. (Eds.), *Insect Pathology* (Second Edition). Academic Press, San Diego, pp. 171–220. <https://doi.org/10.1016/B978-0-12-384984-7.00006-3>
- Vidal, M.C., Murphy, S.M., 2018. Bottom-up vs. top-down effects on terrestrial insect herbivores: a meta-analysis. *Ecology Letters* 21, 138–150. <https://doi.org/10.1111/ele.12874>
- Wang, C., St Leger, R.J., 2007. The MAD1 adhesin of *Metarhizium anisopliae* links adhesion with blastospore production and virulence to insects, and the MAD2 adhesin enables attachment to plants. *Eukaryotic Cell* 6, 808–816. <https://doi.org/10.1128/EC.00409-06>

- Wang, Y.-B., Wang, Y., Fan, Q., Duan, D.-E., Zhang, G.-D., Dai, R.-Q., Dai, Y.-D., Zeng, W.-B., Chen, Z.-H., Li, D.-D., Tang, D.-X., Xu, Z.-H., Sun, T., Nguyen, T.-T., Tran, N.-L., Dao, V.-M., Zhang, C.-M., Huang, L.-D., Liu, Y.-J., Zhang, X.-M., Yang, D. R., Sanjuan, T., Liu, X.-Z., Yang, Z.L., Yu, H., 2020. Multigene phylogeny of the family Cordycipitaceae (Hypocreales): new taxa and the new systematic position of the Chinese cordycipitoid fungus *Paecilomyces hepiali*. *Fungal Diversity* 103, 1–46. <https://doi.org/10.1007/s13225-020-00457-3>
- Wilkinson, D.M., Sherratt, T.N., 2016. Why is the world green? The interactions of top–down and bottom–up processes in terrestrial vegetation ecology. *Plant Ecology & Diversity* 9, 127–140. <https://doi.org/10.1080/17550874.2016.1178353>
- Zhu, G., Ding, W., Xue, M., Zhao, Y., Li, M., Li, Z., 2022. Identification and pathogenicity of a new entomopathogenic fungus, *Mucor hiemalis* (Mucorales: Mucorales), on the root maggot, *Bradysia odoriphaga* (Diptera: Sciaridae). *Journal of Insect Science* 22, 2. <https://doi.org/10.1093/jisesa/ieac010>
- Zimmermann, G., Huger, A.M., Langenbruch, G.A., Kleespies, R.G., 2016. Pathogens of the European corn borer, *Ostrinia nubilalis*, with special regard to the microsporidium *Nosema pyrausta*. *Journal of Pest Science* 89, 329–346. <https://doi.org/10.1007/s10340-016-0749-4>
- Zúbrik, M., Hajek, A., Pilarska, D., Špilda, I., Georgiev, G., Hrašovec, B., Hirka, A., Goertz, D., Hoch, G., Barta, M., Saniga, M., Kunca, A., Nikolov, C., Vakula, J., Galko, J., Pilarski, P., Csóka, G., 2016. The potential for *Entomophaga maimaiga* to regulate gypsy moth *Lymantria dispar* (L.) (Lepidoptera: Erebidae) in Europe. *Journal of Applied Entomology* 140, 565–579. <https://doi.org/10.1111/jen.12295>

## **PUBLICATIONS**

## CURRICULUM VITAE

**Name:** Robin Gielen  
**Date of birth:** 22.01.1993  
**Citizenship:** Estonian  
**Contact:** Department of Zoology, Institute of Ecology and Earth Science,  
J. Liivi 2, 50409, Tartu, Estonia  
**E-mail:** robin.gielen@ut.ee

### Education:

2018 – ... University of Tartu, Zoology and Hydrobiology, PhD  
2016 – 2018 University of Tartu, Biology, M.Sc.  
2012 – 2015 University of Tartu, Biology, B.Sc.  
2009 – 2012 Hugo Treffneri gümnaasium  
2000 – 2009 Mart Reiniku kool

### Honours and awards:

2014 Junior nature protector award, Estonian ministry of environment

### Professional employment:

2022 – 2023 Junior researcher in entomology, University of Tartu

### Research interests:

Entomopathogenic fungi, evolutionary ecology, population dynamics

### Scientific publications:

- Gielen, R.**, Teder, T., Põldmaa, K., Tammaru, T. 2023. Assemblage of entomopathogenic fungi infesting immature stages of Noctuidae (Lepidoptera): High diversity but low effect on host populations. *European Journal of Entomology* 120. DOI: 10.14411/eje.2023.023
- Gielen, R.**, Robledo, G., Zapata, A.I., Tammaru, T., Põldmaa, K. 2022. Entomopathogenic Fungi Infecting Lepidopteran Larvae: A Case from Central Argentina. *Life* 12 (7). DOI: 10.3390/life12070974.
- Gielen, R.**, Põldmaa, K., Tammaru, T. 2022. In search of ecological determinants of fungal infections: A semi-field experiment with folivorous moths. *Ecology and Evolution* 12 (5). DOI: 10.1002/ece3.8926.
- Gielen, R.**, Meister, H., Tammaru, T., Põldmaa, K. 2021. Fungi Recorded on Folivorous Lepidoptera: High Diversity Despite Moderate Prevalence. *Journal of Fungi* 7 (1). DOI: 10.3390/jof7010025
- Põlme, S., Abarenkov, K., Henrik N., R.; Lindahl, B. D., Clemmensen, K. E., Kausrud, H., Nguyen, N., Kjoller, R., Bates, S. T., Baldrian, P., Froslev, T. G., Adojaan, K., Vizzini, A., Suija, A., Pfister, D., Baral, H.-O., Jarv, H., Madrid, H., Norden, J., **Gielen, R.**, Liu, J.-K., ... Tedersoo, Leho. 2021. FungalTraits: a user friendly traits database of fungi and fungus-like stramenopiles. *Fungal Diversity*, 107 (1), 129–132. DOI: 10.1007/s13225-021-00470-0.

**Conference presentations:**

**Gielen, R.**, Põldmaa, K., Tammaru, T. Oral presentation “In search of safe space: Entomopathogenic fungi on folivorous Lepidoptera”. XXII European Congress of Lepidopterology. Laulasmaa, Estonia, 6<sup>th</sup> to 11<sup>th</sup> June 2022.

**Gielen, R.**, Põldmaa, K., Tammaru, T. Oral presentation “Entomopathogenic fungi as selective factors on insect life histories”. Molecular insights to interactoin networks in subarctic and arctic environments. NIBIO Svanhovd Research Station, Norway, 19<sup>th</sup> to 23<sup>rd</sup> August 2019

**Dissertations supervised:**

Triin Sellis, bachelor thesis, 2020, sup. Robin Gielen. *Solitary insects behavioural defence mechanisms against entomopathogenic fungi*. University of Tartu, Faculty of Science and Technology, Institute of Ecology and Earth Sciences, Department of Zoology

**Other activities and memberships:**

Member of the Tartu students’ nature protection organization (since 2013)

*Conference organisation*

Granö research and networking workshop between University of Tartu and University of Turku “Biological interactions from microbes to ecosystem”. 23<sup>rd</sup> to 29<sup>th</sup> August 2020, Tartu, Estonia (co-organiser)

## ELULOOKIRJELDUS

**Nimi:** Robin Gielen  
**Sünniaeg:** 22.01.1993  
**Kodakondsus:** Eesti  
**Kontaktandmed:** Zooloogia osakond, Ökoloogia ja maateaduste instituut,  
J. Liivi 2, 50409, Tartu, Eesti  
**E-mail:** robin.gielen@ut.ee

### Haridustee:

2018 – ... Tartu Ülikool, zooloogia ja hüdrobioloogia, doktoriõpe  
2016 – 2018 Tartu Ülikool, bioloogia, magistriõpe  
2012 – 2015 Tartu Ülikool, bioloogia, bakalaureuseõpe  
2009 – 2012 Hugo Treffneri gümnaasium  
2000 – 2009 Mart Reiniku kool

### Preemiad ja tunnustused:

2014 Noore looduskaitse märk, Keskkonnaministeerium

### Teenistuskäik:

2022 – 2023 Entomoloogia nooremteadur, Tartu Ülikool

### Peamised uurimisvaldkonnad:

Entomopatoogeensed seened, evolutsiooniline ökoloogia, populatsioonidünaamika

### Teaduspublikatsioonid:

- Gielen, R.**, Teder, T., Põldmaa, K., Tammaru, T. 2023. Assemblage of entomopathogenic fungi infesting immature stages of Noctuidae (Lepidoptera): High diversity but low effect on host populations. *European Journal of Entomology* 120. DOI: 10.14411/eje.2023.023
- Gielen, R.**, Robledo, G., Zapata, A.I., Tammaru, T., Põldmaa, K. 2022. Entomopathogenic Fungi Infesting Lepidopteran Larvae: A Case from Central Argentina. *Life* 12 (7). DOI: 10.3390/life12070974.
- Gielen, R.**, Põldmaa, K., Tammaru, T. 2022. In search of ecological determinants of fungal infections: A semi-field experiment with folivorous moths. *Ecology and Evolution* 12 (5). DOI: 10.1002/ece3.8926.
- Gielen, R.**, Meister, H., Tammaru, T., Põldmaa, K. 2021. Fungi Recorded on Folivorous Lepidoptera: High Diversity Despite Moderate Prevalence. *Journal of Fungi* 7 (1). DOI: 10.3390/jof7010025
- Põlme, S., Abarenkov, K., Henrik N., R.; Lindahl, B. D., Clemmensen, K. E., Kausrud, H., Nguyen, N., Kjoller, R., Bates, S. T., Baldrian, P., Froslev, T. G., Adojaan, K., Vizzini, A., Suija, A., Pfister, D., Baral, H.-O., Jarv, H., Madrid, H., Norden, J., **Gielen, R.**, Liu, J.-K., ... Tedersoo, Leho. 2021. FungalTraits: a user friendly traits database of fungi and fungus-like stramenopiles. *Fungal Diversity*, 107 (1), 129–132. DOI: 10.1007/s13225-021-00470-0.

**Konverentsi ettekanded:**

**Gielen, R.,** Põldmaa, K., Tammaru, T. Suuline ettekanne. “In search of safe space: Entomopathogenic fungi on folivorous Lepidoptera”. XXII European Congress of Lepidopterology. Laulasmaa, Eesti, 6–11 juuni 2022.

**Gielen, R.** Põldmaa, K., Tammaru, T. Suuline ettekanne “Entomopathogenic fungi as selective factors on insect life histories”. Molecular insights to interaction networks in subarctic and arctic environments. NIBIO Svanhovd Research Station, Norra, 19–23 august 2019

**Juhendatud väitekirjad:**

Triin Sellis, bakalaureusetöö, 2020, juh. Robin Gielen. *Üksikeluliste putukate käitumuslikud kaitsekohastumused entomopatogeensete seente vastu*. Tartu Ülikool, Ökoloogia ja maateaduste instituut, Zooloogia osakond

**Muud tegevused ja liikmelisus:**

Tartu üliõpilaste looduskaitseringi liige (alates 2013)

*Konverentside korraldamine*

Granö teadusseminar Tartu Ülikooli ja Turu Ülikooli vahel „Bioloogilised koostoimed mikroobidest ökosüsteemideni“. 23–29 august 2020, Tartu, Eesti (TÜ poolne eestvedaja)

## DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

1. **Toivo Maimets.** Studies of human oncoprotein p53. Tartu, 1991, 96 p.
2. **Enn K. Seppet.** Thyroid state control over energy metabolism, ion transport and contractile functions in rat heart. Tartu, 1991, 135 p.
3. **Kristjan Zobel.** Epifüütsete makrosamblike väärtus õhu saastuse indikaatoritena Hamar-Dobani boreaalsetes mägimetsades. Tartu, 1992, 131 lk.
4. **Andres Mäe.** Conjugal mobilization of catabolic plasmids by transposable elements in helper plasmids. Tartu, 1992, 91 p.
5. **Maia Kivisaar.** Studies on phenol degradation genes of *Pseudomonas* sp. strain EST 1001. Tartu, 1992, 61 p.
6. **Allan Nurk.** Nucleotide sequences of phenol degradative genes from *Pseudomonas* sp. strain EST 1001 and their transcriptional activation in *Pseudomonas putida*. Tartu, 1992, 72 p.
7. **Ülo Tamm.** The genus *Populus* L. in Estonia: variation of the species biology and introduction. Tartu, 1993, 91 p.
8. **Jaanus Remme.** Studies on the peptidyltransferase centre of the *E.coli* ribosome. Tartu, 1993, 68 p.
9. **Ülo Langel.** Galanin and galanin antagonists. Tartu, 1993, 97 p.
10. **Arvo Käär.** The development of an automatic online dynamic fluorescence-based pH-dependent fiber optic penicillin flowthrough biosensor for the control of the benzylpenicillin hydrolysis. Tartu, 1993, 117 p.
11. **Lilian Järvekülg.** Antigenic analysis and development of sensitive immunoassay for potato viruses. Tartu, 1993, 147 p.
12. **Jaak Palumets.** Analysis of phytomass partition in Norway spruce. Tartu, 1993, 47 p.
13. **Arne Sellin.** Variation in hydraulic architecture of *Picea abies* (L.) Karst. trees grown under different environmental conditions. Tartu, 1994, 119 p.
13. **Mati Reeben.** Regulation of light neurofilament gene expression. Tartu, 1994, 108 p.
14. **Urmas Tartes.** Respiration rhythms in insects. Tartu, 1995, 109 p.
15. **Ülo Puurand.** The complete nucleotide sequence and infections *in vitro* transcripts from cloned cDNA of a potato A potyvirus. Tartu, 1995, 96 p.
16. **Peeter Hõrak.** Pathways of selection in avian reproduction: a functional framework and its application in the population study of the great tit (*Parus major*). Tartu, 1995, 118 p.
17. **Erkki Truve.** Studies on specific and broad spectrum virus resistance in transgenic plants. Tartu, 1996, 158 p.
18. **Illar Pata.** Cloning and characterization of human and mouse ribosomal protein S6-encoding genes. Tartu, 1996, 60 p.
19. **Ülo Niinemets.** Importance of structural features of leaves and canopy in determining species shade-tolerance in temperate deciduous woody taxa. Tartu, 1996, 150 p.

20. **Ants Kurg.** Bovine leukemia virus: molecular studies on the packaging region and DNA diagnostics in cattle. Tartu, 1996, 104 p.
21. **Ene Ustav.** E2 as the modulator of the BPV1 DNA replication. Tartu, 1996, 100 p.
22. **Aksel Soosaar.** Role of helix-loop-helix and nuclear hormone receptor transcription factors in neurogenesis. Tartu, 1996, 109 p.
23. **Maido Remm.** Human papillomavirus type 18: replication, transformation and gene expression. Tartu, 1997, 117 p.
24. **Tiiu Kull.** Population dynamics in *Cypridium calceolus* L. Tartu, 1997, 124 p.
25. **Kalle Olli.** Evolutionary life-strategies of autotrophic planktonic microorganisms in the Baltic Sea. Tartu, 1997, 180 p.
26. **Meelis Pärtel.** Species diversity and community dynamics in calcareous grassland communities in Western Estonia. Tartu, 1997, 124 p.
27. **Malle Leht.** The Genus *Potentilla* L. in Estonia, Latvia and Lithuania: distribution, morphology and taxonomy. Tartu, 1997, 186 p.
28. **Tanel Tenson.** Ribosomes, peptides and antibiotic resistance. Tartu, 1997, 80 p.
29. **Arvo Tuvikene.** Assessment of inland water pollution using biomarker responses in fish *in vivo* and *in vitro*. Tartu, 1997, 160 p.
30. **Urmas Saarma.** Tuning ribosomal elongation cycle by mutagenesis of 23S rRNA. Tartu, 1997, 134 p.
31. **Henn Ojaveer.** Composition and dynamics of fish stocks in the gulf of Riga ecosystem. Tartu, 1997, 138 p.
32. **Lembi Lõugas.** Post-glacial development of vertebrate fauna in Estonian water bodies. Tartu, 1997, 138 p.
33. **Margus Pooga.** Cell penetrating peptide, transportan, and its predecessors, galanin-based chimeric peptides. Tartu, 1998, 110 p.
34. **Andres Saag.** Evolutionary relationships in some cetrarioid genera (Lichenized Ascomycota). Tartu, 1998, 196 p.
35. **Aivar Liiv.** Ribosomal large subunit assembly *in vivo*. Tartu, 1998, 158 p.
36. **Tatjana Oja.** Isoenzyme diversity and phylogenetic affinities among the eurasian annual bromes (*Bromus* L., Poaceae). Tartu, 1998, 92 p.
37. **Mari Moora.** The influence of arbuscular mycorrhizal (AM) symbiosis on the competition and coexistence of calcareous grassland plant species. Tartu, 1998, 78 p.
38. **Olavi Kurina.** Fungus gnats in Estonia (*Diptera: Bolitophilidae, Keroplattidae, Macroceridae, Ditomyiidae, Diadocidiidae, Mycetophilidae*). Tartu, 1998, 200 p.
39. **Andrus Tasa.** Biological leaching of shales: black shale and oil shale. Tartu, 1998, 98 p.
40. **Arnold Kristjuhan.** Studies on transcriptional activator properties of tumor suppressor protein p53. Tartu, 1998, 86 p.
41. **Sulev Ingerpuu.** Characterization of some human myeloid cell surface and nuclear differentiation antigens. Tartu, 1998, 163 p.

42. **Veljo Kisand.** Responses of planktonic bacteria to the abiotic and biotic factors in the shallow lake Võrtsjärv. Tartu, 1998, 118 p.
43. **Kadri Põldmaa.** Studies in the systematics of hypomyces and allied genera (Hypocreales, Ascomycota). Tartu, 1998, 178 p.
44. **Markus Vetemaa.** Reproduction parameters of fish as indicators in environmental monitoring. Tartu, 1998, 117 p.
45. **Heli Talvik.** Prepatent periods and species composition of different *Oesophagostomum* spp. populations in Estonia and Denmark. Tartu, 1998, 104 p.
46. **Katrin Heinsoo.** Cuticular and stomatal antechamber conductance to water vapour diffusion in *Picea abies* (L.) karst. Tartu, 1999, 133 p.
47. **Tarmo Annilo.** Studies on mammalian ribosomal protein S7. Tartu, 1998, 77 p.
48. **Indrek Ots.** Health state indices of reproducing great tits (*Parus major*): sources of variation and connections with life-history traits. Tartu, 1999, 117 p.
49. **Juan Jose Cantero.** Plant community diversity and habitat relationships in central Argentina grasslands. Tartu, 1999, 161 p.
50. **Rein Kalamees.** Seed bank, seed rain and community regeneration in Estonian calcareous grasslands. Tartu, 1999, 107 p.
51. **Sulev Kõks.** Cholecystokinin (CCK) – induced anxiety in rats: influence of environmental stimuli and involvement of endopioid mechanisms and serotonin. Tartu, 1999, 123 p.
52. **Ebe Sild.** Impact of increasing concentrations of O<sub>3</sub> and CO<sub>2</sub> on wheat, clover and pasture. Tartu, 1999, 123 p.
53. **Ljudmilla Timofejeva.** Electron microscopical analysis of the synaptosomal complex formation in cereals. Tartu, 1999, 99 p.
54. **Andres Valkna.** Interactions of galanin receptor with ligands and G-proteins: studies with synthetic peptides. Tartu, 1999, 103 p.
55. **Taavi Virro.** Life cycles of planktonic rotifers in lake Peipsi. Tartu, 1999, 101 p.
56. **Ana Rebane.** Mammalian ribosomal protein S3a genes and intron-encoded small nucleolar RNAs U73 and U82. Tartu, 1999, 85 p.
57. **Tiina Tamm.** Cocksfoot mottle virus: the genome organisation and translational strategies. Tartu, 2000, 101 p.
58. **Reet Kurg.** Structure-function relationship of the bovine papilloma virus E2 protein. Tartu, 2000, 89 p.
59. **Toomas Kivisild.** The origins of Southern and Western Eurasian populations: an mtDNA study. Tartu, 2000, 121 p.
60. **Niilo Kaldalu.** Studies of the TOL plasmid transcription factor XylS. Tartu, 2000, 88 p.
61. **Dina Lepik.** Modulation of viral DNA replication by tumor suppressor protein p53. Tartu, 2000, 106 p.
62. **Kai Vellak.** Influence of different factors on the diversity of the bryophyte vegetation in forest and wooded meadow communities. Tartu, 2000, 122 p.

63. **Jonne Kotta.** Impact of eutrophication and biological invasions on the structure and functions of benthic macrofauna. Tartu, 2000, 160 p.
64. **Georg Martin.** Phytobenthic communities of the Gulf of Riga and the inner sea the West-Estonian archipelago. Tartu, 2000, 139 p.
65. **Silvia Sepp.** Morphological and genetical variation of *Alchemilla L.* in Estonia. Tartu, 2000. 124 p.
66. **Jaan Liira.** On the determinants of structure and diversity in herbaceous plant communities. Tartu, 2000, 96 p.
67. **Priit Zingel.** The role of planktonic ciliates in lake ecosystems. Tartu, 2001, 111 p.
68. **Tiit Teder.** Direct and indirect effects in Host-parasitoid interactions: ecological and evolutionary consequences. Tartu, 2001, 122 p.
69. **Hannes Kollist.** Leaf apoplastic ascorbate as ozone scavenger and its transport across the plasma membrane. Tartu, 2001, 80 p.
70. **Reet Marits.** Role of two-component regulator system PehR-PehS and extracellular protease PrtW in virulence of *Erwinia Carotovora* subsp. *Carotovora*. Tartu, 2001, 112 p.
71. **Vallo Tilgar.** Effect of calcium supplementation on reproductive performance of the pied flycatcher *Ficedula hypoleuca* and the great tit *Parus major*, breeding in Northern temperate forests. Tartu, 2002, 126 p.
72. **Rita Hõrak.** Regulation of transposition of transposon Tn4652 in *Pseudomonas putida*. Tartu, 2002, 108 p.
73. **Liina Eek-Piirsoo.** The effect of fertilization, mowing and additional illumination on the structure of a species-rich grassland community. Tartu, 2002, 74 p.
74. **Krõõt Aasamaa.** Shoot hydraulic conductance and stomatal conductance of six temperate deciduous tree species. Tartu, 2002, 110 p.
75. **Nele Ingerpuu.** Bryophyte diversity and vascular plants. Tartu, 2002, 112 p.
76. **Neeme Tõnisson.** Mutation detection by primer extension on oligonucleotide microarrays. Tartu, 2002, 124 p.
77. **Margus Pensa.** Variation in needle retention of Scots pine in relation to leaf morphology, nitrogen conservation and tree age. Tartu, 2003, 110 p.
78. **Asko Lõhmus.** Habitat preferences and quality for birds of prey: from principles to applications. Tartu, 2003, 168 p.
79. **Viljar Jaks.** p53 – a switch in cellular circuit. Tartu, 2003, 160 p.
80. **Jaana Männik.** Characterization and genetic studies of four ATP-binding cassette (ABC) transporters. Tartu, 2003, 140 p.
81. **Marek Sammul.** Competition and coexistence of clonal plants in relation to productivity. Tartu, 2003, 159 p.
82. **Ivar Ilves.** Virus-cell interactions in the replication cycle of bovine papillomavirus type 1. Tartu, 2003, 89 p.
83. **Andres Männik.** Design and characterization of a novel vector system based on the stable replicator of bovine papillomavirus type 1. Tartu, 2003, 109 p.

84. **Ivika Ostonen.** Fine root structure, dynamics and proportion in net primary production of Norway spruce forest ecosystem in relation to site conditions. Tartu, 2003, 158 p.
85. **Gudrun Veldre.** Somatic status of 12–15-year-old Tartu schoolchildren. Tartu, 2003, 199 p.
86. **Ülo Väli.** The greater spotted eagle *Aquila clanga* and the lesser spotted eagle *A. pomarina*: taxonomy, phylogeography and ecology. Tartu, 2004, 159 p.
87. **Aare Abroi.** The determinants for the native activities of the bovine papillomavirus type 1 E2 protein are separable. Tartu, 2004, 135 p.
88. **Tiina Kahre.** Cystic fibrosis in Estonia. Tartu, 2004, 116 p.
89. **Helen Orav-Kotta.** Habitat choice and feeding activity of benthic suspension feeders and mesograzers in the northern Baltic Sea. Tartu, 2004, 117 p.
90. **Maarja Öpik.** Diversity of arbuscular mycorrhizal fungi in the roots of perennial plants and their effect on plant performance. Tartu, 2004, 175 p.
91. **Kadri Tali.** Species structure of *Neotinea ustulata*. Tartu, 2004, 109 p.
92. **Kristiina Tambets.** Towards the understanding of post-glacial spread of human mitochondrial DNA haplogroups in Europe and beyond: a phylogeographic approach. Tartu, 2004, 163 p.
93. **Arvi Jõers.** Regulation of p53-dependent transcription. Tartu, 2004, 103 p.
94. **Lilian Kadaja.** Studies on modulation of the activity of tumor suppressor protein p53. Tartu, 2004, 103 p.
95. **Jaak Truu.** Oil shale industry wastewater: impact on river microbial community and possibilities for bioremediation. Tartu, 2004, 128 p.
96. **Maire Peters.** Natural horizontal transfer of the *pheBA* operon. Tartu, 2004, 105 p.
97. **Ülo Maiväli.** Studies on the structure-function relationship of the bacterial ribosome. Tartu, 2004, 130 p.
98. **Merit Otsus.** Plant community regeneration and species diversity in dry calcareous grasslands. Tartu, 2004, 103 p.
99. **Mikk Heidema.** Systematic studies on sawflies of the genera *Dolerus*, *Empria*, and *Caliroa* (Hymenoptera: Tenthredinidae). Tartu, 2004, 167 p.
100. **Ilmar Tõnno.** The impact of nitrogen and phosphorus concentration and N/P ratio on cyanobacterial dominance and N<sub>2</sub> fixation in some Estonian lakes. Tartu, 2004, 111 p.
101. **Lauri Saks.** Immune function, parasites, and carotenoid-based ornaments in greenfinches. Tartu, 2004, 144 p.
102. **Siiri Roots.** Human Y-chromosomal variation in European populations. Tartu, 2004, 142 p.
103. **Eve Vedler.** Structure of the 2,4-dichloro-phenoxyacetic acid-degradative plasmid pEST4011. Tartu, 2005, 106 p.
104. **Andres Tover.** Regulation of transcription of the phenol degradation *pheBA* operon in *Pseudomonas putida*. Tartu, 2005, 126 p.
105. **Helen Udras.** Hexose kinases and glucose transport in the yeast *Hansenula polymorpha*. Tartu, 2005, 100 p.

106. **Ave Suija**. Lichens and lichenicolous fungi in Estonia: diversity, distribution patterns, taxonomy. Tartu, 2005, 162 p.
107. **Piret Lõhmus**. Forest lichens and their substrata in Estonia. Tartu, 2005, 162 p.
108. **Inga Lips**. Abiotic factors controlling the cyanobacterial bloom occurrence in the Gulf of Finland. Tartu, 2005, 156 p.
109. **Krista Kaasik**. Circadian clock genes in mammalian clockwork, metabolism and behaviour. Tartu, 2005, 121 p.
110. **Juhan Javoš**. The effects of experience on host acceptance in ovipositing moths. Tartu, 2005, 112 p.
111. **Tiina Sedman**. Characterization of the yeast *Saccharomyces cerevisiae* mitochondrial DNA helicase Hmi1. Tartu, 2005, 103 p.
112. **Ruth Aguraiuja**. Hawaiian endemic fern lineage *Diellia* (Aspleniaceae): distribution, population structure and ecology. Tartu, 2005, 112 p.
113. **Riho Teras**. Regulation of transcription from the fusion promoters generated by transposition of Tn4652 into the upstream region of *pheBA* operon in *Pseudomonas putida*. Tartu, 2005, 106 p.
114. **Mait Metspalu**. Through the course of prehistory in India: tracing the mtDNA trail. Tartu, 2005, 138 p.
115. **Elin Lõhmussaar**. The comparative patterns of linkage disequilibrium in European populations and its implication for genetic association studies. Tartu, 2006, 124 p.
116. **Priit Kupper**. Hydraulic and environmental limitations to leaf water relations in trees with respect to canopy position. Tartu, 2006, 126 p.
117. **Heli Ilves**. Stress-induced transposition of Tn4652 in *Pseudomonas Putida*. Tartu, 2006, 120 p.
118. **Silja Kuusk**. Biochemical properties of Hmi1p, a DNA helicase from *Saccharomyces cerevisiae* mitochondria. Tartu, 2006, 126 p.
119. **Kersti Püssa**. Forest edges on medium resolution landsat thematic mapper satellite images. Tartu, 2006, 90 p.
120. **Lea Tummeleht**. Physiological condition and immune function in great tits (*Parus major* L.): Sources of variation and trade-offs in relation to growth. Tartu, 2006, 94 p.
121. **Toomas Esperk**. Larval instar as a key element of insect growth schedules. Tartu, 2006, 186 p.
122. **Harri Valdmann**. Lynx (*Lynx lynx*) and wolf (*Canis lupus*) in the Baltic region: Diets, helminth parasites and genetic variation. Tartu, 2006. 102 p.
123. **Priit Jõers**. Studies of the mitochondrial helicase Hmi1p in *Candida albicans* and *Saccharomyces cerevisia*. Tartu, 2006. 113 p.
124. **Kersti Lilleväli**. Gata3 and Gata2 in inner ear development. Tartu, 2007, 123 p.
125. **Kai Rünk**. Comparative ecology of three fern species: *Dryopteris carthusiana* (Vill.) H.P. Fuchs, *D. expansa* (C. Presl) Fraser-Jenkins & Jermy and *D. dilatata* (Hoffm.) A. Gray (Dryopteridaceae). Tartu, 2007, 143 p.

126. **Aveliina Helm.** Formation and persistence of dry grassland diversity: role of human history and landscape structure. Tartu, 2007, 89 p.
127. **Leho Tedersoo.** Ectomycorrhizal fungi: diversity and community structure in Estonia, Seychelles and Australia. Tartu, 2007, 233 p.
128. **Marko Mägi.** The habitat-related variation of reproductive performance of great tits in a deciduous-coniferous forest mosaic: looking for causes and consequences. Tartu, 2007, 135 p.
129. **Valeria Lulla.** Replication strategies and applications of Semliki Forest virus. Tartu, 2007, 109 p.
130. **Ülle Reier.** Estonian threatened vascular plant species: causes of rarity and conservation. Tartu, 2007, 79 p.
131. **Inga Jüriado.** Diversity of lichen species in Estonia: influence of regional and local factors. Tartu, 2007, 171 p.
132. **Tatjana Krama.** Mobbing behaviour in birds: costs and reciprocity based cooperation. Tartu, 2007, 112 p.
133. **Signe Saumaa.** The role of DNA mismatch repair and oxidative DNA damage defense systems in avoidance of stationary phase mutations in *Pseudomonas putida*. Tartu, 2007, 172 p.
134. **Reedik Mägi.** The linkage disequilibrium and the selection of genetic markers for association studies in european populations. Tartu, 2007, 96 p.
135. **Priit Kilgas.** Blood parameters as indicators of physiological condition and skeletal development in great tits (*Parus major*): natural variation and application in the reproductive ecology of birds. Tartu, 2007, 129 p.
136. **Anu Albert.** The role of water salinity in structuring eastern Baltic coastal fish communities. Tartu, 2007, 95 p.
137. **Kärt Padari.** Protein transduction mechanisms of transportans. Tartu, 2008, 128 p.
138. **Siiri-Liis Sandre.** Selective forces on larval colouration in a moth. Tartu, 2008, 125 p.
139. **Ülle Jõgar.** Conservation and restoration of semi-natural floodplain meadows and their rare plant species. Tartu, 2008, 99 p.
140. **Lauri Laanisto.** Macroecological approach in vegetation science: generality of ecological relationships at the global scale. Tartu, 2008, 133 p.
141. **Reidar Andreson.** Methods and software for predicting PCR failure rate in large genomes. Tartu, 2008, 105 p.
142. **Birgot Paavel.** Bio-optical properties of turbid lakes. Tartu, 2008, 175 p.
143. **Kaire Torn.** Distribution and ecology of charophytes in the Baltic Sea. Tartu, 2008, 98 p.
144. **Vladimir Vimberg.** Peptide mediated macrolide resistance. Tartu, 2008, 190 p.
145. **Daima Örd.** Studies on the stress-inducible pseudokinase TRB3, a novel inhibitor of transcription factor ATF4. Tartu, 2008, 108 p.
146. **Lauri Saag.** Taxonomic and ecologic problems in the genus *Lepraria* (*Stereocaulaceae*, lichenised *Ascomycota*). Tartu, 2008, 175 p.

147. **Ulvi Karu.** Antioxidant protection, carotenoids and coccidians in green-finches – assessment of the costs of immune activation and mechanisms of parasite resistance in a passerine with carotenoid-based ornaments. Tartu, 2008, 124 p.
148. **Jaanus Remm.** Tree-cavities in forests: density, characteristics and occupancy by animals. Tartu, 2008, 128 p.
149. **Epp Moks.** Tapeworm parasites *Echinococcus multilocularis* and *E. granulosus* in Estonia: phylogenetic relationships and occurrence in wild carnivores and ungulates. Tartu, 2008, 82 p.
150. **Eve Eensalu.** Acclimation of stomatal structure and function in tree canopy: effect of light and CO<sub>2</sub> concentration. Tartu, 2008, 108 p.
151. **Janne Pullat.** Design, functionlization and application of an *in situ* synthesized oligonucleotide microarray. Tartu, 2008, 108 p.
152. **Marta Putrinš.** Responses of *Pseudomonas putida* to phenol-induced metabolic and stress signals. Tartu, 2008, 142 p.
153. **Marina Semtšenko.** Plant root behaviour: responses to neighbours and physical obstructions. Tartu, 2008, 106 p.
154. **Marge Starast.** Influence of cultivation techniques on productivity and fruit quality of some *Vaccinium* and *Rubus* taxa. Tartu, 2008, 154 p.
155. **Age Tats.** Sequence motifs influencing the efficiency of translation. Tartu, 2009, 104 p.
156. **Radi Tegova.** The role of specialized DNA polymerases in mutagenesis in *Pseudomonas putida*. Tartu, 2009, 124 p.
157. **Tsipe Aavik.** Plant species richness, composition and functional trait pattern in agricultural landscapes – the role of land use intensity and landscape structure. Tartu, 2009, 112 p.
158. **Kaja Kiiver.** Semliki forest virus based vectors and cell lines for studying the replication and interactions of alphaviruses and hepaciviruses. Tartu, 2009, 104 p.
159. **Meelis Kadaja.** Papillomavirus Replication Machinery Induces Genomic Instability in its Host Cell. Tartu, 2009, 126 p.
160. **Pille Hallast.** Human and chimpanzee Luteinizing hormone/Chorionic Gonadotropin beta (*LHB/CGB*) gene clusters: diversity and divergence of young duplicated genes. Tartu, 2009, 168 p.
161. **Ain Vellak.** Spatial and temporal aspects of plant species conservation. Tartu, 2009, 86 p.
162. **Triinu Rimmel.** Body size evolution in insects with different colouration strategies: the role of predation risk. Tartu, 2009, 168 p.
163. **Jaana Salujõe.** Zooplankton as the indicator of ecological quality and fish predation in lake ecosystems. Tartu, 2009, 129 p.
164. **Ele Vahtmäe.** Mapping benthic habitat with remote sensing in optically complex coastal environments. Tartu, 2009, 109 p.
165. **Liisa Metsamaa.** Model-based assessment to improve the use of remote sensing in recognition and quantitative mapping of cyanobacteria. Tartu, 2009, 114 p.

166. **Pille Säälük.** The role of endocytosis in the protein transduction by cell-penetrating peptides. Tartu, 2009, 155 p.
167. **Lauri Peil.** Ribosome assembly factors in *Escherichia coli*. Tartu, 2009, 147 p.
168. **Lea Hallik.** Generality and specificity in light harvesting, carbon gain capacity and shade tolerance among plant functional groups. Tartu, 2009, 99 p.
169. **Mariliis Tark.** Mutagenic potential of DNA damage repair and tolerance mechanisms under starvation stress. Tartu, 2009, 191 p.
170. **Riinu Rannap.** Impacts of habitat loss and restoration on amphibian populations. Tartu, 2009, 117 p.
171. **Maarja Adojaan.** Molecular variation of HIV-1 and the use of this knowledge in vaccine development. Tartu, 2009, 95 p.
172. **Signe Altmäe.** Genomics and transcriptomics of human induced ovarian folliculogenesis. Tartu, 2010, 179 p.
173. **Triin Suvi.** Mycorrhizal fungi of native and introduced trees in the Seychelles Islands. Tartu, 2010, 107 p.
174. **Velda Lauringson.** Role of suspension feeding in a brackish-water coastal sea. Tartu, 2010, 123 p.
175. **Eero Talts.** Photosynthetic cyclic electron transport – measurement and variably proton-coupled mechanism. Tartu, 2010, 121 p.
176. **Mari Nelis.** Genetic structure of the Estonian population and genetic distance from other populations of European descent. Tartu, 2010, 97 p.
177. **Kaarel Krjutškov.** Arrayed Primer Extension-2 as a multiplex PCR-based method for nucleic acid variation analysis: method and applications. Tartu, 2010, 129 p.
178. **Egle Köster.** Morphological and genetical variation within species complexes: *Anthyllis vulneraria* s. l. and *Alchemilla vulgaris* (coll.). Tartu, 2010, 101 p.
179. **Erki Õunap.** Systematic studies on the subfamily Sterrhinae (Lepidoptera: Geometridae). Tartu, 2010, 111 p.
180. **Merike Jõesaar.** Diversity of key catabolic genes at degradation of phenol and *p*-cresol in pseudomonads. Tartu, 2010, 125 p.
181. **Kristjan Herkül.** Effects of physical disturbance and habitat-modifying species on sediment properties and benthic communities in the northern Baltic Sea. Tartu, 2010, 123 p.
182. **Arto Pulk.** Studies on bacterial ribosomes by chemical modification approaches. Tartu, 2010, 161 p.
183. **Maria Põllupüü.** Ecological relations of cladocerans in a brackish-water ecosystem. Tartu, 2010, 126 p.
184. **Toomas Silla.** Study of the segregation mechanism of the Bovine Papillomavirus Type 1. Tartu, 2010, 188 p.
185. **Gyaneshwer Chaubey.** The demographic history of India: A perspective based on genetic evidence. Tartu, 2010, 184 p.

186. **Katrin Kepp.** Genes involved in cardiovascular traits: detection of genetic variation in Estonian and Czech populations. Tartu, 2010, 164 p.
187. **Virve Sõber.** The role of biotic interactions in plant reproductive performance. Tartu, 2010, 92 p.
188. **Kersti Kangro.** The response of phytoplankton community to the changes in nutrient loading. Tartu, 2010, 144 p.
189. **Joachim M. Gerhold.** Replication and Recombination of mitochondrial DNA in Yeast. Tartu, 2010, 120 p.
190. **Helen Tammert.** Ecological role of physiological and phylogenetic diversity in aquatic bacterial communities. Tartu, 2010, 140 p.
191. **Elle Rajandu.** Factors determining plant and lichen species diversity and composition in Estonian *Calamagrostis* and *Hepatica* site type forests. Tartu, 2010, 123 p.
192. **Paula Ann Kivistik.** ColR-ColS signalling system and transposition of Tn4652 in the adaptation of *Pseudomonas putida*. Tartu, 2010, 118 p.
193. **Siim Sõber.** Blood pressure genetics: from candidate genes to genome-wide association studies. Tartu, 2011, 120 p.
194. **Kalle Kipper.** Studies on the role of helix 69 of 23S rRNA in the factor-dependent stages of translation initiation, elongation, and termination. Tartu, 2011, 178 p.
195. **Triinu Siibak.** Effect of antibiotics on ribosome assembly is indirect. Tartu, 2011, 134 p.
196. **Tambet Tõnissoo.** Identification and molecular analysis of the role of guanine nucleotide exchange factor RIC-8 in mouse development and neural function. Tartu, 2011, 110 p.
197. **Helin Räägel.** Multiple faces of cell-penetrating peptides – their intracellular trafficking, stability and endosomal escape during protein transduction. Tartu, 2011, 161 p.
198. **Andres Jaanus.** Phytoplankton in Estonian coastal waters – variability, trends and response to environmental pressures. Tartu, 2011, 157 p.
199. **Tiit Nikopensius.** Genetic predisposition to nonsyndromic orofacial clefts. Tartu, 2011, 152 p.
200. **Signe Värvi.** Studies on the mechanisms of RNA polymerase II-dependent transcription elongation. Tartu, 2011, 108 p.
201. **Kristjan Välik.** Gene expression profiling and genome-wide association studies of non-small cell lung cancer. Tartu, 2011, 98 p.
202. **Arno Põllumäe.** Spatio-temporal patterns of native and invasive zooplankton species under changing climate and eutrophication conditions. Tartu, 2011, 153 p.
203. **Egle Tammeleht.** Brown bear (*Ursus arctos*) population structure, demographic processes and variations in diet in northern Eurasia. Tartu, 2011, 143 p.
205. **Teele Jairus.** Species composition and host preference among ectomycorrhizal fungi in Australian and African ecosystems. Tartu, 2011, 106 p.

206. **Kessy Abarenkov.** PlutoF – cloud database and computing services supporting biological research. Tartu, 2011, 125 p.
207. **Marina Grigороva.** Fine-scale genetic variation of follicle-stimulating hormone beta-subunit coding gene (*FSHB*) and its association with reproductive health. Tartu, 2011, 184 p.
208. **Anu Tiitsaar.** The effects of predation risk and habitat history on butterfly communities. Tartu, 2011, 97 p.
209. **Elin Sild.** Oxidative defences in immunoecological context: validation and application of assays for nitric oxide production and oxidative burst in a wild passerine. Tartu, 2011, 105 p.
210. **Irja Saar.** The taxonomy and phylogeny of the genera *Cystoderma* and *Cystodermella* (Agaricales, Fungi). Tartu, 2012, 167 p.
211. **Pauli Saag.** Natural variation in plumage bacterial assemblages in two wild breeding passerines. Tartu, 2012, 113 p.
212. **Aleksei Lulla.** Alphaviral nonstructural protease and its polyprotein substrate: arrangements for the perfect marriage. Tartu, 2012, 143 p.
213. **Mari Järve.** Different genetic perspectives on human history in Europe and the Caucasus: the stories told by uniparental and autosomal markers. Tartu, 2012, 119 p.
214. **Ott Scheler.** The application of tmRNA as a marker molecule in bacterial diagnostics using microarray and biosensor technology. Tartu, 2012, 93 p.
215. **Anna Balikova.** Studies on the functions of tumor-associated mucin-like leukosialin (CD43) in human cancer cells. Tartu, 2012, 129 p.
216. **Triinu Kõressaar.** Improvement of PCR primer design for detection of prokaryotic species. Tartu, 2012, 83 p.
217. **Tuul Sepp.** Hematological health state indices of greenfinches: sources of individual variation and responses to immune system manipulation. Tartu, 2012, 117 p.
218. **Rya Ero.** Modifier view of the bacterial ribosome. Tartu, 2012, 146 p.
219. **Mohammad Bahram.** Biogeography of ectomycorrhizal fungi across different spatial scales. Tartu, 2012, 165 p.
220. **Annely Lorents.** Overcoming the plasma membrane barrier: uptake of amphipathic cell-penetrating peptides induces influx of calcium ions and downstream responses. Tartu, 2012, 113 p.
221. **Katrin Männik.** Exploring the genomics of cognitive impairment: whole-genome SNP genotyping experience in Estonian patients and general population. Tartu, 2012, 171 p.
222. **Marko Prous.** Taxonomy and phylogeny of the sawfly genus *Empria* (Hymenoptera, Tenthredinidae). Tartu, 2012, 192 p.
223. **Triinu Visnapuu.** Levansucrases encoded in the genome of *Pseudomonas syringae* pv. tomato DC3000: heterologous expression, biochemical characterization, mutational analysis and spectrum of polymerization products. Tartu, 2012, 160 p.
224. **Nele Tamberg.** Studies on Semliki Forest virus replication and pathogenesis. Tartu, 2012, 109 p.

225. **Tõnu Esko**. Novel applications of SNP array data in the analysis of the genetic structure of Europeans and in genetic association studies. Tartu, 2012, 149 p.
226. **Timo Arula**. Ecology of early life-history stages of herring *Clupea harengus membras* in the northeastern Baltic Sea. Tartu, 2012, 143 p.
227. **Inga Hiiesalu**. Belowground plant diversity and coexistence patterns in grassland ecosystems. Tartu, 2012, 130 p.
228. **Kadri Koorem**. The influence of abiotic and biotic factors on small-scale plant community patterns and regeneration in boreonemoral forest. Tartu, 2012, 114 p.
229. **Liis Andresen**. Regulation of virulence in plant-pathogenic pectobacteria. Tartu, 2012, 122 p.
230. **Kaupo Kohv**. The direct and indirect effects of management on boreal forest structure and field layer vegetation. Tartu, 2012, 124 p.
231. **Mart Jüssi**. Living on an edge: landlocked seals in changing climate. Tartu, 2012, 114 p.
232. **Riina Klais**. Phytoplankton trends in the Baltic Sea. Tartu, 2012, 136 p.
233. **Rauno Veeroja**. Effects of winter weather, population density and timing of reproduction on life-history traits and population dynamics of moose (*Alces alces*) in Estonia. Tartu, 2012, 92 p.
234. **Marju Keis**. Brown bear (*Ursus arctos*) phylogeography in northern Eurasia. Tartu, 2013, 142 p.
235. **Sergei Põlme**. Biogeography and ecology of *alnus*- associated ectomycorrhizal fungi – from regional to global scale. Tartu, 2013, 90 p.
236. **Liis Uusküla**. Placental gene expression in normal and complicated pregnancy. Tartu, 2013, 173 p.
237. **Marko Lõoke**. Studies on DNA replication initiation in *Saccharomyces cerevisiae*. Tartu, 2013, 112 p.
238. **Anne Aan**. Light- and nitrogen-use and biomass allocation along productivity gradients in multilayer plant communities. Tartu, 2013, 127 p.
239. **Heidi Tamm**. Comprehending phylogenetic diversity – case studies in three groups of ascomycetes. Tartu, 2013, 136 p.
240. **Liina Kangur**. High-Pressure Spectroscopy Study of Chromophore-Binding Hydrogen Bonds in Light-Harvesting Complexes of Photosynthetic Bacteria. Tartu, 2013, 150 p.
241. **Margus Leppik**. Substrate specificity of the multisite specific pseudouridine synthase RluD. Tartu, 2013, 111 p.
242. **Lauris Kaplinski**. The application of oligonucleotide hybridization model for PCR and microarray optimization. Tartu, 2013, 103 p.
243. **Merli Pärnoja**. Patterns of macrophyte distribution and productivity in coastal ecosystems: effect of abiotic and biotic forcing. Tartu, 2013, 155 p.
244. **Tõnu Margus**. Distribution and phylogeny of the bacterial translational GTPases and the Mqsr/YgiT regulatory system. Tartu, 2013, 126 p.
245. **Pille Mänd**. Light use capacity and carbon and nitrogen budget of plants: remote assessment and physiological determinants. Tartu, 2013, 128 p.

246. **Mario Plaas**. Animal model of Wolfram Syndrome in mice: behavioural, biochemical and psychopharmacological characterization. Tartu, 2013, 144 p.
247. **Georgi Hudjašov**. Maps of mitochondrial DNA, Y-chromosome and tyrosinase variation in Eurasian and Oceanian populations. Tartu, 2013, 115 p.
248. **Mari Lepik**. Plasticity to light in herbaceous plants and its importance for community structure and diversity. Tartu, 2013, 102 p.
249. **Ede Leppik**. Diversity of lichens in semi-natural habitats of Estonia. Tartu, 2013, 151 p.
250. **Ülle Saks**. Arbuscular mycorrhizal fungal diversity patterns in boreo-nemoral forest ecosystems. Tartu, 2013, 151 p.
251. **Eneli Oitmaa**. Development of arrayed primer extension microarray assays for molecular diagnostic applications. Tartu, 2013, 147 p.
252. **Jekaterina Jutkina**. The horizontal gene pool for aromatics degradation: bacterial catabolic plasmids of the Baltic Sea aquatic system. Tartu, 2013, 121 p.
253. **Helen Vellau**. Reaction norms for size and age at maturity in insects: rules and exceptions. Tartu, 2014, 132 p.
254. **Randel Kreitsberg**. Using biomarkers in assessment of environmental contamination in fish – new perspectives. Tartu, 2014, 107 p.
255. **Krista Takkis**. Changes in plant species richness and population performance in response to habitat loss and fragmentation. Tartu, 2014, 141 p.
256. **Liina Nagirnaja**. Global and fine-scale genetic determinants of recurrent pregnancy loss. Tartu, 2014, 211 p.
257. **Triin Triisberg**. Factors influencing the re-vegetation of abandoned extracted peatlands in Estonia. Tartu, 2014, 133 p.
258. **Villu Soon**. A phylogenetic revision of the *Chrysis ignita* species group (Hymenoptera: Chrysididae) with emphasis on the northern European fauna. Tartu, 2014, 211 p.
259. **Andrei Nikonov**. RNA-Dependent RNA Polymerase Activity as a Basis for the Detection of Positive-Strand RNA Viruses by Vertebrate Host Cells. Tartu, 2014, 207 p.
260. **Eele Õunapuu-Pikas**. Spatio-temporal variability of leaf hydraulic conductance in woody plants: ecophysiological consequences. Tartu, 2014, 135 p.
261. **Marju Männiste**. Physiological ecology of greenfinches: information content of feathers in relation to immune function and behavior. Tartu, 2014, 121 p.
262. **Katre Kets**. Effects of elevated concentrations of CO<sub>2</sub> and O<sub>3</sub> on leaf photosynthetic parameters in *Populus tremuloides*: diurnal, seasonal and inter-annual patterns. Tartu, 2014, 115 p.
263. **Küllli Lokko**. Seasonal and spatial variability of zoopsammon communities in relation to environmental parameters. Tartu, 2014, 129 p.
264. **Olga Žilina**. Chromosomal microarray analysis as diagnostic tool: Estonian experience. Tartu, 2014, 152 p.

265. **Kertu Lõhmus**. Colonisation ecology of forest-dwelling vascular plants and the conservation value of rural manor parks. Tartu, 2014, 111 p.
266. **Anu Aun**. Mitochondria as integral modulators of cellular signaling. Tartu, 2014, 167 p.
267. **Chandana Basu Mallick**. Genetics of adaptive traits and gender-specific demographic processes in South Asian populations. Tartu, 2014, 160 p.
268. **Riin Tamme**. The relationship between small-scale environmental heterogeneity and plant species diversity. Tartu, 2014, 130 p.
269. **Liina Remm**. Impacts of forest drainage on biodiversity and habitat quality: implications for sustainable management and conservation. Tartu, 2015, 126 p.
270. **Tiina Talve**. Genetic diversity and taxonomy within the genus *Rhinanthus*. Tartu, 2015, 106 p.
271. **Mehis Rohtla**. Otolith sclerochronological studies on migrations, spawning habitat preferences and age of freshwater fishes inhabiting the Baltic Sea. Tartu, 2015, 137 p.
272. **Alexey Reshchikov**. The world fauna of the genus *Lathrolestes* (Hymenoptera, Ichneumonidae). Tartu, 2015, 247 p.
273. **Martin Pook**. Studies on artificial and extracellular matrix protein-rich surfaces as regulators of cell growth and differentiation. Tartu, 2015, 142 p.
274. **Mai Kukumägi**. Factors affecting soil respiration and its components in silver birch and Norway spruce stands. Tartu, 2015, 155 p.
275. **Helen Karu**. Development of ecosystems under human activity in the North-East Estonian industrial region: forests on post-mining sites and bogs. Tartu, 2015, 152 p.
276. **Hedi Peterson**. Exploiting high-throughput data for establishing relationships between genes. Tartu, 2015, 186 p.
277. **Priit Adler**. Analysis and visualisation of large scale microarray data. Tartu, 2015, 126 p.
278. **Aigar Niglas**. Effects of environmental factors on gas exchange in deciduous trees: focus on photosynthetic water-use efficiency. Tartu, 2015, 152 p.
279. **Silja Laht**. Classification and identification of conopeptides using profile hidden Markov models and position-specific scoring matrices. Tartu, 2015, 100 p.
280. **Martin Kesler**. Biological characteristics and restoration of Atlantic salmon *Salmo salar* populations in the Rivers of Northern Estonia. Tartu, 2015, 97 p.
281. **Pratyush Kumar Das**. Biochemical perspective on alphaviral nonstructural protein 2: a tale from multiple domains to enzymatic profiling. Tartu, 2015, 205 p.
282. **Priit Palta**. Computational methods for DNA copy number detection. Tartu, 2015, 130 p.
283. **Julia Sidorenko**. Combating DNA damage and maintenance of genome integrity in pseudomonads. Tartu, 2015, 174 p.

284. **Anastasiia Kovtun-Kante.** Charophytes of Estonian inland and coastal waters: distribution and environmental preferences. Tartu, 2015, 97 p.
285. **Ly Lindman.** The ecology of protected butterfly species in Estonia. Tartu, 2015, 171 p.
286. **Jaanis Lodjak.** Association of Insulin-like Growth Factor I and Corticosterone with Nestling Growth and Fledging Success in Wild Passerines. Tartu, 2016, 113 p.
287. **Ann Kraut.** Conservation of Wood-Inhabiting Biodiversity – Semi-Natural Forests as an Opportunity. Tartu, 2016, 141 p.
288. **Tiit Örd.** Functions and regulation of the mammalian pseudokinase TRIB3. Tartu, 2016, 182. p.
289. **Kairi Käiro.** Biological Quality According to Macroinvertebrates in Streams of Estonia (Baltic Ecoregion of Europe): Effects of Human-induced Hydromorphological Changes. Tartu, 2016, 126 p.
290. **Leidi Laurimaa.** *Echinococcus multilocularis* and other zoonotic parasites in Estonian canids. Tartu, 2016, 144 p.
291. **Helerin Margus.** Characterization of cell-penetrating peptide/nucleic acid nanocomplexes and their cell-entry mechanisms. Tartu, 2016, 173 p.
292. **Kadri Runnel.** Fungal targets and tools for forest conservation. Tartu, 2016, 157 p.
293. **Urmo Võsa.** MicroRNAs in disease and health: aberrant regulation in lung cancer and association with genomic variation. Tartu, 2016, 163 p.
294. **Kristina Mäemets-Allas.** Studies on cell growth promoting AKT signaling pathway – a promising anti-cancer drug target. Tartu, 2016, 146 p.
295. **Janeli Viil.** Studies on cellular and molecular mechanisms that drive normal and regenerative processes in the liver and pathological processes in Dupuytren’s contracture. Tartu, 2016, 175 p.
296. **Ene Kook.** Genetic diversity and evolution of *Pulmonaria angustifolia* L. and *Myosotis laxa sensu lato* (Boraginaceae). Tartu, 2016, 106 p.
297. **Kadri Peil.** RNA polymerase II-dependent transcription elongation in *Saccharomyces cerevisiae*. Tartu, 2016, 113 p.
298. **Katrin Ruisu.** The role of RIC8A in mouse development and its function in cell-matrix adhesion and actin cytoskeletal organisation. Tartu, 2016, 129 p.
299. **Janely Pae.** Translocation of cell-penetrating peptides across biological membranes and interactions with plasma membrane constituents. Tartu, 2016, 126 p.
300. **Argo Ronk.** Plant diversity patterns across Europe: observed and dark diversity. Tartu, 2016, 153 p.
301. **Kristiina Mark.** Diversification and species delimitation of lichenized fungi in selected groups of the family Parmeliaceae (Ascomycota). Tartu, 2016, 181 p.
302. **Jaak-Albert Metsoja.** Vegetation dynamics in floodplain meadows: influence of mowing and sediment application. Tartu, 2016, 140 p.

303. **Hedvig Tamman.** The GraTA toxin-antitoxin system of *Pseudomonas putida*: regulation and role in stress tolerance. Tartu, 2016, 154 p.
304. **Kadri Pärtel.** Application of ultrastructural and molecular data in the taxonomy of helotialean fungi. Tartu, 2016, 183 p.
305. **Maris Hindrikson.** Grey wolf (*Canis lupus*) populations in Estonia and Europe: genetic diversity, population structure and -processes, and hybridization between wolves and dogs. Tartu, 2016, 121 p.
306. **Polina Degtjarenko.** Impacts of alkaline dust pollution on biodiversity of plants and lichens: from communities to genetic diversity. Tartu, 2016, 126 p.
307. **Liina Pajusalu.** The effect of CO<sub>2</sub> enrichment on net photosynthesis of macrophytes in a brackish water environment. Tartu, 2016, 126 p.
308. **Stoyan Tankov.** Random walks in the stringent response. Tartu, 2016, 94 p.
309. **Liis Leitsalu.** Communicating genomic research results to population-based biobank participants. Tartu, 2016, 158 p.
310. **Richard Meitern.** Redox physiology of wild birds: validation and application of techniques for detecting oxidative stress. Tartu, 2016, 134 p.
311. **Kaie Lokk.** Comparative genome-wide DNA methylation studies of healthy human tissues and non-small cell lung cancer tissue. Tartu, 2016, 127 p.
312. **Mihhail Kurašin.** Processivity of cellulases and chitinases. Tartu, 2017, 132 p.
313. **Carmen Tali.** Scavenger receptors as a target for nucleic acid delivery with peptide vectors. Tartu, 2017, 155 p.
314. **Katarina Oganjan.** Distribution, feeding and habitat of benthic suspension feeders in a shallow coastal sea. Tartu, 2017, 132 p.
315. **Taavi Paal.** Immigration limitation of forest plants into wooded landscape corridors. Tartu, 2017, 145 p.
316. **Kadri Õunap.** The Williams-Beuren syndrome chromosome region protein WBSR22 is a ribosome biogenesis factor. Tartu, 2017, 135 p.
317. **Riin Tamm.** In-depth analysis of factors affecting variability in thiopurine methyltransferase activity. Tartu, 2017, 170 p.
318. **Keiu Kask.** The role of RIC8A in the development and regulation of mouse nervous system. Tartu, 2017, 184 p.
319. **Tiia Möller.** Mapping and modelling of the spatial distribution of benthic macrovegetation in the NE Baltic Sea with a special focus on the eelgrass *Zostera marina* Linnaeus, 1753. Tartu, 2017, 162 p.
320. **Silva Kasela.** Genetic regulation of gene expression: detection of tissue- and cell type-specific effects. Tartu, 2017, 150 p.
321. **Karmen Süld.** Food habits, parasites and space use of the raccoon dog *Nyctereutes procyonoides*: the role of an alien species as a predator and vector of zoonotic diseases in Estonia. Tartu, 2017, p.
322. **Ragne Oja.** Consequences of supplementary feeding of wild boar – concern for ground-nesting birds and endoparasite infection. Tartu, 2017, 141 p.
323. **Riin Kont.** The acquisition of cellulose chain by a processive cellobiohydrolase. Tartu, 2017, 117 p.

324. **Liis Kasari.** Plant diversity of semi-natural grasslands: drivers, current status and conservation challenges. Tartu, 2017, 141 p.
325. **Sirgi Saar.** Belowground interactions: the roles of plant genetic relatedness, root exudation and soil legacies. Tartu, 2017, 113 p.
326. **Sten Anslan.** Molecular identification of Collembola and their fungal associates. Tartu, 2017, 125 p.
327. **Imre Taal.** Causes of variation in littoral fish communities of the Eastern Baltic Sea: from community structure to individual life histories. Tartu, 2017, 118 p.
328. **Jürgen Jalak.** Dissecting the Mechanism of Enzymatic Degradation of Cellulose Using Low Molecular Weight Model Substrates. Tartu, 2017, 137 p.
329. **Kairi Kiik.** Reproduction and behaviour of the endangered European mink (*Mustela lutreola*) in captivity. Tartu, 2018, 112 p.
330. **Ivan Kuprijanov.** Habitat use and trophic interactions of native and invasive predatory macroinvertebrates in the northern Baltic Sea. Tartu, 2018, 117 p.
331. **Hendrik Meister.** Evolutionary ecology of insect growth: from geographic patterns to biochemical trade-offs. Tartu, 2018, 147 p.
332. **Ilja Gaidutsik.** Irc3 is a mitochondrial branch migration enzyme in *Saccharomyces cerevisiae*. Tartu, 2018, 161 p.
333. **Lena Neuenkamp.** The dynamics of plant and arbuscular mycorrhizal fungal communities in grasslands under changing land use. Tartu, 2018, 241 p.
334. **Laura Kasak.** Genome structural variation modulating the placenta and pregnancy maintenance. Tartu, 2018, 181 p.
335. **Kersti Riibak.** Importance of dispersal limitation in determining dark diversity of plants across spatial scales. Tartu, 2018, 133 p.
336. **Liina Saar.** Dynamics of grassland plant diversity in changing landscapes. Tartu, 2018, 206 p.
337. **Hanna Ainelo.** Fis regulates *Pseudomonas putida* biofilm formation by controlling the expression of *lapA*. Tartu, 2018, 143 p.
338. **Natalia Pervjakova.** Genomic imprinting in complex traits. Tartu, 2018, 176 p.
339. **Andrio Lahesaare.** The role of global regulator Fis in regulating the expression of *lapF* and the hydrophobicity of soil bacterium *Pseudomonas putida*. Tartu, 2018, 124 p.
340. **Märt Roosaare.** K-mer based methods for the identification of bacteria and plasmids. Tartu, 2018, 117 p.
341. **Maria Abakumova.** The relationship between competitive behaviour and the frequency and identity of neighbours in temperate grassland plants. Tartu, 2018, 104 p.
342. **Margus Vilbas.** Biotic interactions affecting habitat use of myrmecophilous butterflies in Northern Europe. Tartu, 2018, 142 p.

343. **Liina Kinkar.** Global patterns of genetic diversity and phylogeography of *Echinococcus granulosus* sensu stricto – a tapeworm species of significant public health concern. Tartu, 2018, 147 p.
344. **Teivi Laurimäe.** Taxonomy and genetic diversity of zoonotic tapeworms in the species complex of *Echinococcus granulosus* sensu lato. Tartu, 2018, 143 p.
345. **Tatjana Jatsenko.** Role of translesion DNA polymerases in mutagenesis and DNA damage tolerance in Pseudomonads. Tartu, 2018, 216 p.
346. **Katrin Viigand.** Utilization of  $\alpha$ -glucosidic sugars by *Ogataea (Hanse-nula) polymorpha*. Tartu, 2018, 148 p.
347. **Andres Ainelo.** Physiological effects of the *Pseudomonas putida* toxin grat. Tartu, 2018, 146 p.
348. **Killu Timm.** Effects of two genes (DRD4 and SERT) on great tit (*Parus major*) behaviour and reproductive traits. Tartu, 2018, 117 p.
349. **Petr Kohout.** Ecology of ericoid mycorrhizal fungi. Tartu, 2018, 184 p.
350. **Gristin Rohula-Okunev.** Effects of endogenous and environmental factors on night-time water flux in deciduous woody tree species. Tartu, 2018, 184 p.
351. **Jane Oja.** Temporal and spatial patterns of orchid mycorrhizal fungi in forest and grassland ecosystems. Tartu, 2018, 102 p.
352. **Janek Urvik.** Multidimensionality of aging in a long-lived seabird. Tartu, 2018, 135 p.
353. **Lisanna Schmidt.** Phenotypic and genetic differentiation in the hybridizing species pair *Carex flava* and *C. viridula* in geographically different regions. Tartu, 2018, 133 p.
354. **Monika Karmin.** Perspectives from human Y chromosome – phylogeny, population dynamics and founder events. Tartu, 2018, 168 p.
355. **Maris Alver.** Value of genomics for atherosclerotic cardiovascular disease risk prediction. Tartu, 2019, 148 p.
356. **Lehti Saag.** The prehistory of Estonia from a genetic perspective: new insights from ancient DNA. Tartu, 2019, 171 p.
357. **Mari-Liis Viljur.** Local and landscape effects on butterfly assemblages in managed forests. Tartu, 2019, 115 p.
358. **Ivan Kisly.** The pleiotropic functions of ribosomal proteins eL19 and eL24 in the budding yeast ribosome. Tartu, 2019, 170 p.
359. **Mikk Puustusmaa.** On the origin of papillomavirus proteins. Tartu, 2019, 152 p.
360. **Anneliis Peterson.** Benthic biodiversity in the north-eastern Baltic Sea: mapping methods, spatial patterns, and relations to environmental gradients. Tartu, 2019, 159 p.
361. **Erwan Pennarun.** Meandering along the mtDNA phylogeny; causerie and digression about what it can tell us about human migrations. Tartu, 2019, 162 p.

362. **Karin Ernits**. Levansucrase Lsc3 and endo-levanase BT1760: characterization and application for the synthesis of novel prebiotics. Tartu, 2019, 217 p.
363. **Sille Holm**. Comparative ecology of geometrid moths: in search of contrasts between a temperate and a tropical forest. Tartu, 2019, 135 p.
364. **Anne-Mai Ilumäe**. Genetic history of the Uralic-speaking peoples as seen through the paternal haplogroup N and autosomal variation of northern Eurasians. Tartu, 2019, 172 p.
365. **Anu Lepik**. Plant competitive behaviour: relationships with functional traits and soil processes. Tartu, 2019, 152 p.
366. **Kunter Tätte**. Towards an integrated view of escape decisions in birds under variable levels of predation risk. Tartu, 2020, 172 p.
367. **Kaarin Parts**. The impact of climate change on fine roots and root-associated microbial communities in birch and spruce forests. Tartu, 2020, 143 p.
368. **Viktorija Kukuškina**. Understanding the mechanisms of endometrial receptivity through integration of ‘omics’ data layers. Tartu, 2020, 169 p.
369. **Martti Vasar**. Developing a bioinformatics pipeline gDAT to analyse arbuscular mycorrhizal fungal communities using sequence data from different marker regions. Tartu, 2020, 193 p.
370. **Ott Kangur**. Nocturnal water relations and predawn water potential disequilibrium in temperate deciduous tree species. Tartu, 2020, 126 p.
371. **Helen Post**. Overview of the phylogeny and phylogeography of the Y-chromosomal haplogroup N in northern Eurasia and case studies of two linguistically exceptional populations of Europe – Hungarians and Kalmyks. Tartu, 2020, 143 p.
372. **Kristi Krebs**. Exploring the genetics of adverse events in pharmacotherapy using Biobanks and Electronic Health Records. Tartu, 2020, 151 p.
373. **Kärt Ukkivi**. Mutagenic effect of transcription and transcription-coupled repair factors in *Pseudomonas putida*. Tartu, 2020, 154 p.
374. **Elin Soomets**. Focal species in wetland restoration. Tartu, 2020, 137 p.
375. **Kadi Tilk**. Signals and responses of ColRS two-component system in *Pseudomonas putida*. Tartu, 2020, 133 p.
376. **Indrek Teino**. Studies on aryl hydrocarbon receptor in the mouse granulosa cell model. Tartu, 2020, 139 p.
377. **Maarja Vaikre**. The impact of forest drainage on macroinvertebrates and amphibians in small waterbodies and opportunities for cost-effective mitigation. Tartu, 2020, 132 p.
378. **Siim-Kaarel Sepp**. Soil eukaryotic community responses to land use and host identity. Tartu, 2020, 222 p.
379. **Eveli Otsing**. Tree species effects on fungal richness and community structure. Tartu, 2020, 152 p.
380. **Mari Pent**. Bacterial communities associated with fungal fruitbodies. Tartu, 2020, 144 p.

381. **Einar Kärgerberg**. Movement patterns of lithophilous migratory fish in free-flowing and fragmented rivers. Tartu, 2020, 167 p.
382. **Antti Matvere**. The studies on aryl hydrocarbon receptor in murine granulosa cells and human embryonic stem cells. Tartu, 2021, 163 p.
383. **Jhonny Capichoni Massante**. Phylogenetic structure of plant communities along environmental gradients: a macroecological and evolutionary approach. Tartu, 2021, 144 p.
384. **Ajai Kumar Pathak**. Delineating genetic ancestries of people of the Indus Valley, Parsis, Indian Jews and Tharu tribe. Tartu, 2021, 197 p.
385. **Tanel Vahter**. Arbuscular mycorrhizal fungal biodiversity for sustainable agroecosystems. Tartu, 2021, 191 p.
386. **Burak Yelmen**. Characterization of ancient Eurasian influences within modern human genomes. Tartu, 2021, 134 p.
387. **Linda Ongaro**. A genomic portrait of American populations. Tartu, 2021, 182 p.
388. **Kairi Raime**. The identification of plant DNA in metagenomic samples. Tartu, 2021, 108 p.
389. **Heli Einberg**. Non-linear and non-stationary relationships in the pelagic ecosystem of the Gulf of Riga (Baltic Sea). Tartu, 2021, 119 p.
390. **Mickaël Mathieu Pihain**. The evolutionary effect of phylogenetic neighbourhoods of trees on their resistance to herbivores and climatic stress. Tartu, 2022, 145 p.
391. **Annika Joy Meitern**. Impact of potassium ion content of xylem sap and of light conditions on the hydraulic properties of trees. Tartu, 2022, 132 p.
392. **Elise Joonas**. Evaluation of metal contaminant hazard on microalgae with environmentally relevant testing strategies. Tartu, 2022, 118 p.
393. **Kreete Lüll**. Investigating the relationships between human microbiome, host factors and female health. Tartu, 2022, 141 p.
394. **Triin Kaasiku**. A wader perspective to Boreal Baltic coastal grasslands: from habitat availability to breeding site selection and nest survival. Tartu, 2022, 141 p.
395. **Meeli Alber**. Impact of elevated atmospheric humidity on the structure of the water transport pathway in deciduous trees. Tartu, 2022, 170 p.
396. **Ludovica Molinaro**. Ancestry deconvolution of Estonian, European and Worldwide genomic layers: a human population genomics excavation. Tartu, 2022, 138 p.
397. **Tina Saupe**. The genetic history of the Mediterranean before the common era: a focus on the Italian Peninsula. Tartu, 2022, 165 p.
398. **Mari-Ann Lind**. Internal constraints on energy processing and their consequences: an integrative study of behaviour, ornaments and digestive health in greenfinches. Tartu, 2022, 137 p.
399. **Markus Valge**. Testing the predictions of life history theory on anthropometric data. Tartu, 2022, 171 p.
400. **Ants Tull**. Domesticated and wild mammals as reservoirs for zoonotic helminth parasites in Estonia. Tartu, 2022, 152 p.

401. **Saleh Rahimlouye Barabi.** Investigation of diazotrophic bacteria association with plants. Tartu, 2022, 137 p.
402. **Farzad Aslani.** Towards revealing the biogeography of belowground diversity. Tartu, 2022, 124 p.
403. **Nele Taba.** Diet, blood metabolites, and health. Tartu, 2022, 163 p.
404. **Katri Pärna.** Improving the personalized prediction of complex traits and diseases: application to type 2 diabetes. Tartu, 2022, 190 p.
405. **Silva Lilleorg.** Bacterial ribosome heterogeneity on the example of bL31 paralogs in *Escherichia coli*. Tartu, 2022, 189 p.
406. **Oliver Aasmets.** The importance of microbiome in human health. Tartu, 2022, 123 p.
407. **Henel Jürgens.** Exploring post-translational modifications of histones in RNA polymerase II-dependent transcription. Tartu, 2022, 147 p.
408. **Mari Tagel.** Finding novel factors affecting the mutation frequency: a case study of tRNA modification enzymes TruA and RluA. Tartu, 2022, 176 p.
409. **Marili Sell.** The impact of environmental change on ecophysiology of hemiboreal tree species – acclimation mechanisms in belowground. Tartu, 2022, 163 p.
410. **Kaarin Hein.** The hissing behaviour of Great Tit (*Parus major*) females reflects behavioural phenotype and breeding success in a wild population. Tartu, 2022, 96 p.
411. **Maret Gerz.** The distribution and role of mycorrhizal symbiosis in plant communities. Tartu, 2022, 206 p.
412. **Kristiina Nõomaa.** Role of invasive species in brackish benthic community structure and biomass changes. Tartu, 2023, 151 p.
413. **Anton Savchenko.** Taxonomic studies in Dacrymycetes: *Cerinomyces* and allied taxa. Tartu, 2023, 181 p.
414. **Ahto Agan.** Interactions between invasive pathogens and resident mycobiome in the foliage of trees. Tartu, 2023, 155 p.
415. **Diego Pires Ferraz Trindade.** Dark diversity dynamics linked to global change: taxonomic and functional perspective. Tartu, 2023, 134 p.
416. **Madli Jõks.** Biodiversity drivers in oceanic archipelagos and habitat fragments, explored by agent-based simulation models. Tartu, 2023, 116 p.
417. **Ciara Baines.** Adaptation to oncogenic pollution and natural cancer defences in the aquatic environment. Tartu, 2023, 164 p.
418. **Rain Inno.** Placental transcriptome and miRNome in normal and complicated pregnancies. Tartu, 2023, 145 p.
419. **Daniyal Gohar.** Diversity, genomics, and potential functions of fungus-inhabiting bacteria. Tartu, 2023, 138 p.
420. **Sirli Rosendahl.** Fitness effects of chromosomal toxin-antitoxin systems in *Pseudomonas putida*. Tartu, 2023, 154 p.
421. **Mathilde Frédérique E. André.** New Guinea, a hotspot for Human evolution: settlement history and adaptation in northern Sahul. Tartu, 2023, 202 p.

422. **Vlad-Julian Piljukov.** Biochemical characterization of Irc3 helicase. Tartu, 2023, 137 p.
423. **Gerli Albert.** Carbon use strategies of macrophyte communities in the northeastern Baltic Sea: implications for a high CO<sub>2</sub> environment. Tartu, 2023, 128 p.
424. **Mariann Koel.** The molecular interactions between trophoblast and endometrial cells in embryo implantation. Tartu, 2023, 171 p.