Forest management to mitigate the risk of pest damage

Forest heterogeneity affects bottom-up and top-down mechanisms influencing pest insect population dynamics

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Doctoral thesis
Swedish University of Agricultural Sciences
Uppsala 2018

Acta Universitatis agriculturae Sueciae
2018:21

Cover: what you can find inside my thesis
Drawing: Davide Bellone
Parasitoids: Davide Bellone & Francesca Santaniello
Spider: Melissa Broussard

ISSN 1652-6880
ISBN (print version) 978-91-7760-182-1
ISBN (electronic version) 978-91-7760-183-8

Print: SLU Service/Repro, Uppsala 2018

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Abstract

Mixed forests are proposed as a management strategy that enables high levels of wood production while also supporting ecological and social benefits that are weakened by traditional monoculture-based management strategies. A key ecological benefit of mixed forestry is that it is expected to reduce plant damage caused by specialist insect pests because theory suggests that heterogeneous habitats such as mixed forests should limit fluctuations in pest insect population dynamics. Two main hypotheses have been proposed to explain this reduction in plant damage. The first is based on a bottom-up effect whereby plants grown in a diverse environment have more effective defences against herbivores. The second is based on a top-down effect whereby plant species diversity creates habitat diversity that supports a higher abundance of pests' natural enemies. However, the mechanisms underlying these bottom-up and top-down effects are not fully understood.

To fill this gap, I investigated how heterogeneity affects the bottom-up and top-down mechanisms influencing pest insect population dynamics. As a model organism, I used the European pine sawfly (*Neodiprion sertifer*), an herbivorous insect that frequently reaches outbreak densities and whose larvae cause severe damage when feeding on pine needles. Sawfly performance is known to be affected by pine needle chemistry – particularly the concentration of di-terpenes, which affect larval survival, and nitrogen levels, which affect cocoon weight and thus adult fecundity. Generalist and specialist natural enemies have been showed to cause significant mortality in sawfly larvae and cocoons. Despite their importance, the effects of plant chemistry and natural enemies on insect herbivores have not been studied in the context of forest heterogeneity.

I found that the variation in cocoon weight within groups of sawfly larvae feeding on Scots pine needles increased with the needles' contents of di-terpenes, and that this trend was stronger in mixed forests than monocultures. Additionally, the rate of generalist predation on sawfly larvae was higher in more densely planted spots within forest stands. Predation on sawfly cocoons was favoured by tree diversity, but the presence of dead wood mitigated the negative effect of low tree diversity. In addition, forest heterogeneity had no discernible effect on specialist enemies, which were able to locate their hosts equally well in simple and complex habitats.

This thesis shows that bottom-up effects on sawfly larvae cannot explain the observed reduction in tree damage in heterogeneous habitats. It may be that the higher variation in cocoon weight observed in mixed stands increases the average fecundity of adult sawflies, resulting in higher likelihood of outbreaks. Conversely, heterogeneity promoted top-down effects because it favoured generalist predators without negatively affecting specialists. These results will be useful to forest managers seeking to understand how mixed forestry can be used to mitigate anticipated increases in insect pest damage due to future climate change.

Keywords: Biological control, habitat heterogeneity, bottom-up, top-down, pest, outbreaks

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Preface

*By morning the wind had brought the **locusts**; they invaded all Egypt and settled down in every area of the country in great numbers. Never before had there been such a plague of locusts, nor will there ever be again. They covered all the ground until it was black. They devoured all that was left after the hail, everything growing in the fields and the fruit on the trees. **Nothing green remained on tree or plant in all the land**.*

[Exodus 10, 1-20, *Bible, 500 BC-1000 BC]*

Even centuries ago, people feared damage caused by herbivorous pest insects**.**

Dedication

To myself, because this thesis was impossible twelve years ago.

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Bellone, D., Klapwijk, M.J., Björkman C. Effect of stand type on host plant quality and pine sawfly performance. (manuscript)

II Bellone, D., Björkman, C., Klapwijk, M.J. Combined top-down pressure from generalist and specialist predators facilitated by habitat heterogeneity. *(submitted)*

III Bellone, D, Klapwijk, MJ, Björkman, C. (2017) Habitat heterogeneity affects predation of European pine sawfly cocoons. Ecol Evol. 7:11011–11020

IV Bellone, D., Klapwijk, M.J., Björkman, C. Plant position but not environmental complexity affects aphid parasitism rates. (Manuscript)

Paper III is reproduced with the permission of the publisher

The contribution of Davide Bellone to the papers included in this thesis was as follows:

I Performed the field experiment. The manuscript was written together with Christer Björkman and Maartje J. Klapwijk. Maartje J. Klapwijk executed the data analysis. Jonathan Gerschenzon and Axel Schmidt performed the chemical analysis.

II Performed the field experiment. Developed the research questions and planned the work in collaboration with Christer Björkman and Maartje J Klapwijk. The data analysis was executed in collaboration with Maartje Klapwijk. The manuscript was written in collaboration with both Christer Björkman and Maartje J. Klapwijk.

III Performed the field experiment. The development and planning of the work and the writing of the manuscript was done in collaboration with Christer Björkman and Maartje J. Klapwijk The data analysis was executed in collaboration with Maartje J. Klapwijk.

IV Planned and performed the field experiment. The development of ideas and writing of the manuscript was done in collaboration with Christer Björkman and Maartje J. Klapwijk. The data analysis was done in collaboration with Maartje J. Klapwijk.

1 Introduction

1.1 Boreal forests

Boreal forests are one of the most extended biomes on Earth, covering an area of 1.8 billion ha (Brandt et al. 2013) that accounts for almost half the world's total forest cover (FAO 2015). This area occupies northern latitudes and is characterized by cold-tolerant tree species within the genera *Abies, Larix, Picea, or Pinus* as well as *Populus* and *Betula* (Brandt 2009). Boreal forests provide to local and global populations (Trumbore et al. 2015) a wide range of economic, social, and environmental benefits such as wood, recreation, biodiversity, and carbon sequestration: forests are responsible for 20% of the world's total sequestered carbon. In recent decades, the increase in the global demand of wood and related products has caused large areas of boreal forests to be converted into highly managed plantations (see Box 1: Does the world need wood?).

1.2 Swedish forests

Approximately 75% of the 40.8 million ha of Sweden are covered by boreal forests (Sweden 2015). More than a half of this area is represented by managed forest plantations with an annual standing volume that exceeds 3000 million m^3 (Sweden 2015). Norway spruce (*Picea abies*) accounts for 40% of this volume, Scots pines (*Pinus sylvestris*) for 38%, and birches for 12% (*Betula* spp.); the remainder consists of other tree species and dead wood. The importance of managed forest plantations in Sweden is highlighted not only by the wide percentage of land cover but also by its economic importance: Sweden is the world's third largest exporter of forest-related products (pulp, paper and sawn wood) after Canada and the USA.

Box 1. Does the world need wood?

Wood is one of the most remarkable material that has accompanied human civilizations since prehistoric times (Sutton 1999). Its incredible physical and structural proprieties make it useful in a wide range of industrial sectors. The most common use is in the **construction industry**, because its low density compared to other conventional materials (i.e., steel or concrete) allows it to carry a significant part of a structure's load (Ramage et al. 2017). Special treatments can make wood into a higher performance material (Song et al. 2018) for long-span or tall structures, as shown by several recent futuristic architectural challenges (Forestry Sutimoto 2018) (Fig.1, Left). Wood is also one of the major raw materials used in the **pulp and paper** industry (Fig.1, right) due to its content of carbohydrate-based cellulose fibres and materials such as lignin, which acts as an adhesive substance for the cellulose fibres (Thompson et al. 2001). Wood represent also a potential source for the production of **bioenergy and biofuel** that could replace non-renewable fossil fuels which reserve are also limited (Sowlati 2016). Most recently, industrial groups have explored other **cutting-edge applications** of wood in green electronics, biological devices and other energy applications (Zhu et al. 2016) (Fig.1 Right).

Figure 1 **Left** New development concept for a wooden high-rise building (Forestry Sutimoto 2018). **Right** paper production (FAO 2016) and future applications of wood (Zhu et al. 2016).

Due to mentioned applications and a global demand showing a constant increase (FAO 2016), the answer to our question is "**YES, the world needs wood**".

1.3 Forest management

In keeping with a global trend over the last century (Nichols et al. 2006), Swedish forest plantations have been traditionally managed as even-aged monoculture stands that tend to provide simplified habitats. This approach is favored because it helps to maximize wood production by concentrating resources on the growth of a single desirable species, enables the use of simple nursery practices, and affords a uniform harvest (Piotto 2008). However, maximizing wood production by monoculture is often detrimental to other ecological or social benefits provided by forests (Bennett et al. 2009). Therefore, researchers and forest managers have explored alternative management strategies to better support these benefits while also maintaining high wood production.

Proposed alternative management strategies include short rotation forestry (Weih 2004) and continuous cover forestry (Kuuluvainen et al. 2012), both of which can match or exceed the wood production of traditional monoculture management (Roberge et al. 2016; Laiho et al. 2011) and at the same time promoting ecological services such as biodiversity conservation (Noss 2001) or resistance to natural disturbance (Peura et al. 2018). While these positive results are encouraging, a third management strategy based on mixtures of tree species has been the focus of increasing research effort (Bravo-Oviedo et al. 2014) and has attracted the attention of forest managers (Coll et al. 2018). Forest management strategies based on **mixed forests** have shown promising results with respect to wood production as well as ecological and social services (Gamfeldt et al. 2013), and are therefore advocated as one of the most interesting alternatives to traditional monoculture management.

1.4 Swedish mixed forests

In Sweden, the most common species in **tree mixtures** are spruce, birch and Scots pine. Recent research has shown that mixing conifers and broadleaves provides several advantages over traditional monoculture management (Felton et al. 2016). One of the most important benefits of mixed forests is the increase in **biodiversity**, for instance population of birds and saproxylic beetles or richness of understory vegetation and lichens (Felton et al. 2010). Mixed forests are considered heterogeneous habitats where tree species diversity tends to favour greater structural complexity (Ehbrecht et al. 2017). This heterogeneity is associated with greater **species richness and abundance** favored by their coexistence, persistence, and diversification of local species (Stein et al. 2014). The presence of broadleaves in coniferous plantations may also reduce the risk of fire due to their lower **fire susceptibility** (Gonzáles et al. 2005) or decrease of **wind throw** damage due to their greater stability (Griess & Knoke 2011).

A major concern for forest managers interested in mixed forestry practices is the potential reduction in **wood production** relative to traditional monoculture management. However, recent studies have shown that there are no cost in productivity when trees are used in a mixture but instead mixed forestry management could favor tree growth (Chamagne et al. 2017). Trees growing in mixed plantations may benefit from species complementarity, leading to reduced competition for resources such as nutrients, water, or light. This may increase tree growth and also create opportunities to plant trees more densely (Pretzsch et al. 2015).

Mixed forests could also provide various **social services** that consist of a series of recreational actives (Eriksson 2012). For instance, **picking berries** is one of the most important social habit in Swedish forests (Lindhagen 2012). Mixed forests may favour these activities because tree diversity is known to increase the diversity and abundance of berry species (Gamfeldt et al. 2013) including cowberry (*Vaccinium vitis-idaea*), bilberry (*Vaccinium. myrtillus*), cloudberry (*Rubus chamaemorus*), and raspberry (*Rubus idaeus*). Another activity practiced in Nordic countries is **moose hunting**. It has been shown that tree diversity (especially mixes of birches and pines) can increase the presence of this mammals (Vehviläinen & Koricheva 2006; Milligan & Koricheva 2013).

In recent years, another aspect of mixed forests has attracted the attention of researches. It is expected that the increase in global temperatures due to **climate change** will enhance the performance of herbivorous insects (Bale et al. 2002), leading to more severe and frequent tree damage. Higher temperatures could facilitate a shift to new or alternative food resources (i.e. trees) through changes in plant-insect phenology (Pureswaran et al. 2015) or increases in insects' distribution areas (Heimonen et al. 2015). However, a recent meta-analysis (Jactel & Brockerhoff 2007) has showed that **herbivorous pest insects** caused **less damage** in mixed forests than in monoculture stands. The mechanisms responsible for this effect are not fully understood, but it seems to primarily stem from reduced activity by specialist herbivores. The purpose of this thesis is to explain the origins of this effect by determining the mechanisms responsible for the reduced herbivorous damage suffered in plantations with high tree diversity, and the related differences between monocultures and mixed stands.

1.5 Pest damage: monocultures vs. mixed forests

All forests are subject to insect herbivory. In general, endemic levels of herbivory are not severe and plants can often recover through the presence of physiological mechanisms such as compensatory growth (Crawley 1987). However, explosive increases in the abundance of herbivorous insects can sometimes cause severe plant damage. These increases occur periodically and over very short periods of time (Estay et al. 2012). Species that exhibit such periodic dynamics, oscillating from low to high population densities (Maguire et al. 2015), are referred to as **outbreak species** (Wallner 1987).

Outbreaks can have very severe consequences for plants. For example, the most recent outbreak of the Mountain pine beetle (*Dendroctonus ponderosae*) in North America killed over 700 million m^3 of trees spread over 18.1 million ha (Cooke & Carroll 2017). Outbreaks can also have many indirect negative consequences; for example, a reduction in the number of trees may remove suitable nesting sites for birds (Ayres & Lombardero 2000).

It is supposed that heterogeneous habitats are more stable and resilient towards disturbances, including outbreaks (Oliver et al. 2010). **Mixed stands**, being highly heterogeneous, may promote stability in herbivorous pest insect population dynamics, limiting their fluctuations and reducing plant damage. Understanding the mechanisms that promote herbivorous pest insect population stability could be could greatly benefit forest managers by enabling them to develop strategies for reducing the expected increases in plant damage associated with outbreaks.

1.6 Habitat heterogeneity and associational resistance

The “Associational resistance” mechanism (Barbosa et al. 2009) is a process that has been suggested to reduce plant damage in heterogeneous habitats such as mixed stands. It suggests that plants surrounded by hetero-specific neighbours suffer lower levels of herbivory. Associational resistance has been explained in terms of bottom-up and top-down processes. The bottom-up explanation is also known as the resource concentration hypothesis, which explains resistance in terms of reduced plant accessibility to herbivorous insects; the top-down explanation is known as the enemy hypothesis, which explains the outcome in terms of higher herbivore mortality due to a greater abundance of natural enemies.

1.6.1 Bottom-up: the resource concentration hypothesis

The “Resource concentration hypothesis” predicts that specialist herbivores reach higher density and abundance when their specific host plants grow in dense patches such as monocultures (Tahvanainen & Root 1972). Contrarily, plants growing in mixed stands might benefits from hetero-specific neighbours because specialist herbivores could have difficult to locate their specific host plant. Suggested mechanisms are related to the disorienting effects of different tree species, which could work as physical (Dulaurent et al. 2012) or chemical barrier (Jactel et al. 2011).

Other associational effects occurring in mixed stands could lead to a different pattern compare to what suggested by the “resource concentration hypothesis”. For example, greater tree diversity could increase plant damage by increasing the population of generalist herbivores that might benefit from a greater diversity of food resources (Jactel & Brockerhoff 2007). Alternatively, the presence of hetero-specific neighbours could concentrate specialist herbivore s on individual trees (Plath et al. 2012). In addition, lower damage in monoculture might occur as a consequence of the “dilution effect” where the same number of herbivores and relative damage could be spread out among more host plants.

Results from studies on association effects can be difficult to interpret and might lead to a wrong interpretation. For instance, a reduction in plant damage in mixed stands could be due to a reduction in the density of a preferred specialist host plant or the ability of hetero-specific trees to “hide” preferred host plants from specialist herbivores (Hambäck et al. 2014). Therefore, empirical studies must be carefully designed to control for such confounding factors and thereby minimize the risk of misinterpretation.

1.6.2 Bottom-up: secondary metabolites

Studies that investigate the effects of mixed stands on specialist herbivores have mostly focused on the resource concentration hypothesis. However, plants are not passively subject to herbivory but own chemical defences consisting of secondary metabolites, toxic organic compounds contained in plant tissues such as leaves (Fraenkel 1959; Feeny 1976). Effects on herbivorous insects include the disruption of cell membranes, inhibition of nutrient or ion transport, inhibition of signal transduction processes and metabolism, and disruption of hormonal control of physiological processes (Mithöfer & Boland 2012). In addition, secondary metabolites can also be released in response to herbivore attacks in order to attract and orientate herbivorous natural enemies (Pinto et al.

2004; Li et al. 2014) or to induce defence responses in neighbouring plants (Zakir et al. 2013).

The amounts of resources that plants allocate to the production of secondary metabolites depends on the C:N ratio, i.e. the ratio of resources needed for growth (carbon) to the availability of nutrients (nitrogen) (Koricheva et al. 1998). In general, an excess of carbon available for growth or a reduction in nutrient availability can favour the allocation of carbon for the production of secondary metabolites. Thus, the production of secondary metabolites varies in relation to factors affecting the C:N ratio. For instance, tree diversity may affect the light availability (and thus photosynthesis), leading to changes in secondary metabolite concentration (Abdala-Roberts et al. 2014). Alternatively, tree diversity could promote the uptake of soil nutrients (i.e. nitrogen) which might lead an increase in chemical defence related to leaf nitrogen (Mraja et al. 2011). Positive effects of soil nutrients (i.e. nitrogen) has also been observed in conifers (Bjorkman et al. 1991), where the production of resin ducts containing secondary metabolites depends on soil nitrogen availability.

1.6.3 Top-down: the enemy hypothesis

The “enemy hypothesis” (Root 1973) suggests that heterogeneous habitats, i.e. mixed forests, provide favourable conditions for predators and parasitoids, thereby increasing herbivorous pest insect mortality. Favourable conditions include a greater abundance of preferred food resources (i.e. arthropods in the canopy) (Sobek et al. 2009) or in their absence, the presence of alternative food sources such as pollen and nectar. Higher habitat heterogeneity is often related to higher structural complexity (Ehbrecht et al. 2017), which promotes the presence of natural enemies by increasing the availability of shelter and/or breeding sites (Langellotto & Denno 2004; Bereczki et al. 2014; Letourneau et al. 2015). These factors could also reduce negative interactions and favour complementarity (Jonsson et al. 2017). Mixed stands might offer all these benefits, of increasing the pressure natural enemies on herbivorous pest insects thus reducing in plant damage.

Generalist and specialist natural enemies

Natural enemy species can be classified as either generalists or specialists based on the number of resources upon which they can feed. Generalists have a wide range of possible food resources making them a more constant presence and a relatively higher abundance compared to specialists, as generalists are not dependent on one or a few prey species. A more stable abundance of generalist predators is thought to result in more stable predation pressure over time, which helps to prevent increases in prey abundance and severe pest damage (Gould et al. 1990; Klemola et al. 2002). In addition, an increase in the abundance of a certain resource, for instance a herbivorous insect, could cause in generalists a “switching behaviour” (Murdoch 1969), leading them to preferentially exploit this newly abundant resource.

Sometimes, the control by generalists fails, leading to a rapid increase in herbivorous pest insect density (Hassel & May 1986; Berryman 1996). In such cases, specialists show a delayed density-dependent response that commonly leads to crashes in the prey and specialist predator populations (Hassel & May, 1986). However, from a plant perspective, a delayed response occurs too late when damage are already severe.

Understanding which parameters that contribute to forest heterogeneity and promote the presence of generalists and specialists could prevent or interrupt severe plant damage and reduce herbivorous pest insect population density.

2 Aim of the thesis

In this thesis, I investigated monocultures and mixed forests to better understand how forest heterogeneity can affect bottom-up and top-down effects on herbivorous pest insects. The final goal was to contribute new knowledge about ecological processes affecting herbivorous pest populations in relation to habitat heterogeneity. An additional aim is to provide information that forest managers can use to counteract and prevent increased levels of plant damage that are expected to result from the expansion of herbivorous pest insect populations due to climate change.

I investigated the following issues:

- How forest heterogeneity affects plant chemistry and herbivorous insect populations (bottom-up). **Paper I**

- How forest heterogeneity affects the top-down pressure of generalist and specialist natural enemies on herbivorous insect larvae (top-down). **Paper II**

- How forest heterogeneity affects the top-down pressure of a generalist natural enemy on herbivorous insect cocoons (top-down). **Paper III**

- How habitat heterogeneity affects the efficiency of a specialist natural enemy in finding herbivorous insects (top-down). **Paper IV**

3 Materials and methods

3.1 Study model

To investigate the role of forest heterogeneity on bottom-up and top-down effects on herbivorous insects, I used the European pine sawfly, *Neodiprion sertifer* (Geoffroy, Hymenoptera, Diprinonidae), which is a gregarious feeders on pine species (Fig. 2). *N. sertifer* has shown irregular population dynamics that lead to outbreaks which can cover thousands of hectares and last for several years (Lyytikäinen-Saarenmaa & Tomppo 2002).

N. sertifer is a univoltine species where females lay eggs in one batch during late August - early September on needles of current year shoots. Eggs overwinter until May and upon hatching, the larvae feed gregariously on the needles (Fig. 2) (Kolomiets, 1979). At the end of June, the last instar larvae moult into pre-pupae and drop from the pine branch to spin cocoons (Fig.2) in the forest topsoil. Adults emerge from cocoons in late August to start reproducing.

Figure 2. Larvae of *N. sertifer* feeding on Scots pine needles. Photo by Bellone Davide

3.2 Bottom-up

Scot pine chemistry affects sawfly performance through change in defence levels and nutritional value. Chemical defences in pine needles include di-terpenes that have been shown to cause severe mortality and reduced growth in young sawfly larvae (Larsson et al., 1986). Nutritional values, represented by nitrogen, have instead a positive effect on insect performance, increasing their weight and promoting their growth (Mattson 1980). Di-terpenes (Bjorkman et al. 1991; Nerg et al. 1994) and nitrogen (Bjorkman et al. 1991; Björkman et al. 1998) were shown to be positively related to soil nitrogen availability, which could differ between monocultures and mixed stands, leading to differences in the concentration of di-terpenes and nitrogen which could affect differently sawfly performance.

In **Paper I,** I investigated differences in the di-terpene and nitrogen concentrations of Scots pine needles from trees grown in monocultures and mixed stands, and the effects of these differences on sawfly larvae performance (which was measured in terms of cocoon weight). I selected six monocultures and six mixed stands. Twenty needles were sampled from ten experimental pines selected at random from each stand. The needles were ground and analysed to determine their concentrations of di-terpenes and nitrogen**.** The number of stems of individual tree species and the total number of trees around each experimental pine were recorded because both parameters could potentially affect the concentrations of di-terpenes and nitrogen in needles.

Figure 3. Larvae of *N. sertifer* caged with a plastic mesh netting. Photo by Bellone Davide

To determine sawfly performance, 20-25 larvae were moved on each of the experimental pines and caged with a plastic mesh netting (Fig.3) to exclude natural enemies. Larvae were left on the pine branch, free to feed, until they span cocoons, at which point they were collected and weighed with a microbalance. The concentrations of nitrogen and di-terpenes in pine needles were used to explain the observed sawfly performance.

3.3 Top-down

Several natural enemies affect *N. sertifer* in all its life stages. **Sawfly larvae** are subject to top-down pressure by common predators in forest stands including ants, spiders and parasitoids. **Ants** are considered one of the most important generalist predators of terrestrial arthropods, and exert strong pressure on *N. sertifer* (Olofsson 1992). The reported effects of **spiders** (Fig. 4, left) are inconsistent: some studies suggest their contributions to sawfly mortality are negligible (Eisner et al. 1974) while others suggest they are severe (Nakamura 1981). **Specialist parasitoids** (Fig. 4, right) represent one of the main cause of sawfly mortality, exerting a strong top-down pressure during the late larval stage (Olofsson 1987). Forest heterogeneity may affect the abundance and activity of generalist and specialist natural enemies by altering the abundance of alternative resources such as food or shelter.

Paper II describes a study where I investigate on the top-down pressure exerted by **generalist predators** and **specialist parasitoids** on *N. sertifer* larvae in several forest stands that differed in heterogeneity. Twenty-two forest stands that differed in the proportions of Scots pine and tree densities were selected. Within each stand, I chose five experimental pines. A group of 20-25 sawfly larvae was moved on one branch of each experimental pine. Larvae were exposed to generalist predators and specialist parasitoids until they reached the 4th instar. The remaining larvae were then counted and caged with a plastic mesh net until they span cocoons. The difference between the initial number of larvae moved on the pine branch and the remaining ones was used to determine the **predation rate** by generalist predators. The remaining cocoons were reared under natural conditions to determine whether an adult sawfly or a parasitoid emerged. Cocoons from which no adult or parasitoid emerged were dissected to see if they contained a larva or a parasitoid. The **parasitism rate** was determined as the number of successfully emerged or dead parasitoids in the sawfly cocoons, and the survival was determined as the number of adult sawfly that emerged or were found dead in their cocoons. To measure forest heterogeneity, the number of stems of individual tree species, the total number of trees, and the presence or absence of dead wood were measured around each experimental pine to explain the observed predation and parasitism rates.

Figure 4. **Left**: a spider carrying a sawfly larva (2nd instar). **Right**: a flying parasitoid searching for sawfly larvae on a Scots pine branch. Photo by Bellone Davide

Small mammals are considered important generalist predators of *N. sertifer* **cocoons** (Hanski & Parviainen 1985; Olofsson 1987). Their activity and abundance could be affected by forest heterogeneity, i.e. tree species composition (Liebhold *et al.* 1998; Coppeto *et al.* 2006) and shrub cover (Arnan et al. 2014) as well as the presence of dead wood (Manning & Edge 2008) .

To investigate how forest heterogeneity affects sawfly cocoon predation by small mammals, I performed a manipulative experiment involving dead wood (**Paper III**). Dead wood is a parameter increasing complexity on forest ground layer providing shelter to small mammals which could increase their abundance and consequently the predation on sawfly cocoon. The amount of dead wood was manipulated in ten different forest stands. Ten experimental pines were selected from each stand. Dead wood was removed from the surroundings of half the selected pines and added to the surroundings of the other half, creating two piles (Fig. 5, left). Two groups of 15 cocoons were placed close to the two piles and the experimental pines and left hidden for two weeks (Fig. 5, right). Disappeared and missed cocoons were assumed to have been predated.

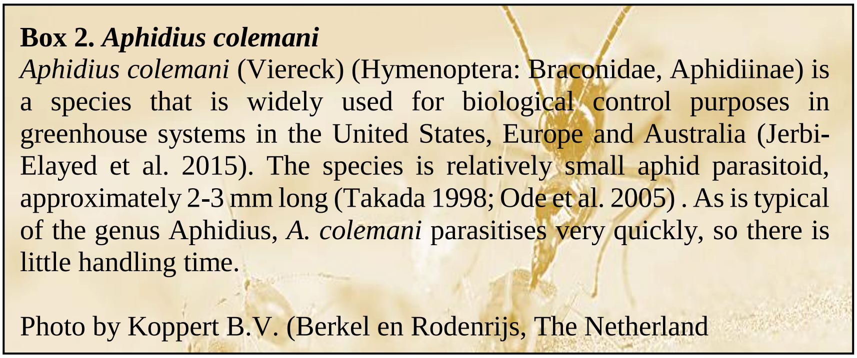
Figure 5. **Left**: two piles of dead wood close to an experimental pine. **Right**: the author hiding cocoons in the topsoil. Photo by Kevin Censtrières

To explain the observed predation rates, I measured several parameter relating to forest heterogeneity around each experimental pine, namely the number of stems of individual tree species, the total number of trees, the presence or absence of dead wood, and the mean height of understory vegetation.

Habitat heterogeneity is known to increase the abundance and efficiency for **specialist parasitoids**. However, it also has the potential to increase structural and chemical complexity, which could reduce top-down pressure by interfering with the parasitoids' searching behavior. In **paper IV**, I investigated the effect of habitat heterogeneity on the top-down pressure exerted by a **specialist parasitoid**. In partcular, I measured the efficiency of the well-known parasitoid *Aphidius colemani* (see Box 2, *Aphidius colemani*) at locating and parasitizing its host, the bird cherry-oat aphid *Rhopalosiphum padi* (Hemiptera: Aphididae). These model organisms were chosen because a) it was straightforward to obtain enough *Aphidius colemani* to perform the experiment, b) there are to the several knowledge and information about *A. colemani* in the literature, c) by working in a controlled environment rather than a forest habitat, I was able to focus on the mechanisms underpinning parasitoids' ability to search for and locate their hosts.

Parasitoid efficiency was tested inside a plastic cage using four different treatments corresponding to a gradual increase in plant diversity and complexity. The most homogenous treatment consisted of an oat monoculture (Fig. 6). The other treatments were oat and red clover (*Trifolium pratense*), oat and bird's-foot trefoil (*Lotus corniculatus,* Linnaeus), and oat and a fake odorless plastic plant resembling bird's-foot trefoil to determine whether any changes in efficiency were due mainly to increased structural complexity (i.e. plant shape) or whether the plants' smell played any role. A female of *A. colemani* was placed inside the cage and left free to locate and parasitize a host for seven minutes. The difference between the initial number of aphids placed on an oat plant and the number of aphids parasitized was used to calculate the parasitism rate.

Figure 6. Preparing oat plants. Photo by Irene Piccini



Box 2. *Aphidius colemani*

Aphidius colemani (Viereck) (Hymenoptera: Braconidae, Aphidiinae) is a species that is widely used for biological control purposes in greenhouse systems in the United States, Europe and Australia (Jerbi-Elayed et al. 2015). The species is relatively small aphid parasitoid, approximately 2-3 mm long (Takada 1998; Ode et al. 2005) . As is typical of the genus Aphidius, *A. colemani* parasitises very quickly, so there is little handling time.

Photo by Koppert B.V. (Berkel en Rodenrijs, The Netherland

4 Results and discussion

The work presented in this thesis was performed to determine how forest heterogeneity affects bottom-up and top-down effects on herbivorous pest insects using the European pine sawfly, *Neodiprion sertifer,* as a model organism. I performed experimental and observational studies, considering several parameters contributing to forest heterogeneity and how they would have affect plant chemistry and natural enemies of *N. sertifer*.

4.1 Bottom-up

Scots pines differed in needle nitrogen concentration (**Paper I**) in relation to the interaction between stand type, tree density and pine proportion (Fig. 7). Pines grown in monocultures increased needle nitrogen concentrations when surrounded by a relatively high number of pines and in denser areas. Pines grown in mixed stands had lower needle nitrogen concentrations when grown in denser areas and areas relatively high numbers of pines. The different responses observed for Scots pines surrounded by conspecifics and hetero-specific trees at the same density may be due to differences in root system architecture and resource acquisition between tree species (Jose et al. 2006).

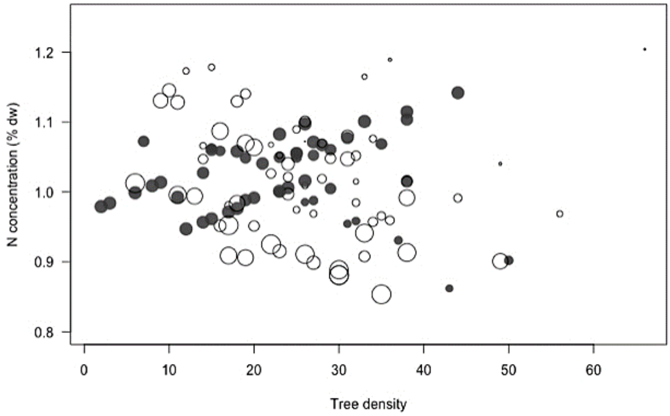


Figure 7. Nitrogen concentrations in Scots pine needles in relation to the 3-way interaction between stand type, tree density, and the proportion of pines around each experimental Scots pine tree. The sizes of the symbols represent the proportion of pines around the tree; larger circles indicate a higher proportion of pines relative to deciduous trees. The colours of the symbols represent the stand type; filled circles represent Scots pine monocultures and open circles represent mixed forest stands

No relationship was found between the concentrations of nitrogen or di-terpenes in pine needles and the average sawfly performance (i.e. cocoon weight) at the larval group level. However, the variability of the weight of female cocoons within larval groups was higher in mixed forest stands compared to than in monocultures (Fig. 8 left).

Female cocoon weight is strongly correlated with realized fecundity (Larsson et al. 2000), so the observed within-group variability in cocoon weight indicates that sawfly populations in mixed stands exhibited a greater variation in fecundity than those in monoculture stands. Higher levels of variation in the fecundity of individuals within the same group could theoretically lead to stronger fluctuations in population densities in mixed stands compared to monocultures, increasing the likelihood of outbreaks. This is inconsistent with the common belief that insect population dynamics are more stable in heterogeneous habitats such as mixed forests than in more homogenous habitats (Oliver et al. 2010; Haddad et al. 2011).

The variation in cocoon weight within larval groups correlated with the di-terpene concentration of the pine needles (Fig. 8 right). Specifically, the maximum fecundity of sawfly females that developed on trees with high di-terpene concentrations was higher than that of females that developed on trees with low di-terpene concentrations.

Two alternative and mutually compatible hypotheses were proposed to explain the higher variation in cocoon weight on trees with high di-terpene concentrations. First, plasticity within larval groups could result in performance differences between individuals that are exaggerated on needles with high di-terpene levels. Second, since high di-terpene concentrations are beneficial to sawfly larvae in later developmental stages because they deter predators (Larsson et al. 1986; Björkman et al. 1997; Bjorkman et al. 1991), individuals belonging to the same group may compete to maximize their intake of di-terpenes, leading to increased variability in performance.

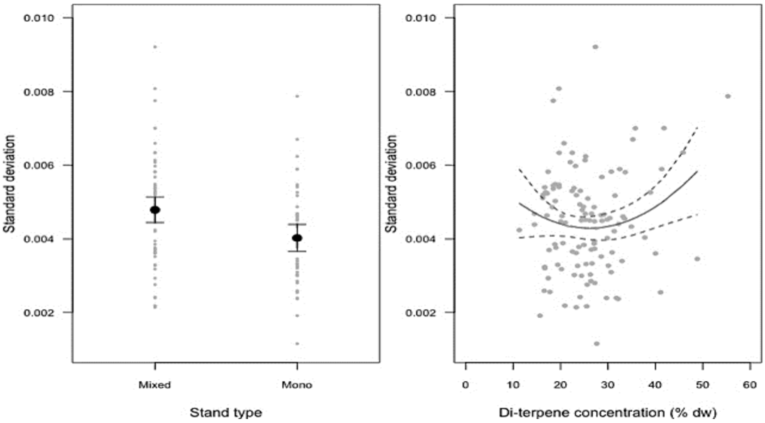


Figure 8. **Left** The mean standard deviation of cocoon weights within larval groups for mixed stands and monocultures; the error bars represent the confidence interval of the mean. **Right** The standard deviation of the cocoon weights within a larval group as a function of the measured di-terpene concentration in the sampled needles from the experimental trees.

4.2 Top-down

The proportion of larvae predated (**Paper II**) was positively affected by the total number of trees surrounding the experimental trees, in particular birches (Fig.9 A-B). This was probably due to the ecology of the most common generalist predators, ants and spiders. These generalists constitute a large part of the predator community exerting top-down pressure on herbivorous insects in boreal forests (Olofsson 1987; Tanhuanpää et al. 2001; Vehviläinen et al. 2008). The abundance of ants can be related to the density of birches increase aphid abundance (Riihimäki et al. 2005). Higher tree densities could also increase structural complexity (e.g. in terms of tree architecture), which promotes the presence, movement and predation pressure exerted by spiders (Kaitaniemi et al. 2007; Vehviläinen et al. 2008).

Specialist parasitoids were not affected by tree species diversity, tree density, dead wood, or the interactions between these parameters (**Paper II**). The reason behind this result could be related to the higher dependence of specialists on the occurrence of their preferred host. This host specificity may have led to the development of efficient searching behaviour based on visual or chemical cues that makes the effect of forest structure inconsequential.

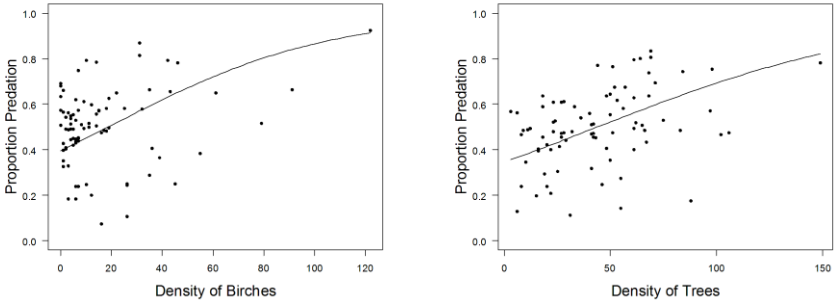


Figure 9. **Left** The proportion of *Neodiprion sertifer* larvae predated increased with the number of birches. **Right** The proportion of *Neodiprion sertifer* larvae predated increased with the total number of trees surrounding each experimental pine tree.

The efficiency of parasitoids in finding their specific host regardless higher habitat heterogeneity was supported by results obtained on a smaller spatial scale (**Paper IV)**. Plant diversity had no effect on the number of aphids parasitized despite clear differences in structure and chemical complexity between the four treatments. The structural complexity of a single host plant (Prado & Frank 2013; Andow & Prokrym 1990) or within a plant group (White & Andow 2006; Bezemer et al. 2010), has been shown to affect negatively parasitoids by reducing their host location ability. High structural complexity could also produce high chemical complexity, which can enhance or reduce the ability of parasitoids to detect suitable hosts (Bukovinszky et al. 2005; Kehoe et al. 2016; Vinson 1976; Hatano et al. 2008). The differences between our findings and previous reports may be related to the use of different parasitoid and plant species, suggesting a species-specific response to complexity.

A positive effect of forest heterogeneity on top-down pressure exerted by generalist predators was also observed in the predation of sawfly cocoons by small mammals (**Paper III**). The proportion of cocoons fed upon was positively related with tree density ($\log_e$) in forest stands (Fig. 10). It has been shown that small mammals exhibit a preference for habitats that offer shelter and from their natural enemies (Ecke *et al.* 2002; Sundell et *al.* 2012), including forest stands with high tree densities.

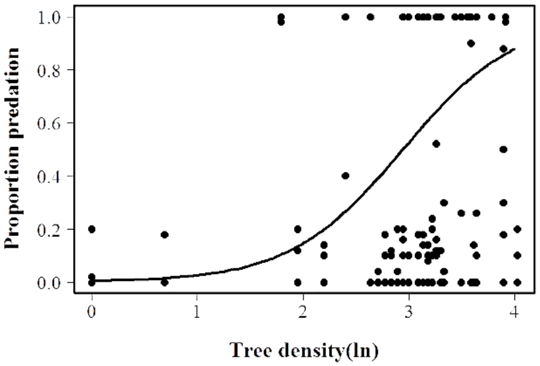


Figure 10. Proportion of sawfly cocoons preyed upon in relation to the natural logarithm of tree density surrounding the experimental pines

The effect of dead wood on sawfly cocoon predation depended on the interaction between the pine proportion in forest stands and the presence/absence of dead wood (**Paper III**). The predation rate declined more when dead wood was removed in an environment that otherwise would not provide much shelter opportunities. Adding dead wood decreased predation rates when the proportion of pine increased, but this relationship was less pronounced (Fig. 11).

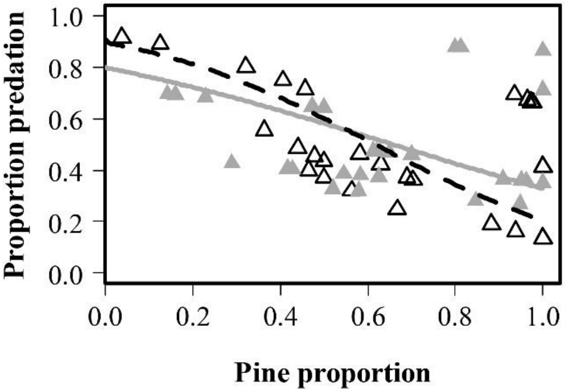


Figure 11. Proportion of sawfly cocoons preyed upon in relation to two dead wood manipulation treatments and the proportion of pines around each experimental pine. Solid line and filled grey points represent the wood addition treatment while dotted line and empty points represent wood removal treatment

Dead wood contributes to habitat heterogeneity (McElhinny et al. 2005) by providing shelter for small mammals thus have the potential to increase their feeding activity (Kollberg et al. 2014). The difference between the two dead wood treatments can be caused by the effect of small mammal behavior as well as variations in natural conditions of forest stands that differ in pine proportion. The higher predation rates in stands with a lower proportion of pine can be a consequences of higher abundance of alternative food resource provided by heterogeneous thus allowing high densities of small mammals (Sullivan & Sullivan 2012). Conversely, stands with high proportions of pine are often considered poor and dry habitats (Kouki et al. 1998); in such cases, dead wood could provide alternative food sources, which can be important for small mammals (Ecke et al. 2001). Removing dead wood from poor stands could therefore lead to a reduction in small mammal presence and consequently a decrease in cocoon predation.

5 Conclusion and future research

I believe that this project brought new important arguments habitat heterogeneity in promoting bottom-up and top-down effects on herbivorous pest insect populations. I also believe that these finding could provide relevant information to forest managers to improve their management practices to deliver high productivity in combination with other ecological benefits.

Paper I showed that although bottom-up effects could be an important regulatory mechanism of herbivorous population in heterogeneous habitats, they had relatively little impact on sawfly larval performance under the studied conditions. Plant chemistry, in particular di-terpenes, caused an increase in the variation of cocoon weight within larval groups and this variation was higher in mixed stands compare to monocultures. This variation could lead to high weight females, to which is related a higher fecundity potentially increasing the likelihood of outbreaks in mixed forests. The bottom-up effects observed showed here are in contrast with previous research, suggesting that top-down pressure could contribute more to reducing herbivore damage in more diverse habitats. Future research should investigate on other aspects of the relationship between habitat heterogeneity and bottom-up effects. For instance, how herbivorous performance could be affected by the chemistry of different plant genotypes or perform similar studies in forest stands with substantially higher levels of tree species diversity.

Paper II and **III** showed that top-down pressure exerted by generalist and specialist natural enemies contribute for most of the mortality of sawfly larvae and cocoons. A next step would be to determine how forest heterogeneity could affect other natural enemies such as birds and pathogens, and how such natural enemies could affect other sawfly life stages such as eggs or adults. A complete study of top-down pressure on sawfly larvae could be helpful for managing forest stands in order to promote a natural biocontrol. However, a good natural biocontrol should also take in consideration those parameters of habitat heterogeneity parameters that enhance the ability of different natural enemies to locate their prey, as discussed in **paper II** and **IV**.

In addition to the contributions to bottom-up and top-down effects in mixed forests, this thesis raises some more general questions on the role of habitat heterogeneity in counteracting herbivorous pest insects and its other benefits. For instance, dead wood, which increases forest heterogeneity on forest ground, promotes the activity of natural herbivore enemies but also promotes biodiversity since several species (i.e. arthropods and fungi) depend on decaying wood. Therefore, the results presented here suggest that further research is warranted to determine how forest heterogeneity could provide several benefits combining economic, ecological and social services.

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Acknowledgements

Christer I still remember the first time I saw you! You were playing the bass with the Kommandos SLU and I thought that my supervisor was so cool and years after I am still convinced about this. I will never stop thanking you for all your work in helping me to reach my PhD! You taught me that there is always a plan B and C and D, so to never give up!
Maartje You were the first person that I met in Uppsala when you pick me up at the airport! I do not know how many thanks I should tell to you and sorry if sometimes I was really stubborn. But thanks for showing me that there is always a solution for every problem. And yes, you can have the skulls in my office!

Both you are the best supervisors that a PhD can get!

Michelle how I managed my work before you arrived at SLU? Thank you for teaching me how to book a flight on the internet because apparently I am not able anymore to do it. But if you need help to fix a toilette call me! Thank you for being a great colleague but more important a great friend! PS you still own me 8 beers! **Karin** thank you because without you my works would have been impossible. And a great thanks from my socks since they were the most happy when you taught me how to use the sewing machine! A great thanks to all **forest entomology** group for all the nice meetings and excursions I have done with you!

Thanks to my **Italian family** in Uppsala**. Francesca** because sometimes Milan and Rome are closer than you think! There will always be a place for you on the bench at the post office in Gozzano! Valborg can be an all night long chat in front a fire with a good bottle of wine! Bella Zi! **Laura** because most of the funniest things I have done in Uppsala you were present, i.e. crash in a bachelorette party believing that was a raggaeton party, sleeping in an uncomfortable back of a van without sleeping bag or pillow in the legendary first party in Norredatorp, driving thousands km in two days for the best road trip ever across Sweden and Norway. **Anna** because I was not the only one with the passion of cooking with microwave and because Pinerolo is not only a city in an

Italian trash movie! Call me when you still need some fashion suggestions! And for sure thank you for helping me in exporting some piemontèis tradition with **Cecilia** and **Cristiano**, Boja Fauss! Looking forward for next coffee in Turin! **Silvia** for having fed me during your staying in Uppsala. If I learnt a minimal amount of cooking, it was all thanks to you but at least I taught you how to clean the bathroom! Sharing the flat with you was really great and still sorry for the snake! Remember, when you feel angry just go out for an ice-cream. **Irene** for the best Katuska party that I ever attended and for teaching me how much dung beetles can be cool! **Laia** Sometimes I am still wondering on the story about the spider and the Barcelona underground! **Simone & Gianvito** I am still waiting for the big adventure in Länna and other plans that we will for sure fail! But it could be cool having some cheap Ica pizza playing Fifa with your risvoltini and zoccoli. **Edo & Beppe** thanks for teaching me that bouldering and fishing are practised also in Italy!

The Flat + the House, how much fun is living with me? **Alva,** thank you all the times you made fun of me and vice versa, **Staffan** after 2 years you showed me your paintings! Great job man (and keep the moustache)! And have you meeeet **Thad** and **Anna**? Thanks both for listening to my stories and not getting bored! **Daniela,** I'm still sorry to have left your party but there were too many people to stay downstairs! **Dimitrije** let´s go to Katushka! Brabumba. **Kate** you redefine my definition of being an active person, but please Adele as alarm... maybe not... **Louise** you brought so much happiness inside the house, you are always positive. That is something really cool! Oh yes, I learn what is a queer! **Anke**, next time can I come with you to scuba-diving on the west coast? **Jelena** thanks for not getting angry when I lost your bike keys (especially because I haven't told you yet), **Renee** we should start to learn bouldering seriously right? **Dani** next dinner is still about eggs and beans?

Pernilla & Preeti Thanks for the discussion about pop-culture…ehmm science that we have done or I have heard from Preeti office! **Romain**, I miss our late fika at the department with your chocolate and the discussion about football and southern life! Thanks for showing me Katushka style! See you at the carnival in Mainz! **Kim** thanks for sharing the office with me! After a while I think I learned some swedishness and you some crazy Italian habits (yes, we can speak without hands)! Sorry for being a little bit messy (do not go to see how the office is looking now). **Jörg** thank you to always find a part of my manuscript were I can cite you! Thanks to: **Guiomar** because at the end everyone will die alone! **Giovanni** because I am not the only one that likes Gigi Dag in the department. **Ludo** why the anti-drug dog checked only me at the airport? **Guille** because at every party we need Kalimotxo, **Ineta** because SLU will need a PhD that makes photos after me. **Kirsten** because sometimes it is really cool listening to a perfect English accent, **Julian** without you I would be still half way to Norredatorp, **Adam** because we all need a Swedish that explain what is Vasaloppet, **Chloë** because I still have to ice-skating close to the amazing place (house rumors) where you live **Yayuan** because.. hej how tasty were the rice balls at the Chinese dinner? **Mathieu** because you asked to be in the acknowledgements! So, here you are! **Joe & Kevin** because good field data are obtained with a great field assistant. Thanks to all PhDs, postdocs, students, researchers, docents and professors that I did not mention and shared with me SLU life.

Thanks **to Carolina Rediviva,** I will miss your cozy, relaxing and inspiring atmosphere since sometimes it is nice to not work in the office! **Upland nation** because sometimes we just need a place to recover from the hard work during the week! **Palermo** because there is the best fake Italian pizza ever. **Bernadotte brothers,** we crash the Korpen cup! Thanks for letting me play with you guys! Bra Spela! And a great thanks to all people that I met in Uppsala and that did a part of this long journey with me!

Gio, Team, Panny, Coq Thanks because I still remember how much you were happy when I had the possibility to start my PhD, even if I am still not sure you understood what it is. **Sbordoni**, because what I achieved today started 12 years ago in a rainy day in Unimi when we met for the first time! **Poldo, Emi, Bijoux, Bianca, Leo, Attila** thank you even if you cannot read because, well…you are cats. But thanks to keep my bed warm when I was away and to be happy (mostly for getting food) when I was coming back home (yes, I am a cat person).
E infine un grazie enorme alla mia famiglia per avermi supportato in tutti questi anni. In particolar modo, un grazie enorme a mia **madre** per aver fatto molti sacrifici per permettermi di studiare e avermi sempre spronato a impegnarmi anche quando le cose non andavano bene. Se ho ottenuto questo PhD é anche in gran parte merito tuo! Grazie!